THE EFFECT OF HOME RANGE REDUCTION ON THE
ECOLOGY OF RED HOWLER MONKEYS IN CENTRAL
AMAZONIA

by
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Selwyn College
Cambridge
To my grandmothers, Mome and Bita,
*In memoriam*
“What escapes this eye...is a much more insidious kind of extinction: the extinction of ecological interactions”.

D.H. Janzen
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ABBREVIATIONS

Co 2.5-ha: forest fragment of 2.5 ha in Colosso camp
Co 12-ha: forest fragments of 12 ha in Colosso camp
Km41: Continuous forest in Km41 camp
BDFFP: Biological Dynamics of Forest Fragments Project
INPA: Brazil’s National Institute for Amazon Research
SUFRAMA: Manaus Free Trade Authority
ISS: instantaneous scan sampling
SZ: Sleeping zone
GD: group defaecations
ID: individual defaecations
RS: random sites
PREFACE

The work described in this thesis was conducted from the Wildlife Research Group, Department of Anatomy, University of Cambridge under the supervision of Dr David J. Chivers. This thesis is the result of my own research, except where explicitly stated otherwise. No part of this thesis has been submitted to this or any other University for any degree or diploma. The text does not exceed 80,000 words.

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The effect of home range reduction on the ecology of red howler monkeys in central Amazonia

Marcela Santamaría Gómez

The loss of effective seed dispersers in forest remnants has been stated to disrupt dispersal services that alter the dynamics of tropical forests. Howler monkeys are efficient seed dispersers that prove to be exceptionally tolerant to habitat fragmentation by surviving in very small forest fragments. In this context, the effect of home range reduction, caused by habitat fragmentation, on the feeding ecology of red howler monkeys (Alouatta seniculus) and on their subsequent role as primary seed dispersers in Central Amazonia, are examined.

At the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus (Brazil), two howler groups living in 2.5 ha and 12 ha fragments (Groups 1 and 2 respectively) were habituated during a four-month period. Systematic data on the diet, activity budgets and use of space were collected for each group on a monthly basis, between January 2002 and January 2003. Comparisons on seed dispersal were also made from howlers’ faecal analysis between the two fragments (Co 2.5-ha and Co 12-ha) and a continuous forest reserve (Km41).

At the three study sites, a strong seasonality in plant-part production was recorded within howlers’ home ranges, dividing the year in three seasons: fruiting (January-May), leafing (June-September) and flowering (October-December), but low fruit availability was found within the small fragment. Both groups showed a frugi-folivorous diet, with drastic seasonal variations based on plant-part availability. Group 1 responded to low fruit supply by eating more flowers and by repeatedly crossing a secondary-vegetation gap (50 m) to obtain fruit from an adjacent continuous forest. Forest fragmentation reduced drastically howlers’ home range from about 20 ha at Km41 to 7.2 ha and 2.5 ha at the fragments (63% and 88% reduction, respectively). Home range was composed of 60% of edge habitat for Group 1 and only 26% for Group 2. A more drastic reduction in the home range of Group 1 resulted in a net decline in food plants, which affected time allocation decisions of this group: howlers living in the small fragment rested more and fed less
throughout the study. Group 1 seems to live in a more demanding environment and is presumably at its limits of flexibility, whereas Group 2 is well adjusted to a less-disturbed habitat.

Although the reduction of howlers’ home range decreases the number of plant species and seeds dispersed, howlers were effective seed dispersers for most of the species they consumed at the three study sites. In fragments, up to 77% of small to large seeds of fruit species exploited by Groups 1 and 2 were dispersed by endozoochory, and howlers’ digestion lasting about 20 hours, had a positive or neutral effect on germination success. Despite that Group 1 deposited seeds at shorter distances from fruit sources than Group 2, up to 93% of seeds were moved away from the parental crown by both groups.

Although howlers are generally regarded as less effective dispersers, because they produce large faecal clumps with high seed aggregation, this is not always the case. Five main points emerged from this study in terms of deposition patterns, which indicate that the view of categorising a species as a “good or bad” disperser is misguided:

1. Howlers defaecated mainly in synchrony (ca 80%), but also separately (20%);
2. In both defaecation types, howlers dispersed seeds in latrines and random sites in the forest, but more often in the former (up to 66%);
3. Seed deposition displayed a spatially clumped-distribution and this patchiness was associated not only to sleeping areas but to latrines located outside them;
4. In latrines, howlers deposited more seeds of more species than in random sites, but at both fragments seed densities were similar between defaecation sites,
5. The fate of seeds delivered in howlers’ multi-species seed depositions varied greatly according to seed species at all sites and to seed-density at Km41. Nonetheless, after nearly one year, 51% seedlings survived in Km41, 50% in Co 12-ha and 23% in Co 2.5-ha.

In conclusion, howlers living in small and medium fragments are contributing in the maintenance of regeneration processes through seed dispersal and, consequently, the species is a key element to be considered in management and restoration programmes of fragmented landscapes.
CHAPTER 1
HABITAT FRAGMENTATION, AMAZONIA AND MONKEYS

1.1 INTRODUCTION
The loss of effective seed dispersers in forest remnants has been stated to disrupt dispersal services that consequently alter the structure and dynamics of tropical forest (Chapman and Chapman 1995, Onderdonk and Chapman 2000, Peres and van Roosmalen 2002, Andresen 2003, Bruna 2003). Howler monkeys are prevalent and efficient seed dispersers (Andresen 2002a) that prove to be exceptionally tolerant to habitat fragmentation by surviving in very small forest fragments (Rylands and Keuroghlian 1988). It is important, therefore, to assess their potential contribution in maintaining the regeneration ability of forest remnants, to make recommendations for the conservation, management and restoration of forest fragments. This assessment is pertinent given the increasing rate of habitat alteration and fragmentation of tropical forests (Loiselle and Dirzo 2002). In this context, the effect of home range reduction caused by habitat fragmentation, on the feeding behaviour and seed dispersal role of red howler monkeys in Central Amazonia, is examined in this thesis.

1.1.1 Tropical deforestation and habitat fragmentation
Tropical forests harbour the highest species diversity and ecological complexity of land communities in the world (Lewin 1986, Wilson 1988, Laurance and Bierregaard 1997, Hoekman and Quiñones 2000). Representing only 7% of the earth’s land surface, they sustain more than half of the plant and animal species (Myers 1984, Wilson 1988). Yet, tropical forests are being destroyed and modified throughout the world at an alarming rate through clearing, burning, logging and over-hunting (Laurance and Bierregaard 1997). In fact, Whitmore (1997) estimated that 200,000 km² of tropical forest were lost each year during the 1980s.

The effects of forest disruption are varied. On a large scale, tropical deforestation releases greenhouse gases to the atmosphere, such as carbon dioxide, which contribute to global warming (Houghton 1991, Laurance et al. 1998a). On a regional scale, forest

Fragmented tropical forests have been studied for more than three decades. During the 1970s and 1980s, scientists were mainly concerned with species extinction in forest remnants and approached the problem from the framework of island biogeography theory (MacArthur and Wilson 1967). Forest patches persisting in the landscape were considered “islands”, encircled by a “sea” of modified habitats (Laurance and Bierregaard 1997), in which larger areas contained more species than smaller ones (MacArthur and Wilson 1967). Although this theory has been very useful, it soon became clear that the analogy between fragments and islands was incomplete and that forest fragmentation was a much more complex process that could affect not only biological diversity, but also ecological interactions (e.g. seed dispersal) and forest functions (e.g. evapotranspiration) (Gascon and Bierregaard 2001).

Currently, three basic components of forest fragmentation are widely recognised to alter biological diversity and forest integrity: the isolation and size of the fragment, the creation of edges, and the matrix, defined as the surrounding vegetation altered by humans. The following features promote biological and structural changes in fragmented landscapes (Gascon et al. 2001):

*Forest fragment size and isolation.* Fragmentation results not only in reduction in size, but also in isolation of forest remnants (Laurance and Bierregaard 1997). Local species extinction and/or population declines are the most frequently-reported outcomes of forest reduction. In fact, a fragment may be too small to provide resources for animals with large home ranges or specialised diets (Harris 1984). Moreover, ecological processes and tight associations are also affected when species disappear with decreasing area, leading to cascading extinction (Gascon and Bierregaard 2001). Due to species-area effects,
smaller fragments will generally support fewer species, resulting in loss of individuals, species and habitats. Biological diversity can also decline by initial exclusion, since forest fragments will be a small representation of the original habitat and species could be eliminated by chance when fragments are created. Furthermore, isolation effects will reduce or prevent the normal dispersal and migration of species, which is critical for long-term population viability (Harris 1984, Lovejoy et al. 1986, Skole and Tucker 1993, Noss and Csuti 1994). In this last case, time since isolation and distance from other remnants and continuous forest are key features determining the fate of fragments (Saunders et al. 1991).

Yet, responses by faunal species are reported to be varied. In Central Amazon, for instance, coprophagous and leaf-litter beetles, euglossine bees, birds and primate species declined after isolation, according to the predictions mentioned above (Powell and Powell 1987, Rylands and Keuroghlian 1988, Klein 1989, Stouffer and Bierregaard 1995, Diham 1998). In contrast, species richness in butterflies, amphibians and terrestrial small mammals increased after isolation, but with a striking shift in community composition (Tocher et al. 1997, Brown and Hutchings 1997, Malcolm 1997). Vulnerability of faunal groups appears closely related to differential responses to edge effects and the landscape matrix. These findings re-emphasise the fact that species disappearance cannot always be attributed to “area effects” (Laurance and Bierregaard 1997).

**Edge creation.** Tropical forests generally exhibit natural boundaries or ecotones, where gradual transitions between two habitat types occur (Laurance and Bierregaard 1997, Gascon and Bierregaard 2001). In contrast, forest fragmentation increases forest edges creating an abrupt transition from forest to modified habitat encircling the fragment. In particular, smaller, linear and recently-created remnants display sharper margins. Edge effects have physical and biotic consequences that can penetrate more than 250 m into the forest (Laurance 1997). The margins of fragments are highly exposed to winds and lateral penetration of sunlight, driving drastic changes in microclimatic conditions (Laurance 1997). Temperature rises, while relative humidity and soil moisture drop near edges (Kapos et al. 1997). Consequently, rates of tree mortality and damage, especially to larger ones, as well as rates of turnover increase along forest edges (Ferreira and Laurance 1997).
As a result, more tree-fall gaps are formed, contributing to a great proliferation of sun-loving plants, such lianas and vines. Thus, as a general result of edge creation, vegetation structure and composition are altered and a substantial loss of biomass occurs (Laurance et al. 1997). Given that plants play a central role in forest structure and functioning, floristic modifications in fragments trigger cascading alterations in animal species and ecological processes.

**Habitat Matrix.** Forest remnants are usually embedded in a habitat modified by humans, termed the matrix that influences fragmented flora and fauna communities (Laurance 1997, Tocher et al. 1997). Effects of matrix habitats on fragment dynamics was only recognised in the mid-1980s, due to the emergence of landscape ecology (Harris 1984, Logsdon et al. 2001). Landscape pattern analyses provide a more integrative approach for understanding not only remaining forest-cover, but also a spatial and temporal configuration of forest remnants embedded in matrix habitats (shapes, sizes and degrees of isolation). The matrix can act as a selective filter for species movement, dispersal and colonisation between fragments and continuous forests. Some species can cross and move between forest patches (e.g. frogs, Tocher et al. 1997), while others avoid the matrix, which acts like a physical barrier (e.g. understorey insectivorous birds, Bierregaard and Stouffer 1997). Species responses appear to change according to the level of disturbance and the expanses and types of matrix habitats. Remnants surrounded by severely-altered habitats, like pastures and agricultural areas, are more inhospitable to species movement than secondary-growth vegetation that resembles the forest structure of the original habitat (Laurance 1990, Malcolm 1991). Furthermore, species associated with the appearance of a new matrix will be able to colonise and invade forest patches and edges. These invader species might displace some native species via competition and/or predation, leading to important changes in the original forest species assemblages and altering multi-species interactions (Bierregaard et al. 2001a).

### 1.1.2 The Amazon

The Amazon rainforest constitutes the largest wild tropical forest remaining on earth. Totalling five million square kilometres of land, it occurs in nine countries with 60%
found in Brazilian territory (Higuchi 2001). The Amazonian basin is drained by the world’s largest river by volume, the Amazon. This ecosystem spans most of the South American continent, and covers a distance of nearly 2000 km with elevations that do not exceed 300 m. Viewed from the air, the Amazon forest looks homogeneous, but this is misleading. In fact, the Amazon is extremely heterogeneous with different types of rivers with white, clear and black waters, and different forest types (flooded: várzea and igapó, non-flooded: terra firme). This variation results in different arrays of plant and animal species and very high levels of diversity, endemism and ecological complexity.

Like other tropical regions, the Amazon is also seriously affected by forest removal. Human population growth and economic pressures are transforming Amazonian forests into a landscape dominated by human activities (Gascon et al. 2001). Although forest clearance has not yet been as devastating as in the Atlantic forest of southeast Brazil (only 8% remaining) (Skole and Tucker 1993, Bierregaard et al. 2001b, Chiarello 2003), deforestation has been significant. In fact, about 12 to 14% of the Brazilian Amazon has already been clear-cut and 40% has been fragmented (Skole and Tucker 1993, Higuchi 2001, Cochrane and Laurance 2002). Forests have been opened for the expansion of road networks, conversion into farmlands, timber, oil and mineral extraction, and for hydro-electric projects (Smith 1981, Gascon et al. 2001). These activities usually result in human settlements and always end in the expansion of the colonisation frontier. In the 1970s the Brazilian government, in particular, motivated colonisation of the Amazon through the construction of the Trans-Amazon highway, mainly as a safety valve for poverty in the northeast region (Smith 1981).

Closer analysis shows that the amount of deforestation differs from state to state within the Brazilian “legal Amazon”, which includes the forested basin and drier savannas to the south (Gascon et al. 2001). Past clearing and heavy forest loss occurred mainly in the southwest (Rondonia state) for farming development, and in the northeast (Belém state) for timber extraction, particularly of mahogany trees. In Amazonas state (central Amazonia), deforestation has occurred at a slower pace, with only 5% of the region cleared. Forest removal has been mainly concentrated around the capital of Manaus and along main roads (Gascon et al. 2001). Recently, intense development pressures have been promoting major changes in forest cover in the central Amazon, causing great
concern among conservationists (Gascon et al. 2001). Firstly, the implementation of low-impact logging timber extraction is generally not consistent with approved management plans. Secondly, timber stocks are becoming scarce worldwide and the Central Amazon represents the largest natural resource of hardwood timber. In fact, there is a movement from southeast Asia to Amazonia by Malaysian and Chinese companies. Thirdly, the city of Manaus has expanded alarmingly since 1967, when a duty-free district was established. It is estimated that Manaus harbours 1.5 millions inhabitants and employment opportunities are declining. By 2013, the city will lose the duty free status and it is predicted that the number of jobs will drop dramatically, which may increase pressure on forest areas becoming more accessible through recent road improvements. Finally, road construction is known to have a dramatic impact on forest cover, by generating new accesses to undisturbed forests and causing emergence of secondary roads. Since 1995, the Federal Government has invested considerable funds to improve the main highway of the State (BR 174) that links Manaus to Venezuela in the north (Gascon et al. 2001). It also proposed that the area along this road should become the next big agricultural frontier, although soils are already known to be inadequate for that purpose (Gascon et al. 2001). Moreover, large-scale projects, such as extensive soybean plantations, are being widely promoted (Gascon et al. 2001).

Although a Brazilian Forest Code was established in 1965, with modifications in 1984, 1986 and 1996, the Code is still open to misinterpretations (Gascon et al. 2001). In fact, large-scale projects quoted as “Avança Brasil” were planned during the previous Brazilian government and threaten to accelerate Amazon deforestation. These infrastructure projects include paving two roads in Central Amazon, a gas pipeline crossing Indian lands, and two hydro-electric dams. Fortunately, a recent report from the new Federal Government revealed that these planned infrastructure projects will be seriously reassessed. This may redirect the near-future prospect for the Amazon region.

1.1.3 Primate, frugivory and seed dispersal

Forest conversion results in the reduction of the amount of primary forest available for native flora and fauna (Bierregaard and Stouffer 1997), which in turn assists human settlements through the construction of new roads. As a result, more people (including
hunters) have easier access to, and use of, forest remnants, which seriously affects some animal species through subsistence and commercial hunting (Redford and Robinson 1987, Redford 1992, Peres and Terborgh 1995, Cowlishaw and Dunbar 2000, Cullen et al. 2000). In the Amazon, wildlife serves as a major protein source for local communities (Peres 1990, 1999, Bodmer 1995), for which an estimated 19 million mammals, birds and reptiles are killed for food each year in the Brazilian Amazon alone (Redford 1992). The most commonly-hunted game animals are the large-bodied species (Bodmer 1995), which are the major contributors to the total biomass and density of the forest (Peres 1999). These animals are principally frugivores (Redford 1992, Peres and van Roosmalen 2002).

Numerous empirical and theoretical studies have focussed on the interactions between fruit plants and their consumer vertebrates to understand their evolutionary and ecological implications. In tropical rain forests, these studies have been conducted for two main reasons. First, 60-95% of tropical-plant species produce fruit adapted for vertebrate consumption and seem to rely on frugivorous animals for seed dispersal (Howe and Smallwood 1982, Willson et al. 1989, Howe 1990, Jordano 1992). Second, fruit-eating vertebrates constitute the dominant rain-forest animal group (more that 75%, see Terborgh 1986) and depend on fruit plants for their survival (Bourlière 1985, Chapman and Chapman 1995). Frugivores play a central role in rain-forest regeneration through seed dispersal, and are crucial for its maintenance and preservation (Howe 1984, Terborgh 1986, Chapman 1989, Willson et al. 1989, Redford 1992, Lambert and Garber 1998). Fruit, compared to leaves, are a resource that shows a patchier distribution, both in space and time (Milton and May 1976, Leighton and Leighton 1983, Terborgh 1986, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000). Consequently, frugivores are very sensitive to habitat fragmentation, because they require larger home ranges than folivores to find enough food resources for their survival. Furthermore, frugivores, and particularly large-bodied animals, are also more affected by hunters, especially in fragments (Chiarello 2003). Thus, large-bodied frugivores are more prone to extinction in small fragments and their loss in forests may cause serious disruptions to the fruit-frugivore interactions and seed dispersal patterns of many plant species (Terborgh and Winter 1980, Strahl and Grajal...
Frugivores represent a significant proportion of the avian and mammal biomass in some Neotropical forests (Eisenberg and Thorington 1973). Primates, rodents, tapirs and peccaries are, for instance, the most important components in Cosha Cashu Biological Station (Peru; Terborgh 1986) and Tinigua National Park (Colombia; Stevenson 1996, 2002). All Neotropical primates are frugivores to a greater or lesser extent, and spend important periods of time foraging on the fruit of many tropical forest tree species (Terborgh 1983, Peres 1994a, Chapman 1995, Chapman and Onderdonk 1998, Oliveira and Ferrari 2000). Consequently, their role in seed dispersal is significant. Yet, primates are very sensitive to hunting pressure and habitat fragmentation (Peres 1990, Peres 1997, Chiarello 2003). Given that 90% of primate populations are found in tropical forests, most of them have arboreal habits, and hunting increases with forest reduction, forest loss coupled with hunting are considered the most dominant threats for primate populations (Mittermeier and Cheney 1987, Peres 2000, Robinson and Bennett 2000, Bennett et al. 2002, Ferrari et al. 2003, McCann et al. 2003).

It is difficult to draw common threads to predict primates’ persistence in forest remnants, because species respond differently to disturbed habitats and because available data are limited. The process is complex, but the nature of fragmentation (sensu Marsh 2003) and some features of primate behaviour can provide important insights into understanding primates’ responses to forest reduction. On one hand, primate survival in forest patches seems affected by the type of surrounding matrix, the time and degree of isolation, forest and species protection status, the degree of human use, the vegetation quality and availability of food resources, connectivity and their location in the landscape (Saunders et al. 1991, Cowlishaw and Dunbar 2000, Chapman et al. 2003, Chiarello 2003, Marsh 2003, Rodríguez-Toledo et al. 2003). Indeed, Marsh (2003) suggests that the permeability of the matrix is one of the key factors for primate persistence in fragments. On the other hand, primates’ ability to thrive in fragments depends, but not always, on species-specific traits, such as home range size requirements, degree of frugivory, behavioural and dietary plasticity, and capacity to use the matrix. Finally, some authors (Chapman et al. 2003, Rodríguez-Vargas 2003) suggest that fragmented primate
populations may function as metapopulations and, in this way, may escape the hazards of genetic, environmental and demographic stochasticity.

1.1.4 Red howler monkeys

Of the large-bodied Neotropical primates, howler monkeys are the only species that are able to survive in forest fragments of less than 10 ha (Milton and May 1976, Rylands and Keuroghlian 1988, Chiarello 1994, Crockett 1998, Estrada et al. 1999a, Cosson et al. 1999, Silver and Marsh 2003). Although they are the most folivorous primates in the Neotropics, their diet includes a considerable proportion of fruit when available (Mittermeier and van Roosmalen 1981, Julliot and Sabatier 1993, Chiarello 1994, Silver et al. 1998, Stevenson et al. 2000a). Howlers are recognised as primary seed dispersers, since they swallow most of their seeds without damaging them (Julliot 1996a, Estrada and Coates-Estrada 1984, Andresen 1999, Andresen 2002a). They are regarded as less-effective dispersers, however, because of the synchronous defaecation pattern of the groups, which results in seed aggregation (Howe 1980, Mittermeier and van Roosmalen 1981, Peres and van Roosmalen 2002). This pattern is considered disadvantageous for the plants, because seed and seedling mortality are dependent on plant density (Janzen 1970, Connell 1971). Andresen (2000, 2002a) recently demonstrated, however, that seeds dispersed by howlers in Central Amazon have a higher probability of being buried by dung beetles, which considerably enhances seed survival. This is because seeds in large faecal clumps have a higher probability of being buried by dung beetles, and thus avoid rodent predation. Data also revealed that howlers are important seed dispersers at the plant community level, since they dispersed the seeds of 137 species during a 25-month study period (Andresen 2002a).

As such, howlers may contribute to maintaining the regeneration ability of forest remnants (Neves and Rylands 1991, Estrada and Coates-Estrada 1996, Estrada et al. 1999a, Andresen 2002a) due to several key attributes: they are fruit-eaters, efficient and important dispersers, and they are able to survive in small forest fragments. In this context, the study of howler monkeys in fragmented forest is important, especially since information on these animals in tropical forest remnants remains scarce (Estrada et al. 1999a, Bicca-Marques 2003). This is pertinent given the increasing rate of habitat
alteration and fragmentation of tropical forests (Loiselle and Dirzo 2002). The survival of intact forests will partly depend on maintaining processes such as seed dispersal (Laurance 1999, Cowlishaw and Dunbar 2000, Laurance et al. 2001). Recommendations for the conservation, management, and restoration of fragmented forests can only be possible by understanding how the process of forest regeneration may be affected by habitat disruption (Andresen 2000).

1.2 HOWLER MONKEYS

1.2.1 Howlers in continuous forest

**Taxonomy and distribution.** In the latter half of the last century, Platyrhine systematics followed the traditional classification, which divided New World monkeys into two families: Callithrichidae and Cebidae (Ford and Davis 1992, Rylands et al. 1996/1997). Therefore, howler monkeys (genus: *Alouatta*) were traditionally classified in the Alouattinae subfamily of the Neotropical Cebidae family, which also included all sub-families other than marmosets and tamarins (Hershkovitz 1977). Recent classifications based on cladistic analyses of morphological characters (teeth and skeleton) have placed *Alouatta* in the family Atelidae, sub-family Atelinae, which also includes the genera *Ateles, Brachyteles, Lagothrix* (Rosenberger 1981, Ford 1986, Ford and Davis 1992). Members of this sub-family share the prehensile tail and the large size (Ford and Davies 1992), but *Alouatta*, being the closest relative of this group, belongs to the tribe Alouattini, whereas the other genera constitute the tribe Atelini (Rosenberger 1981, Ford and Davies 1986).

The systematic of the genus *Alouatta* is controversial (Crockett 1998, Rylands and Brandon-Jones 1998). Hill (1962) proposed that *Alouatta* is comprised of six species. Some subspecies have been elevated, however, to the species level, and consequently nine species of howler monkeys are currently recognised by Rylands et al. (2000): mantled howlers (*A. palliata*), Central American black howlers (*A. pigra*), red-handed howlers (*A. belzebul*), brown howlers (*A. guariba*), South American black howlers (*A. caraya*), red howlers (*A. seniculus*), coiba island howlers (*A. coibensis*), Bolivian red howlers (*A. sara*), and ursine howlers (*A. arctoides*). Groves (2001) has proposed an additional species, *Alouatta macconelli*, which is not accepted by Rylands et al. (2000).
Recently, Cortés-Ortiz et al. (2003) inferred the phylogenetic relationship of nine of the ten species of *Alouatta* species recognised by Groves (2001), using mitochondrial and nuclear genes. They found that howler species originated in the late Miocene and Pliocene, and that the initial genus diversification was caused by the geographical barriers created during the final formation of the northern Andes in the late Miocene.

*Alouatta* has the broadest distribution of New World primates, living in 19 countries from southern Mexico to northern Argentina (Figure 1.1) (Crockett and Eisenberg 1986). Howlers appear to represent the largest biomass of primates at all sites where such estimations have been made and this has been considered an important criterion of ecological dominance (Eisenberg and Thorington 1973). Howlers inhabit the widest range of habitat types, from wet evergreen to highly-seasonal semi-deciduous forests and are found from sea level to > 3,200 m (Hernández-Camacho and Cooper 1976). The nine howler species recognised have allopatric distributions, but some small areas of sympatry may exist: *A. pigra* - *A. palliata* in Mexico (Smith 1970), *A. palliata* - *A. seniculus* in Colombia (Hernández-Camacho and Cooper 1976, Defler 1994), and *A. caraya* - *A. guariba* in Argentina (Crespo 1954).

*Alouatta seniculus*, the species of this study, has the broadest distribution of the genus, occurring in 10 countries: Ecuador, Peru, Bolivia, Venezuela, Colombia, Brazil, Guiana, French Guiana, Surinam and Trinidad. Nine subspecies have been listed for the genus (Hill 1962), but its systematics is still under discussion (Rylands and Brandon-Jones 1998). Red howler monkeys occur mainly in the Amazon basin, but can also be found in a diverse array of forest types including mangroves, deciduous forest, cloud forest, and gallery forest (Mittermeier and van Roosmalen 1981, Rylands et al. 1995, Rylands et al. 1996/1997).

**Morphology and associate behaviour.** *Alouatta*, with members of the genus *Ateles*, *Brachyteles*, and *Lagothrix*, are among the largest Neotropical primates, ranging from 4.5 to 11.3 kg in weight (Ford and Davies 1992, Defler and Rodríguez-Machado 2003). Howlers are sexually dimorphic in body size with males larger than females, especially for *A. seniculus* and *A. caraya*. Only one species, *A. caraya*, and one subspecies, *A.
Figure 1.1: Distribution of the genus Alouatta (source: Crockett 1998).
*guariba clamitans*, are sexually dichromatic with males changing colour at puberty (Crockett 1998). For *A. seniculus*, the average body weight varies from 4.5 – 6 kg for females to 6.5 – 8 kg for males (Thorington *et al.* 1979, Ayres 1986).

Two specific morphological features characterise the genus: the increased hyoid/larynx complex and the prehensile tail. The enlarged hyoid bone and larynx act as a resonator and amplifier when the monkeys produce their characteristic calls. The hyoid bone is larger in males than in females and its size varies across species. *Alouatta seniculus* has the most developed hyoid, while *A. palliata* has the smallest (Schön Ybarra 1988). Roars are produced only by males, but often occur in chorus with all members of the group involved in this activity. Roars are produced most often at dawn as a way to announce group location in the area and, thus, to avoid confrontations (Chivers 1969, Sekulic 1982, Sekulic and Chivers 1986, Vercauteren Drubbel and Gautier 1993). They have also been heard at night (Vercauteren Drubbel and Gautier 1993, A.A. Marques, pers. comm., M. Santamaría pers. obs.). Calls during the day occur less frequently and are given in the presence of a predator, as well as when interacting with neighbouring groups or other primate species (Sekulic 1982).

The prehensile tail, another peculiarity of the genus and family, serves as a support device during locomotion, foraging, and crossing gaps (Crockett and Eisenberg 1986, Neville *et al.* 1988, Crockett 1998). The locomotion of howlers is quadrupedal and they generally move at a slow pace (Milton 1980, Mittermeier and van Roosmalen 1981, Braza *et al.* 1981). Howlers are arboreal species that usually move in the middle and upper vegetation strata. However, they can descend to the ground in particular situations, such as for eating soil (Izawa and Lozano 1990), drinking water (Gilbert and Stouffer 1989), chasing individuals of other troops (M. Santamaría, pers. obs.), or when crossing from one vegetation patch to another (Braza *et al.* 1981).

*Population structure and densities.* Howlers live in cohesive and stable groups, but the mean group size shows both intra- and inter-specific variation. Fluctuations in group size can result from numerous factors, such as rainfall affecting resource availability, hunting, habitat destruction, yellow fever epidemics and natural disasters (e.g. hurricanes) (Crockett and Eisenberg 1986). Intra-specific variations within sites may be due to
different densities of food resources in group home ranges. *Alouatta palliata* has the largest mean troop size of the genus, with values up to 23 individuals (Milton 1980). For *A. seniculus*, group size varies from 5 to 11 individuals, but generalisations are difficult because recently-formed groups are smaller than those that have existed for years (Crockett and Eisenberg 1986).

Striking differences in home range size occur across the geographic distribution of howlers (Crockett and Eisenberg 1986). These findings have been strongly associated with habitat characteristics, given that howlers are found in a diverse array of forest types (Mittermeier and van Roosmalen 1981, Rylands *et al.* 1995, Rylands *et al.* 1996/1997). In fact, the area required and used by a group will depend on variables such as density, diet, distribution and abundance of food resources, troop size, and presence of other sympatric primate species (Milton and May 1976, Crockett and Eisenberg 1986, Neville *et al.* 1988). Studies of howlers conducted in areas larger than 1,000 ha report home ranges varying from 4.5 to 182 ha and mean daily travel distance from about 260 to 760 m (Bicca-Marques 2003). For red howlers living in the Amazon basin, home ranges in continuous forest vary between 21 and 182 ha (Julliot 1992, Rylands and Keuroghlian 1988, Santamaría and Rylands 2003, Queiroz 1995, Palacios and Rodríguez 2001, Stevenson *et al.* 2000a) (Figure 1.2). The highest value (182 ha) was reported in southeast Colombian Amazon (Caparú station) (Palacios and Rodríguez 2001) and it is attributed to a particularly low howler population density in the area (4 individuals/km²), which in turn is a result of the edaphic poverty of the region (Defler 1995).

Population densities of howlers also vary considerably. Most estimates range from < 10 to about 100 individuals/km² (Crockett 1998). Howler monkey densities were estimated for 23 lowland Amazonian forests and compiled for 83 other Neotropical forest sites by Peres (1997), showing large variations (from 3.3 to 115 individuals/km²). He found that howler densities could be predicted by indirect measures of habitat quality, such as forest structure, seasonality and soil fertility, once hunting is controlled. In the Amazon region, red howler densities vary also considerably among forest types, with values between 4 and 94 individuals/km² (Ayres 1986, Queiroz 1995, Peres 1997) (Figure 1.3). In particular, várzea forests, based on rich-nutrient soils, appear to support higher densities than *terra firme* forests growing on nutrient-deficient soils (Peres 1997). Foliage of poor
Figure 1.2: Home range size recorded for *Alouatta seniculus* in different localities of the Amazon region.
1= Julliot 1992  
2= Rylands and Keuroghlian 1988  
3= Santamaría and Rylands 2003  
4= Queiroz 1995  
5= Palacios and Rodríguez 2001  
6= Stevenson *et al.* 2000a

Figure 1.3: Population densities reported for *Alouatta seniculus* in different localities of the Amazon region.
1= Mittermeier and van Roosmalen 1981  
2= Gilbert and Setz 2001  
3= Peres 1997  
4= Julliot 1992  
5= Palacios and Rodríguez 2001  
6= Queiroz 1995  
7, 8 = Peres 1997  
9= Ayres 1986  
10= Stevenson 2002  
11= Terborgh 1983
quality (toughness and high levels of secondary compounds) is produced in soils of low fertility that in turn affects densities of arboreal folivores, such as howlers (Peres 1997). The large variance in howler densities described might also be partly attributed to the different methods applied by the studies summarised in figure 1.3. In fact, at least three different methods (strip censuses, variant of line transect, home range mapping) were used to estimate howlers densities, which in turn could result in biased density estimates of howler populations. For instance, detectability and rate of encounters of howlers may vary according to the habitat type (e.g. várzea, terra firme) and the time of day that censuses are conducted. Moreover habituated howlers are not easily seen when the groups are resting and resting may occur at any time of the day (Chapter 5).

Social organisation and reproduction. The social organisation of howler monkeys has been described as uni-male, multi-male, and age-graded (Eisenberg 1979). Red howlers’ social structure is similar to a harem, in which only the dominant male has access to the females. In this species, groups are generally composed of a dominant breeding male, several females, sub-adult males, and juveniles of different ages (Gaulin and Gaulin 1982). Infanticides after male invasions have been reported for A. palliata (Clarke 1981), A. seniculus (Crockett and Sekulic 1984) and A. caraya (Rumiz et al. 1986).

The life span of howlers has been reported only for A. palliata, at Barro Colorado Island, as 16½ years for males and 15½ years for females (Froehlich et al. 1981). Howler reproduction is not seasonal and births can occur during any month (Neville et al. 1988). Nevertheless, some birth clusters have been reported for A. palliata (Glander 1980) and A. seniculus, but they cannot be classified as reproductive peaks (Crockett and Eisenberg 1986). The mean gestation length has been estimated at 191 days with small variations from 180 to 194 days. The menstrual cycle length varies between 16 to 20 days and ovulation occurs over two to four days (Crockett and Sekulic 1982). Observers can detect ovulation by monitoring the proximity between females and males. For A. seniculus, sexual maturity is achieved between 43 and 54 months for females and between 58 and 66 months for males (one year later than for A. palliata and A. caraya). Both males and females of A. seniculus may disperse from their natal social group, but who leaves and what happens after emigration differs between sexes (Pope 2000). The probability of a
female dispersing from its natal group increases with the number of females already breeding within the group. A migrant female can establish membership in a group only by forming a new party with other solitary migrants. By contrast, males that emigrate move to adjacent groups or stay as solitaries until they establish new groups with other solitaries migrants (Pope 2002).

Activity patterns. Howler monkeys are diurnal species that allocate between 63 and 79% of their time to resting and spend little time moving, foraging and in social activities (Smith 1977, Milton 1980, Gaulin and Gaulin 1982, Limeira 1997, Stevenson et al. 2000a, Pavelka and Houston Knopff 2004). Figure 1.4 summarises the activity pattern for *Alouatta seniculus* recorded by four studies. The long periods of inactivity in howlers are explained as adaptations to process important amounts of, and extract sufficient nutrients from, foliage (Milton 1998). This pattern contrasts with frugivorous species like *Ateles* spp. that have a digestive tract adapted to rapid fruit digestion and, thus, they can spend less time resting (40 to 54%) (Milton 1978, Crockett and Eisenberg 1986, Stevenson et al. 2000a). Social interactions are rare in howler monkeys. Less than 2% of howler activity is spent in allogrooming, with an average duration of about 1 minute (Gaulin and Gaulin 1982, Crockett and Eisenberg 1986). Adult females perform most allogrooming on their own infants. Intra-specific encounters generally occur between neighbouring groups, particularly in the overlapping areas of their home ranges and specifically in a resource-feeding context. Aggressive episodes usually lead to the displacement of one group from the area and/or from the forage resource (Chivers 1969, Crockett and Eisenberg 1986).
accidental ingestion may occur when, for instance, fig fruits containing wasps are eaten (Simmen and Sabatier 1996).

Annual diet of *A. seniculus* has been reported for different areas of continuous forest, but particularly for the Amazon region of French Guiana (Julliot and Sabatier 1993), Peru (Andresen 1999), Brazil (Gilbert 1994a, Queiroz 1995), and Colombia (Stevenson *et al.* 2000a, Palacios and Rodríguez 2001). They conform to the same pattern described for the genus: a diet rich in both leaves and fruit, with particularly high leaf consumption in terra firme forests (Figure 1.5). An accentuated folivory has been detected for some sites, however, because fruits can be very scarce in those forests during the dry season. In French Guiana, for example, Julliot and Sabatier (1993) found that fruit consumption could vary from 0 to 50.8%. In the Central Amazon, Santamaría and Rylands (2003) found that diet was composed of almost 100% leaves in three months of the dry season. Howlers also show a higher diet diversity in the Amazonian region (> 100 species) when compared to other Neotropical areas (ca. 60 species) (Smith 1977, Milton 1980, Gaulin and Gaulin 1982). This is because areas with high plant diversity, like the Amazon basin, offer a larger number of potential resources for primates (Neves and Rylands 1991, Maisels and Gautier-Hion 1994).

**Figure 1.5:** Annual diet composition recorded for *Alouatta seniculus* in different localities of the Amazon region.

1= Julliot and Sabatier 1993
2= Gilbert 1994a
3= Queiroz 1995
4= Palacios and Rodríguez 2001
5= Andresen 1999
6= Stevenson *et al.* 2000a.
Leaf-eating primates have to face the problem of low ready-energy content of leaves. Howlers have resolved this issue by behavioural rather than physiological adaptations (Milton 1998). In fact, howlers lack the complex sacculated stomachs of the folivorous colobines of the Old World (Baukop 1978). Instead, they have a simple, acidic (PH < 4.5) and not particularly large stomach (Chivers and Hladik 1980). The caecum is slightly enlarged, but its dimensions are very similar to Ateles paniscus, a ripe-fruit specialist (Milton 1998). Both colobines and howlers depend on fermentative processes, but these take place in different sections of the gut, i.e. in the forestomach and in the caecum and colon, respectively (Chivers and Hladik 1980, Milton 1998). The behavioural adaptations of howlers to a folivorous diet include long periods of inactivity, direct travel from food patch to food patch, high selectivity in feeding, avoidance of rapid travel that could raise body temperature, and body postures that may help in conserving body heat (Milton 1998).

**Seed dispersal.** Few howler studies have focused on the role of howlers in seed dispersal (Estrada and Coates-Estrada 1984, Chapman 1989, Julliot 1996a, 1997, Andresen 1999, 2002a, Yumoto et al. 1999, Peres and van Roosmalen 2002, Stevenson et al. 2002, Wehncke et al. 2004). Howlers are recognised as primary seed dispersers, since they swallow most of their seeds without damaging them. The size of seeds swallowed and dispersed ranges between 0.1 mm to 40 mm long (Estrada and Coates-Estrada 1984, Julliot 1996a, Andresen 2002a, Peres and van Roosmalen 2002). Large seeds of indehiscent husks conform a “large-primate fruit syndrome” (sensu Peres and van Roosmalen 2002); they are almost exclusively dispersed by Alouatta, Ateles and Lagothrix spp. that have the ability to handle and swallow large seeds due to their large bodied-size.

The time elapsed between fruit ingestion and first seed to appear varies between 16 to 62 hours, with a mean of about 21 hours (Milton 1980, Julliot 1996a, Yumoto et al. 1999). These long retention times are related to their digestive system adapted for leaf fermentation (Milton 1980). The effect of endozoochory is extremely variable and seems to depend on intrinsic traits of seeds (Estrada and Coates-Estrada 1984, Julliot 1996a, Stevenson et al. 2002). Red howler monkeys at Tinigua National Park (Colombia) tended
to increase the germination rate but to delay the time of germination (Stevenson et al. 2002). In French Guiana, Julliot (1996a) found that red howlers enhanced, decreased or did not affect germination for seventeen seed species.

Dispersal distances seem to vary according to howlers’ home range size, especially for maximum distances that a seed can reach. A group of red howlers ranging in 25 ha in Colombian Amazon moved seeds at a mean of 317 m with a maximum distance of 637 m (Yumoto et al. 1999). In French Guiana, a troop of red howlers having a home range of 45 ha dispersed seeds from 0 to 550 m with a mean of 255 m (Julliot 1996a). In Mexico, Estrada and Estrada-Coates (1984) reported a low mean of 112 m for five species dispersed by a group of Alouatta palliata ranging in 60 ha, but with a maximum distance of 811 m.

Howlers living in the Amazonian basin are reported to disperse a larger number of seed species in comparison to other Neotropical forest primates (up to 30 species; Milton 1980, Estrada and Coates-Estrada 1984). In French Guiana, Julliot (1996a) recorded 110 species dispersed by red howler monkeys. In central Amazonia, Andresen (2002a) found 137 species in howler monkey defaecations and concluded that in this area, howlers were highly prevalent seed dispersers at the plant community level. In contrast, howlers are regarded as poor quality dispersers because of the defaecation pattern, which results in seed aggregation (Howe 1980, Mittermeier and van Roosmalen 1981, Peres and van Roosmalen 2002). This pattern is considered disadvantageous, because, similar to seeds that fall under the parental tree, dispersed seeds may suffer high seed and seedling mortality (Andresen 2000). Howlers’ defaecation pattern has been related to two main behavioural traits. Firstly, large faecal clumps are produced usually by the whole group that defaecates in synchrony (ca 750%, Andresen 2002a). Secondly, howlers often use specific sleeping areas in the forest and display a bimodal rhythm of deposition that leads to high concentration of faeces around sleeping sites.

In Central Amazonia, however, red howler monkeys were described recently as efficient seed dispersers in an undisturbed and continuous forest (Andresen 2001, 2002a). Andresen demonstrated that large defaecations attracted more and larger dung beetles than scattered depositions, increasing the number of seeds buried and thereby compensating the negative effects of high seed density. In this way, seeds buried had a
higher chance of escaping predation by rodents on the ground surface (which are also attracted to howler depositions), and eventually germinating (Andresen 2001, 2002a).

In French Guiana, Julliot (1997) surveyed seedlings of six howlers food plants under sleeping sites and on control plots. She found that, for four species, seedlings were concentrated under their sleeping sites, suggesting that red howlers may contribute to the spatial heterogeneity of the forest through their aggregative dispersal pattern.

In Costa Rica, Wehncke et al. (2004) compared the defaecation patterns of *Cebus capucinus* and *Alouatta palliata* and found that howlers produced larger faecal clumps, spent longer times in fruiting trees, had shorter seed dispersal distances and produced a clumped pattern where 67% of neighbouring faeces were deposited within 1-5 m. The early seed fate of *Acacia collinsii*, in terms of seed removal by rodents, was assessed, indicating that *Cebus* deposition resulted in better conditions for the short-term survival of seeds than the pattern of *Alouatta*. The discrepancy between this result and the study of Andresen (2002a) may be attributed to different ecological scenarios, such as the inactivity of dung beetles during the study period in Costa Rica.

### 1.2.2 Howlers in fragmented habitats

Because of their ability to exploit leaves, to have a flexible home range size, and to live in small groups (Rylands and Keuroghlian 1988), howlers tolerate habitat fragmentation. They can persist in extremely small forest fragments of less than 10 ha and are the only fruit-eating primate that thrives in such areas (Rylands and Keuroghlian 1988, Chiarello and Galetti 1994, Chiarello 1994, Crockett 1998). Nevertheless, seven of the 20 howler species and subspecies with adequate population data are classified as threatened according to the IUCN Mace-Lande System. Howler populations can be decimated by major habitat disturbances (e.g. flooding from dam construction) and epidemic diseases like yellow fever and bot-fly parasitism. This genus seems to be more prone to these diseases than other Neotropical primates. Because of their large body size, howlers are a preferred prey of humans and, thus, hunting constitutes the main cause of declining howler populations (Crockett 1998). In fact, higher densities have been reported for areas protected from human hunting than from unprotected ones (Peres 1997). In some areas,
howlers are hunted for the magical and medicinal properties attributed to the hyoid bone (Mittermeier 1987).

A recent compilation of studies of primates living in fragments (Marsh 2003) denotes an important effort toward an understanding of how primates adjust to the disturbed conditions in forest isolates. Although nine of the 19 studies in this book reported on different howler species, only two studies were conducted on red howlers (Gilbert 2003, Bicca-Marques 2003). As pointed out by Bicca-Marques (2003), information on feeding behaviour of *A. seniculus* living in fragments remains scarce.

*Diet and activity patterns.* Studies of behavioural ecology in forest fragments have been carried out for *Alouatta palliata* in lowland rain forest in Mexico (Estrada *et al.* 1999a, Juan *et al.* 2000, Rodríguez-Luna *et al.* 2003) and upland-riparian forest in Costa Rica (Clarke *et al.* 2002), for *Alouatta pigra* in north central Belize (Marsh 1999, Silver *et al.*, 1998, Ostro *et al.* 1999, Silver and Marsh 2003), for *Alouatta guariba* in Brazilian Atlantic forest (Mendes 1989, Chiarello 1993, 1994), for *Alouatta belzebul* in logged and unlogged forest in Brazilian eastern Amazonia and finally, for *Alouatta seniculus* in cloud forest in Colombian Andes (Gaulin and Gaulin 1982) and *terra firme* forest in Brazilian central Amazon (Neves and Rylands 1991). Responses of howlers to diet composition varied profoundly across species and sites (Figure 1.6), indicating again how difficult it is to generalise the outcomes of forest reduction on primates (Marsh 2003, Chiarello 2003).

In a forest fragment (3.6 ha) at Los Tuxtlas Mexico, a mantled howler troop (*Alouatta palliata*) ate mainly young leaves and fruit, with a strong preference for tree species of Moraceae and Cecropiaceae in their annual diet (Estrada *et al.* 1999a). On the other hand, Juan *et al.* (2000) observed that, in a large fragment (250 ha), howlers used more plant species, ate more fruit (72%) than leaves (24%), and spent more time travelling and less resting than in two smaller patches (3.2 and 35 ha). In particular, at the smaller fragment (3.2 ha), diet consisted of nearly only leaves (98%). Rodríguez-Luna *et al.* (2003) provided data on a 10-member howler group that was released in an 8.3 ha island in Lake Catemaco, Mexico. Seven years later, the group size increased significantly to 57 members, leading to changes in social structure (cohesive vs. sub-group) and increasing fruit consumption and use of vines.
Figure 1.6: Diet composition recorded for several howler species in forest fragments of different sizes.

1= Neves and Rylands 1991  2= Gaulin and Gaulin 1982  3= Mendes 1989

In Costa Rica, Clarke et al. (2002) evaluated the effects of partial deforestation of the home range of a long-studied mantled howler troop. As a result of losing 10% of its former home range (24 ha) due to a canal construction, a mantled howler troop increased their feeding time and day range, while reducing group size and social interactions. Long-term responses to deforestation resulted in the expansion of the group into new areas and the exploitation of new stands of fruit trees, Montinia calabura (Elaeocarpaceae), which grew on edges just after the deforestation.

At the Community Baboon Sanctuary (CBS) in Belize, Marsh (1999) compared six groups of Alouatta pigra living in remnants from 1.3 to 80 ha in size. Independent of fragment area and floristic composition, howlers displayed a similar home range (about 3 ha), diet, and number of plants exploited, even though the plant species eaten were different. In another study, Ostro et al. 1999 examined the effects of translocations on the ranging behaviour of Alouatta pigra. Four groups were translocated from CBS into a continuous forest sanctuary, Cockscomb Basin Wildlife Sanctuary (CBWS, 400 km²). Population density was higher in CBS than in CBWS, resulting in smaller home ranges in.
the former than in the latter. After six months, newly-translocated groups established their home ranges. From the same translocation study, Silver and Marsh (2003) outlined two main lessons gained that clarify howlers’ ability to thrive in fragments. Firstly, they exhibited a high degree of dietary flexibility, given that novel food sources were exploited soon after translocation. Secondly, they adjusted time budgets for resting and foraging in order to minimise energy expenditure.

In the Brazilian Atlantic forest, Chiarello (1994) observed a brown howler group, *Alouatta guariba*, at Santa Geneva Reserve (250 ha), and Mendes (1989) followed a group at Caratinga Biological Station (560 ha). The diet was richer in leaves than in fruit (Mendes 1989, Chiarello 1994), but included a large proportion (41%) of liana leaves only at Santa Geneva (Chiarello 1994). The marked seasonal food availability at the two Atlantic forest sites (Morellato and Leitão-Filho 1996, Strier 1992) may explain the accentuated folivory recorded for the brown howlers. In addition, the scarcity of trees with fleshy fruits may have led the howler group living in Santa Geneva to increase their leaf consumption, particularly liana leaves, since these are more available due to forest disturbance (Chiarello and Galetti 1994).

In Brazilian eastern Amazonia, activity patterns and diet were recorded for a group living in a mosaic of unlogged and logged forest, during a 10-month period (Pinto et al. 2003). The group ranged in 17.8 ha of which 7 ha were unlogged and 10.8 ha were logged. For both areas, fruit availability was similar and no behavioural modifications were recorded for the group in terms of diet and activity patterns. The authors suggested that the low logging intensity (25 m³/ha) and the proximity of the unlogged area may have minimised the impact of habitat disturbance for the howler group that seemed to recover rapidly after the three years of the harvesting (time between logging and the study).

In a fragment (270 ha) in the Colombian Andes, a red howler troop fed mainly on both young leaves and fruit, and displayed particularly long resting times (78.5%; Gaulin and Gaulin 1982). In central Amazonia, Neves and Rylands (1991) reported a diet richer in leaves for a red howler group, *Alouatta seniculus*, living in a 12 ha fragment, where there was a considerable percentage (27%) of seeds consumed (Neves and Rylands 1991). This is the only study known with such a high percentage of seed ingestion, even though a
group of red howlers in an undisturbed forest in Colombian Amazon included 4% of seeds on its annual diet (Stevenson et al. 2000a).

Bicca-Marques (2003) compiled the information available for six howler species living in 27 Neotropical forests that range in size between 1.3 and 1,240,000 ha. In that study, fragment size could only predict howlers’ home range size, diet richness, and leaf and fruit diversity. The author stressed that howlers cope with habitat reduction without showing a distinct pattern in their feeding ecology and behaviour.

**Population structure and densities.** In contrast to behavioural studies, other researchers have approached the problem of habitat fragmentation on primates from a population perspective. Effects of habitat fragmentation on howler densities have been assessed in Mexico, Nicaragua, French Guiana and Brazil. Estrada and Coates-Estrada (1988, 1996) analysed population structure and density of *Alouatta palliata* between different forest size patches in Los Tuxtlas, Mexico. In general, the number of howlers was positively correlated with the size of the fragment and negatively correlated with the time of isolation and the distance to the nearest forest. In the same area, Rodríguez-Toledo et al. (2003) found that 59 out of 64 forest fragments were smaller than 10 ha. Moreover, only 19% of the sampled remnants had howlers and their presence was positively related to well-preserved fragments (measured as canopy height). In Chiapas (Mexico), Estrada et al. (2002) estimated a forest loss of 33% between 1984 and 2001. In this fragmented landscape, 22 out of the 44 forest fragments were occupied by groups of *Alouatta pigra*, ranging in size from 1.9 to 35 ha. Mean isolating distances of fragments with howlers were significantly smaller (0.3 ± 0.3 km) than for fragments with no howler monkeys (1.6 ± 0.7 km). As a conservation measure, the creation of vegetation corridors would establish connectivity between fragments and the protected forest of the Palenque National Park, ensuring the dispersal opportunities for howlers.

In Nicaragua, McCann et al. (2003) assessed the conservation status of mantled howlers living in a buffer zone of shade-coffee plantations that encircles a natural reserve (650 ha). Surprisingly, 84 out of 97 mainly unimale groups were recorded at the coffee plantations, and shade trees seemed to be vital for their survival. Some agro-forestry
systems seem to support howler persistence like those shade-coffee plantations, but only with highly regulated practices.

In the Brazilian Atlantic forest, the population of brown howlers seemed to have increased (1.8 individuals/km²) in a 20-year period at Santa Geneva Reserve (250 ha), even though densities were not estimated before the creation of the reserve. The population increase seemed to be attributed to low predation pressure and abundance of liana leaves, which are two resulting effects of forest fragmentation (Chiarello and Galetti 1994). Similar density values (1.2 individuals/km²) were reported for the same species living at Caratinga Biological Station (560 ha; Mendes 1989).

In northern Argentina, the effect of logging on a population of *Alouatta caraya* was assessed by comparing changes in howler density before (1984-1992) and after the disturbance (1993-1995). The total number and absolute density of howlers living in five forest fragments (5 to 10 ha) remained unchanged after disturbance (0.06 individuals/ha). Yet, since the area of suitable forest was reduced by 32% after intense logging, ecological density increased accordingly (0.92 individuals/ha) (Kowalewski and Zunino 1999).

Recolonisation and persistence in fragments. In Costa Rica, the expansion of a population of *A. palliata* was assessed over a 28-year period after the establishment of the Santa Rosa National Park, on lands reclaimed from ranchers. Subsequent to protection, the population of *Alouatta palliata* expanded to the new area by a substantial increase in size via the formation of new groups (Fedigan and Jack 2001). The main finding of this research was that, by allowing the regeneration of forest in a period of time of 28 years, the size of howler populations could be enhanced.

In the southern Brazilian Amazon, Ferrari et al. (2003) assessed the effect of the Santarem-Cuiaba highway on local primate communities in 11 forest fragments (70 to 4,500 ha) and one continuous forest reserve. In general, larger fragments contained more species, but primate abundance tended to increase in smaller patches, especially for *Alouatta belzebul*.

At the Biological Dynamics of Forest Fragment Project in central Amazonia (BDFFP), red howlers (*Alouatta seniculus*) were the only primate species remaining in six reserves (2 of 100 ha and 4 of 10 ha each) after isolation, while black spider monkeys (*Ateles*
paniscus), brown capuchins (Cebus apella) and bearded-black sakis (Chiropotes satanas) disappeared immediately from all of them (Rylands and Keuroghlian 1988). Golden-handed tamarin (Saguinus midas) and white-faced saki (Pithecia pithecia) remained in the 100 ha fragments only (Rylands and Keuroghlian 1988). Recolonisation of the fragments has occurred at different rhythms and seems to be related to changes in the matrix. For instance, spider monkeys have been observed in 10 ha fragments when the matrix was a tall secondary-growth vegetation. A survey carried out in 1995 (Gilbert and Setz 2001) revealed a decline in densities of the six primate species in 10 ha fragments, and a slight increase of primate densities in 100 ha and continuous forest reserves, compared to estimates recorded in 1984 after isolation (Rylands and Keuroghlian 1988). Finally, for the same study area, Gilbert (1997) found that endoparasitic infestation was greater in small forest fragments (10 and 100 ha) than in larger fragments (1000 ha) and continuous forest (> 5000 ha).

Seed dispersal. In northern Belize, Marsh and Loiselle (2003) evaluated the recruitment of trees dispersed by Alouatta pigra in six forest fragments (1.25 to 3 ha) with howlers and in one remnant without howlers. Fruit species dispersed by howlers did not show a general advantage at the sapling stage of recruitment, despite the abundance of howlers in the area. The authors suggest that the lack of differences may reflect site and species-specific responses to local environmental and disturbance conditions.

The close interaction between dung beetles and faeces produced by howlers in forest fragments has been assessed in two studies (Estrada et al. 1999b, Andresen 2003). They suggest that the regeneration capacity of plant species would certainly be affected by the absence of their primary and secondary seed dispersers and the subsequent disruption of howlers-dung beetles ecological interactions. In Mexico, a study relating the presence of howlers and dung beetles was conducted in 38 isolated forest fragments of sizes varying between 2 and 150 ha and with distances to the nearest forest from 20 to 800 m. The decline or disappearance of howler populations resulted in major declines in dung-beetle numbers and species (Estrada et al. 1999b).

At the BDFFP, Andresen (2003) found that 1 ha fragments had half the number of dung beetle species captured in continuous forest and in 10 ha fragments. She suggested that
howler monkeys are probably the most important dung source for beetles in the 10 ha fragments and, thus, the maintenance of a rich dung-beetle community in forest fragments may be closely related to the presence of howler monkeys. Dung beetles acted as secondary seed dispersers by relocating seeds primarily dispersed by howlers in the fragments.

According to all the studies mentioned above, it appears difficult to find a general trend for howlers thriving in fragments. As Marsh (2003) pointed out, generalisations of primate responses facing forest loss and isolation are difficult to find since information available is generally gathered from different localities (Laurance et al. 1997) and through different methods and sampling designs. Furthermore, Chiarello (2003) proposed a more local approach to the problem of forest loss that should be outlined within a specific array of local conditions, such as forest protection status, degree of human use and surrounding matrix.

Finally, some authors suggest that fragmented primate populations may persist as metapopulations (Chapman et al. 2003, Rodríguez-Vargas 2003). Metapopulations occur both naturally or are created as a result of habitat loss and habitat fragmentation caused by human action. A metapopulation is a set of partially isolated populations belonging to the same species that are able to exchange individuals and recolonise sites in which the species has recently become extinct (Hanski 1999). In this way, fragmented primate populations may escape the hazards of genetic, environmental and demographic stochasticity (Chapman et al. 2003, Rodríguez-Vargas 2003). Information on landscape structure, fragment occupation, population dynamics and individual movements are necessary in order to determine if local populations are structured as metapopulations (Rodriguez-Toledo et al. 2003).
CHAPTER 2
RESEARCH DESIGN:
Objectives, study site and general methods

2.1 OBJECTIVES AND QUESTIONS

The main objective in this study was to evaluate the effect of home range reduction caused by habitat fragmentation on the feeding ecology of *Alouatta seniculus* and on the howlers’ subsequent role as seed dispersers in Brazilian central Amazon. Changes in the basic ecology were assessed over 13 months for two groups of howlers living in 2.5 ha and 12 ha fragments. Comparisons of seed dispersal were also conducted through analysis of howlers faeces across a continuous forest and the two fragments. The following questions were addressed:

1. Do temporal patterns of leafing, flowering and fruiting within howlers’ home ranges differ between a 2.5 ha fragment, a 12 ha fragment and a continuous forest?

2. What are the effects of fluctuations in food supply on the diet, activity budgets and use of space of the howler groups living in the fragments?

3. Do these behavioural responses by howlers differ between fragments due to reduction in home ranges?

4. Do dispersal patterns and seed shadows created by howlers vary across the fragments and the continuous forest?

2.2 EXPECTED RESULTS

Habitat fragmentation always results in the reduction in size and isolation of forest remnants (Laurance and Bierregaard 1997, Gascon *et al.* 2001). Consequently, at the onset of this study howlers living in the fragments were assumed to exhibit smaller home ranges than those living in the continuous forest. This assumption was corroborated
during preliminary observations conducted between September and December 2001. In the 12 ha fragment, the focal group used about half of the fragment, whereas a neighbouring troop was observed occupying the rest of the fragment. At the 2.5 ha fragment, the focal group was the only one using the fragment. Clearly, these home ranges sizes were smaller, when compared to a home range of 21 ha recorded in 1998 for a howler group living in the same continuous forest (Santamaría and Rylands 2003). Thus, expected results are based on the fact that habitat fragmentation decreases howlers’ home range.

It is well documented that fluctuations in food supply have important implications for primate ecology. Such fluctuations drive seasonal changes in primate diets, ranging, habitat use, activity patterns and reproduction (Leighton and Leighton 1983, Terborgh 1986). Thus, in a fragmented scenario, primate responses need to be predicted by accounting for seasonal changes in plant-part production.

Fruit availability is predicted to be lower in forest fragments than in continuous forest due to two factors. Firstly, habitat reduction causes an elevated mortality of large trees (Ferreira and Laurance 1997). Secondly, fruiting trees, compared to leaves, display a clumped distribution in both space and time (Milton and May 1976, Leighton and Leighton 1983, Terborgh 1986, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000). Both factors would reduce the number of fruiting trees available to consumers, especially in smaller fragments. Consequently, howlers living in the 2.5 ha fragment are expected to show a more folivorous diet. Moreover, habitat fragmentation alters plant diversity with smaller fragments showing lower species richness (Tutin and White 1999). Thus, an effect is predicted in the array of food species available to howlers. Consequently, diet would be less rich for the group living in the 2.5 ha fragment. To process a diet richer in leaves, howlers at the 2.5 ha fragment would rest more and move less.

Changes in the behavioural ecology of howlers living in fragments would result in modifications of their defaecation patterns and thus influence their role as seed dispersers. A larger number of fruit species would be available in larger home ranges and, accordingly, howlers would consume and disperse more seed species at the continuous
site than in the fragments. In addition, reduction of howlers’ home range would diminish the richness and abundance of deposition sites produced by them. Yet, howlers are expected to play an important role in the dispersal of large seeds (> 20 mm long) in fragments, where other frugivorous primates (e.g. *Ateles paniscus*) are absent (Rylands and Keuroghlian 1988, Gilbert and Setz 2001, Gilbert 2003).

At the study sites, howlers use specific sites for defaecations, but also drop faeces at random, when foraging, resting and travelling throughout their ranging area (Gilbert 1997, M. Santamaría pers. obs.). Accordingly, I classified these sites as latrines (sites where howlers defaecated at least twice throughout the study) and random sites (used only once). It is predicted that howlers would deposit more seeds in latrines than at random sites, owing to their prevailing behaviour to move and defaecate from specific supports. Deposition sites would be produced more in latrines in the fragments than in the continuous forest, however, because howlers in fragments would re-use more often specific supports according to a smaller area available.

Finally, seed shadows generated by howlers across sites would show a spatially-clumped distribution according to howler behaviour: (a) defaecations produced by the whole group synchronously; (b) defaecations performed from specific supports, and the creation of latrines (c) use of dormitories plus bimodal rhythm of deposition that leads to high concentration of faeces around sleeping sites. The degree of seed shadow patchiness, however, would be affected through home range reduction. In the continuous forest, deposition sites would be more concentrated than in fragments, because more area of the forest ground would fail to receive seeds in larger than in smaller home ranges.

### 2.3 STUDY SITE

#### 2.3.1 Historic background

This research was carried out at the Biological Dynamics of Forest Fragments Project (BDFFP), a large-scale experimental project studying the effects of fragmentation on Central Amazonian *terra firme* forests (Lovejoy *et al.* 1986, Lovejoy and Bierregaard 1990). The project began in 1979 as the “Minimal Critical Size of Ecosystems” and as a joint effort by Brazil’s National Institute for Amazon Research (INPA) and World Wildlife Fund (WWF-US). It was originally conceived to identify the minimum size of
tropical forest required to maintain the biotic diversity represented in an intact ecosystem. The project took advantage of the Brazilian law that states that Amazonian landowners have to maintain 50% of the forest intact within their property. Agreements and arrangements were made with the ranch owners to re-direct their clear-cutting and to establish a replicated series of isolated forest fragments of different sizes (1, 10, 100, and 1,000 ha) (Figure 2.1). Twenty-four square primary forest reserves were set up in three large cattle ranches (Dimona, Porto Alegre and Esteio), which are under control of the Manaus Free Trade Authority (SUFRAMA). The ranches are located about 80 km north of the city of Manaus (2°30’ S, 60° W), embedded in unbroken primary forest extending over 200 kilometres to the north, east and west (Bruna et al. 2002). Surveys of different plant and animal groups were conducted by several researchers before and after fragment isolation, to detect changes in species richness and composition in response to fragment size (see review Gascon and Bierregaard 2001).

The project underwent profound transformations between 1987-1989, when it was renamed as the BDFFP and became project administered jointly by INPA and the Smithsonian Institution, Washington, D.C. Its main goal also changed, since it became clear that forest remnants were not representing “true islands” and that more complex modifications were occurring after forest fragmentation. Subsequently, research efforts were focussed on two additional and key components of forest fragmentation: the creation of forest edges and the appearance of a modified landscape in which fragments are embedded, the matrix. Moreover, studies were conducted on fragmentation effects, not only at population and community levels, but also in a more integrative approach through ecological processes (e.g. decomposition) (Gascon and Bierregaard 2001).

2.3.2 Characteristics of the BDFFP reserves

Encompassing an area of 1,000 km², the BDFFP inland reserves consist of non-flooded forest, referred to as *terra firme* forests that are broadly classified as a lowland tropical moist forest. The terrain is undulating and dissected by first- and second-order streams, with altitudes ranging from 50 to 100 m above sea level. The predominant soils, known as yellow latosols, are nutrient-poor, acidic, with high clay content and low available
Figure 2.1: Location of the reserves of the Biological Dynamics of forest fragments Project (source BDFFP). The two forest fragments and the continuous forest of this study are located in the yellow circle.
water capacity (Fearnside and Filho 2001). Annual rainfall ranges between 1,900 and 3,500 mm (based on 12 years of BDFFP records), with a dry season from June to October that may become more severe during El Niño droughts (Laurance 2001). There is little variation in day length and mean annual temperature is 26°C, with minimum values of 19°C to 21°C and maximum ones of 35°C to 39°C (Laurance 2001). Canopy height ranges from 30 to 37 m with emergent trees up to 55 m (Rankin-de-Merona et al. 1990).

The *terra firme* forests of the Manaus region comprise a high diversity of tree species, a high level of floristic endemism and a large number of rare tree species. Around 1,250 tree plant species (including morpho-species) have been identified at the BDFFP (S. Laurance, pers. comm.), of which only 160 species are not considered rare (Laurance 2001). These undisturbed forests are characterised by having a high density of trees with small dbh (diameter at breast height) and a few with a high dbh (Oliveira 1997, Oliveira and Mori 1999). According to Oliveira and Daly (1999), two attributes explain the striking floristic diversity of the Manaus region. Firstly, several phyto-geographic provinces within Amazonia converge in this area and, secondly, it is a key centre of re-convergence for populations from Pleistocene refugees. The dominant families in terms of density, diversity and biomass are Lecythidaceae, Leguminosae, Sapotaceae and Burseraceae (Oliveira 1997, Laurance 2001). Plant-part productivity exhibits a supra-annual cycle, with a distinct fruiting peak occurring mainly in the rainy season, and a flowering peak concentrated during the dry season (Oliveira 1997). Moreover, because the density and abundance of flowering and fruiting plants is low (Gentry and Emmons 1987, Spironello 2001), central Amazonia is considered a fruit-poor area in comparison to other Neotropical forests (Bierregaard et al. 1992).

Nine primate species are known from the north of the Amazon River and east of the Rio Negro in Brazil. Six species are found in the study area: golden-handed tamarin (*Saguinus midas*), white-faced saki (*Pithecia pithecia*), bearded saki (*Chiropotes satanas*), brown capuchin (*Cebus apella*), black spider monkey (*Ateles paniscus*), and red howler monkeys (*Alouatta seniculus*) (Rylands and Keuroghlian 1988, Schwarzkopf and Rylands 1989). Baseline data on primates before and after isolation were first gathered by Rylands and Keuroghlian (1988), showing that only howler monkeys remained in all 10 ha fragments just after the isolation process, while spider monkeys and bearded sakis
disappeared immediately. Primate re-colonisations have been recorded and seem strongly related to a more mature matrix (Gilbert and Setz 2001, Gilbert 2003). In fact, forest fragments do not remain isolated continuously, since vegetation around them regenerates rapidly (Bierregaard et al. 2001a). As a result, primate composition seems to be highly dynamic at the BDFFP reserves.

2.3.3 The study sites

Fieldwork was conducted in three sites located at the cattle ranch named Esteio: two forest fragments in Colosso camp of 2.5 ha (hereafter Co 2.5-ha) and 12 ha (hereafter Co 12-ha) respectively, and a 1,000 ha continuous forest reserve by Km41 camp (hereafter Km41). This latter reserve functions as one of the BDFFP control sites because it has not been disturbed and is surrounded by continuous forest. All reserves within the BDFFP are protected from hunting, selective logging and other harvesting activities. Furthermore, all fragments were fenced after their initial isolation to prevent cattle intrusions (Bruna 2003).

At Km41, a grid of 100 m x 100 m covers 3 km² of the reserve. In Co 2.5-ha, the area is divided in 20 m x 20 m quadrats totalling a 1 ha plot, while in Co 12-ha, 9 plots of 1 ha divided almost the whole area into quadrats of the same size (20 m x 20 m). In these plots, all trees with a dbh > 10 cm marked with a number are being identified by the Phyto-demographic Project of the BDFFP (Gascon and Bierregaard 2001). Distances outside the plot system were measured from each external quadrat to the existing fence, and subsequently from it to the forest edges. Thus, both fragments were entirely divided into a grid system.

Following the definition of fragment size by Marsh (2003), Co 2.5-ha is a small remnant (< 10 ha). It was first isolated in August 1980 by burning a belt of forest around the fragment that was 150 m in width. In 1988, 1992, 1995 and 2000, the fragment was re-isolated by burning and clearing-up the surrounding vegetation, mainly composed of Cecropia spp. (Cecropiaceae) and Vismia spp. (Clusiaceae) (Gascon et al. 2001). Two aspects of the history of this fragment remain unclear, but have profound implications for the survival of the howler group living in it. First, its real size is 2.5 ha, which is more than twice its original planned size (1 ha). Second, since 1992, a narrower belt was burnt reducing the distance between the forest patch and the adjacent forest to only 50 m. The
presence of large avian frugivores (e.g. guans and toucans) and potential primate predators (e.g. harpy eagle) is perhaps explained by the proximity of the adjacent continuous forest.

The second fragment under study, Co 12-ha, is classified as a medium-sized fragment (10-100 ha, Marsh 2003), but actually is very close to small-sized fragments. It was first isolated in August 1980 by burning a band of 700 m wide of forest around it. The regenerating second growth composed of *Cecropia* sp. and *Vismia* sp. was burnt and cleared again in 1982, 1985, 1987, 1989, 1994 and 2000. For an unknown reason, this fragment is 2 ha larger than was originally planned and, since 1989, only a belt of 100 m surrounding the fragment has been kept clear. Again, large frugivorous birds and primate predators were also regularly observed using the fragment. A cattle-pasture 400 m long separates the two fragments (Figures 2.2 and 2.3), while about 12 km of forest separates the Colosso camp study area from Km41 camp.

### 2.4 GENERAL METHODS

This study included two fieldwork phases. The groups of *Alouatta seniculus* were contacted and habituated during a pre-sampling period of four months, September to December 2001, while systematic data on the study troops were recorded on a monthly basis between January 2002 and January 2003.

#### 2.4.1 Pre-sampling period

*Vegetation plots.* With the aim to survey plant-part availability to howlers, vegetation plots (20 m x 20 m) were established within the home range of each monkey group, at each study site. In Km41, plots were set up within the home range of the group that resisted habituation. The home range was estimated at 20 ha according to data obtained in 1998 for another howler group (Santamaría and Rylands 2003). As the howlers under study showed a difference in home range sizes, I established a different number of plots across study sites: five in Co 2.5-ha, nine in Co 12-ha and 16 in Km41.
Figure 2.2: The Co 2.5-ha and Co 12-ha forest fragments, after the first isolation burn in October 1980 (source: Bierregaard et al. 2001a).

Figure 2.3: Satellite image of the Co 2.5-ha and Co 12-ha forest fragments in 2002 (source: BDFFP).
Howler groups in continuous forest. Previously, in 1998, I studied a howler group in the continuous forest reserve of Km41 (Santamaría and Rylands 2003). When I returned in 2001, I found the original howler group no longer existed in their home range, but instead only a lone male and a couple (female with a male juvenile) were located in the area. After about 100 search-hours/person, we concluded that the group had disintegrated, possibly due to the death of the alpha male. In fact, in July 2001, a carcass of an adult male was found (P. Stouffer, pers. comm.) close to the home range of the group. Subsequently, habituation began on a second troop encompassing an adjacent home range. Although about 120 hours were invested in following the new group, we did not succeed in habituating it. The alpha male was particularly aggressive to observers and continuous observations of more than two hours were hardly possible. Thus, no behavioural data could be recorded from this site.

Howler groups in forest fragments. Habituation of the two groups living in the fragments was also conducted during this period. The process was particularly difficult and time consuming at Co 12-ha, where animals were secretive and would hide from the observers. After three months, the group became calmer and could be observed continuously. In contrast, the habituation process was easy at Co 2.5-ha, since in such a small fragment the presence of researchers cannot be unnoticed and thus the group was already used to observers. During this pre-sampling period, ad libitum observations (Martin and Bateson 1993) were carried out to record group size, group composition, ranging area, plant species used and food categories ingested. In this period, observation protocols were also refined and field assistants were trained in data collection of howlers and phenological data collection.

The group of Co 2.5-ha (hereafter Group 1) was observed for 60 hours during this pre-sampling period and used the whole fragment, with intensive use of forest edges. There are no available baseline data on primates for this reserve before isolation, but four surveys conducted later at the BDFFP (Gilbert 2003) reported that a howler group was living in this fragment, at least since 1991-1992. A single adult male bearded saki was observed on the 1995-1997 and 2000-2001 surveys. During my research, September
2001-January 2003, the howler group was the only resident primate species of the fragment, leading to a howler density of 2.4 individuals/ha.

In Co 12-ha, the study group (hereafter Group 2) was followed for 125 hours during this pre-sampling period and about half the fragment (6 ha) was exploited. Another neighbouring howler group, composed of 5-6 members, was observed using the rest of the forest fragment. Thus, this fragment shows a howler density of 1 individual/ha. The presence of this second group was first reported in 1985 (Neves 1985). After isolation in 1980, one howler group and one golden-handed tamarin group remained in the fragment (Rylands and Keuroghlian 1988), but dynamic changes in primate composition were recorded in this fragment that appear related to a more mature matrix (Gilbert and Setz 2001, Gilbert 2003). In two surveys (1991-92 and 1992-93), a group of white-faced sakis was also observed using the fragment. Additionally, the presence of an adult male bearded saki and an adult female black spider monkey were noticed in two following surveys (1995-96 and 2000-01 by Gilbert and Setz 2001, Gilbert 2003). During my study, September 2001-January 2003, the fragment was inhabited by two resident howler groups, one bearded saki (and three individuals visiting the fragment occasionally), and one golden-handed tamarin group (but not known if it was a permanent resident).

2.4.2 Sampling period

Vegetation plots. All the trees marked in the plots were monitored on a monthly basis in the three locations. Between January 2002 and January 2003, direct observation for the presence and absence of leaf flushing, flowering (including buds) and fruiting was recorded. Monthly monitoring was completed within 3-5 days, depending on weather conditions. Data were gathered by one or two field assistants and myself.

Continuous forest. Due to the impossibility of collecting systematic data on a howler group at Km41, only the defaecation patterns and seed dispersal were compared across the three sites through faecal analyses. Faeces were collected from three howler groups (hereafter Groups 3, 4 and 5), but especially from one of them (Group 3). Thus, comparisons were performed mainly between this group and Groups 1 and 2 living in the fragments. During the second week of each month, howlers were located in the early
morning by their characteristic dawn calls, and faeces were recovered from the ground when detected. In addition, we searched for depositions within the groups’ home range. Independently, two field assistants and myself regularly looked for faeces in latrines already marked and search for new locations through olfactory cues. Monthly sampling effort was 150 person-search-hours. Seed survival of dispersed seeds was also assessed for some natural seed shadows produced by howlers and then compared across the three sites.

The three howler groups had adjacent home ranges and lived around the Km41 field station. All points of collected faeces and opportunistic encounters of the three groups were mapped in Arc View version 3.2 and then the convex-polygon method was applied (Mohr 1947). Home range sizes of Groups 4 and 5 were not estimated, because points were concentrated in a small area. In particular, Group 5 was ranging in a rugged area that made it difficult to locate faeces and group encounters. Home range size of Group 3 was estimated at 22 ha, a value similar to the one recorded for another howler group observed in the same reserve in 1998 (21 ha; Santamaría and Rylands 2003).

*Forest fragments.* Between January 2002 and January 2003, systematic data on howlers’ diet, activity budget, ranging and seed dispersal were recorded and compared between the two groups of howlers living in Co 2.5-ha and Co 12-ha, respectively. Each group was observed continuously from 0530-0550 to 1730-1820h, during four consecutive days of the first week of each month. The start and end of daily observations were determined in relation to slight variations (of about 20 minutes) in sunrise and sunset throughout the year. Due to logistic and ecological reasons, monthly observations were conducted in parallel by one field assistant with Group 1 and myself with group 2. In this way, synchronous observation periods reduced a confounding effect caused by temporal variability in food supply in different sites. Three field assistants with prior experience of primate observation recorded behavioural howler data on Group 1, each one over a period of 4–5 months, whereas I observed Group 2 throughout the study. The field assistants were always trained on observation protocols during 2–3 weeks before starting to collect data systematically.
Total observation time for Group 1 was 611 hours, whereas Group 2 was followed for 696 hours. Observation times varied, between the two groups because Group 1 crossed the surrounding belt to the adjacent continuous forest in April, May and August 2002 and January 2003. Only two-three observation days were recorded for Group 1 over these months. Furthermore, this group could not be followed during these travels, since they were extremely silent when leaving the fragment. In addition, Group 2 often left the sleeping site very early at 0430 hours, for an unknown reason. Thus, I standardised the data on the basis of including only data from full days and observations after 0530 hours (when monkeys could be seen). Thus, 570 hours and 47 full days were obtained for Group 1, while 641.5 hours corresponding to 52 full days were completed for group 2 (Table 2.1).

Table 2.1: Number of full days (N) and total hours of observation (T.O.) of the two troops under study between January 2002 and January 2003.

<table>
<thead>
<tr>
<th>Month</th>
<th>Co 2.5-ha</th>
<th></th>
<th>Co 12-ha</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>T.O. (hr.min)</td>
<td>N</td>
<td>T.O. (hr.min)</td>
</tr>
<tr>
<td>January</td>
<td>4</td>
<td>45:40</td>
<td>4</td>
<td>47:18</td>
</tr>
<tr>
<td>February</td>
<td>4</td>
<td>48:30</td>
<td>4</td>
<td>48:45</td>
</tr>
<tr>
<td>March</td>
<td>4</td>
<td>48:25</td>
<td>4</td>
<td>49:40</td>
</tr>
<tr>
<td>April</td>
<td>2</td>
<td>24:46</td>
<td>4</td>
<td>49:25</td>
</tr>
<tr>
<td>May</td>
<td>3</td>
<td>36:30</td>
<td>4</td>
<td>49:40</td>
</tr>
<tr>
<td>June</td>
<td>4</td>
<td>49:20</td>
<td>4</td>
<td>48:40</td>
</tr>
<tr>
<td>July</td>
<td>4</td>
<td>48:45</td>
<td>4</td>
<td>48:30</td>
</tr>
<tr>
<td>August</td>
<td>3</td>
<td>36:00</td>
<td>4</td>
<td>48:50</td>
</tr>
<tr>
<td>September</td>
<td>4</td>
<td>48:00</td>
<td>4</td>
<td>48:20</td>
</tr>
<tr>
<td>October</td>
<td>4</td>
<td>49:30</td>
<td>4</td>
<td>52:10</td>
</tr>
<tr>
<td>November</td>
<td>4</td>
<td>48:40</td>
<td>4</td>
<td>49:40</td>
</tr>
<tr>
<td>December</td>
<td>4</td>
<td>48:50</td>
<td>4</td>
<td>50:40</td>
</tr>
<tr>
<td>January</td>
<td>3</td>
<td>36:40</td>
<td>4</td>
<td>49:50</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>47</strong></td>
<td><strong>570:00</strong></td>
<td><strong>52</strong></td>
<td><strong>641:50</strong></td>
</tr>
</tbody>
</table>

Instantaneous scan sampling at 10-minute intervals was used to quantify systematic behavioural data on diet, activity budgets and ranging of each group (Martin and Bateson 1993). This method was chosen because howler monkeys are not very active and they have strong cohesion, performing most activities together (Milton 1980, Julliot and Sabatier 1993). Infants were not included in the sampling until they reached about one
year of age. Details of the method are presented in Chapters 4 and 5. In total, 3,450 scans for Group 1 and 3,914 for Group 2 were collected. Group composition changes throughout the study and, consequently, the number of members sampled, varied along the study. In the small fragment, four to six members were included in the sampling, while in the medium fragment, 4 to 5 individuals were recorded (see below for changes in group composition). All members of each group (4-6 in Group 1 and 4-5 in Group 2) were recorded in more than 80% of the total scans (mean$_{\text{Group 1}} = 4.5$, mode = 5; mean$_{\text{Group 2}} = 4.1$, mode 4; figure 2.4).

![Figure 2.4](image)

**Figure 2.4**: Percentage of number of animals seen per scan for (a) Group 1 and (b) Group 2, between January 2002 and January 2003.
2.4.3 Group composition

The composition of howler groups followed in the two forest fragments was defined according to four age classes: infants, juveniles, sub-adults and adults. Individuals of 0 to 11 months were considered infants. They were carried by their mothers first ventrally (one month), then dorsally (about five months) and finally not at all but were similar in size to the ones carried dorsally. Individuals between 12 to 23 months were considered juveniles and were visibly smaller than sub-adults and adults. Sub-adult males included individuals of about 23 to 35 months that were smaller than adult males but similar in size to adult females. Finally, adults were composed from individuals of 36 months onwards. For the groups observed occasionally in the continuous forest, adults and sub-adults were pooled in one single category, as they are difficult to identify in the field when groups are not systematically observed.

Continuous forest. During the monthly searches for faeces in Km41, composition of Groups 3, 4 and 5 were noted, but changes in composition could not be detected. By January 2003, Group 3 was formed of two males, three females and one infant. In May 2002, a newly-formed group, Group 4, was observed occupying the area of the group followed in 1998 (Santamaria and Rylands 2003). In the following month, a new-born infant (about one week) was part of the group composed of three males and two females. Finally, in January 2002, Group 5 was composed of two males, two females and one infant. Thus, group size varied between 5-6 members that included 2-3 males, 2-3 females and one infant.

Forest fragments. Composition of the two howler troops changed due to births and migrations and/or deaths of some individuals. In September 2001, Co 2.5-ha group was composed of six members: an adult male, a juvenile/subadult male, two adult females, and two male infants about five to six months old (Table 2.2). In March, the young males (already juveniles; see table 2.2) were completely independent of their mothers, foraging like the adults and thus were included in the sampling. In April 2002 and for the first time, the group was observed crossing the surrounding vegetation to the adjacent continuous forest. Three days later, the group returned to the fragment, where it was
observed that one of the young juveniles had seriously injured his arm. He could barely move on his own and finally died. Group size was reduced to five individuals until the end of the sampling period. In a later survey in September 2003, I recorded a new infant (unidentified sex) of about four months of age, since it was still carried by its mother (Table 2.2).

Table 2.2: Variation in the composition of the study groups between September 2001 and September 2003.
A:  Adult; Sa: Sub-adult; J: Juvenile; I: infant
?: unknown month
* Members not sampled. Infants = 0 to 11 months old, juveniles =12 to 23 months old, subadults = 24 to 35 months old and adults 36 months onwards.
In September 2001, the group in Co 12-ha was composed of four members: one alpha male, a subadult male and, two adult females (Table 2.2). Two male infants were born during the research period, one in November 2001 and the other in April 2002. Only the first-born infant was included in the sampling from October onwards, when he was almost one year old (Table 2.2). During the survey in September 2003, the group composition changed to seven individuals in total: an adult male (not the alpha one) had moved out of the troop, while two male infants were born. One was about 3-4 months old and the other one around was 6 months old (Table 2.2).

2.5 LIMITATIONS OF THIS STUDY

This study had some limitations that can be partly attributed to logistic problems. Because howler monkeys have been widely studied and, in particular, *Alouatta seniculus* is not an endangered species, funding was limited. Consequently, fewer howler groups could be followed and observed than previously planned. My discussions and conclusions on feeding behaviour in fragments are based mainly on the two focal groups and in this sense, they may be restricted. Yet, primates’ responses to forest reduction depend not only on species-specific traits, but also on the local environmental conditions in which fragments are found. Thus, my research represents a study case in which particular fragmentation conditions are occurring, and the responses of howlers are evaluated in this context.

The unexpected disappearance of the howler group previously observed in 1998 in Km41 (Santamaría and Rylands 2003) and then the impossibility of habituating a new group, resulted in a lack of a howler control group. Yet, when possible, results obtained for the howlers in fragments were compared with information recorded in 1998 (Santamaría and Rylands 2003) and with other howler studies conducted in undisturbed forests of the Amazonian basin (e.g. Julliot 1992). Yet, data on some components of seed dispersal were collected in the continuous forest, Km41, allowing comparisons between the three study sites.
2.6 THESIS STRUCTURE

This dissertation is organised into five chapters that are the result of a simultaneous sampling effort (Chapters 3 to 7). In the final chapter (Chapter 8), I collate the results and discuss their implications for conservation.

Temporal patterns of leafing, flowering and fruiting within howlers’ home ranges at the three study sites are presented in Chapter 3. The subsequent two chapters comprise temporal variations in ranging behaviour, activity budgets and foraging strategies within and between the two howler troops. In Chapter 6, data on frugivorous behaviour, defaecation rhythm, gut passage time and seed dispersal distance are presented and compared between the two groups living in fragments. Finally, in Chapter 7, howlers are compared across the three sites in terms of defaecation patterns (latrines and random sites), seed shadow characteristics and spatial distribution, and seedling survival in natural seed shadows.

The specific methods and statistical analyses completed for the different variables recorded are explained in detail in the corresponding chapter. Since one of the main objectives of this study was to evaluate howler responses to food availability, I pooled data in three seasons, according to the phenological pattern obtained and described in detail in Chapter 3:

a. A fruiting season: January-May (rainy period),
b. A leaf flushing season June-September (dry period),
c. A flowering season: October-December (dry-wet transition period).

For each site, differences in the variables recorded for howlers were analysed among the three seasons, while comparisons across sites were performed within each season. Most of the data recorded were not normally distributed and hence, non-parametric statistics were generally performed. All analyses used a p < 0.05 and were two-tailed tests. Parametric tests were applied only when assumptions of normality and equal variances were not violated. All statistic analysis were performed using the SPSS package version 11.
CHAPTER 3
FOREST FRAGMENTATION AND CHANGES IN
RESOURCE AVAILABILITY

3.1 INTRODUCTION

It is well documented that tropical forests display seasonal rhythms in plant-part production (Foster 1982, Terborgh 1986, van Schaik et al. 1993, Peres 1994a, Chapman et al. 1999) and that abiotic (rainfall, temperature, solar irradiance) and biotic (pollinators, seed dispersers/predators, herbivores) factors underlie these temporal patterns (Frankie et al. 1974, Tutin and Fernandez 1993, van Schaik et al. 1993, Newstrom et al. 1994). Solar irradiance and rainfall appear, however, to have major roles in triggering phenological patterns of woody tropical plants (van Schaik et al. 1993, Wright and van Schaik 1994, Wright 1996). Although exceptions occur, particularly in aseasonal forests, leaf flushing and flowering are mainly produced during peaks of solar irradiance (e.g. dry season), while fruiting is concentrated at the end of the dry season and during the rainy season (Frankie et al. 1974, Foster 1982, Rathcke and Lacey 1985, van Schaik et al. 1993, Newstrom et al. 1994).

Fluctuations in food supply have important implications for animals that feed on plant parts. Several studies have focused on understanding how primary consumers cope with these changes and endure periods of food abundance and scarcity (Terborgh 1983, Peres 1994a, Kaplin et al. 1998, Chapman et al. 1999, Stevenson et al. 2000a, Brugiére et al. 2002, McConkey et al. 2003). In fact, phenological patterns affect primate socio-ecology, as these drive seasonal changes, not only in primate diets, but also in their ranging, habitat use, activity patterns and reproduction (Leighton and Leighton 1983, Terborgh 1986, Peres 1994a). Little is known, however, about how forest fragmentation is likely to disrupt phenological patterns in tropical forests (Restrepo et al. 1999, Laurance et al. 2003) and, if so, how animals surviving in forest fragments are likely to respond.

In this chapter, I describe and compare temporal patterns of leafing, flowering and fruiting for a 13-month period within howlers’ home ranges living in a small (Co 2.5-ha) and a medium (Co 12-ha) forest fragments and a continuous forest reserve (Km41) in
Central Amazon. Additional information on canopy cover, as an indicator of habitat quality, is also included for each site. These data will be linked in the next two chapters concerning the feeding and activity patterns of howlers living in the two forest fragments. The main questions addressed in this chapter are:

(1) Is there a more open canopy in the fragments than in the continuous forest?
(2) What are the leafing, flowering and fruiting patterns within howlers’ home range at each study site?
(3) Are there differences in these patterns between sites?

Small forest fragments (< 10 ha) are subjected to higher exposure to winds especially near forest edges, which in turn causes an elevated mortality and damage of large trees and the formation of canopy-gaps (Ferreira and Laurance 1997). These vegetation structural changes would result in an open and discontinuous canopy, which would affect habitat quality for arboreal species such as howlers. Thus, it is predicted that more light would penetrate through the forest in the small forest fragment, followed by the medium one and then by the continuous forest reserve.

It is expected that leafing, flowering and fruiting will vary between months in each study site, given that tropical forests are known to display seasonal rhythms in plant-part production (Foster 1982, Terborgh 1986, van Schaik et al. 1993, Peres 1994a, Chapman et al. 1999). These seasonal patterns will differ across sites due to forest fragmentation. In particular, fruit availability is predicted to decline in fragments, given that, firstly, habitat reduction causes an elevated mortality of large trees (Ferreira and Laurance 1997). Secondly, fruiting trees, compared to leaves, exhibit a clumped distribution in time and space (Milton and May 1976, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000). Consequently, both factors would reduce the number of trees fruiting within howlers’ home ranges.
3.2 METHODS

3.2.1 Rainfall variation

Data on monthly rainfall has been recorded by the BDFFP and, since 1988, it has been available to researchers. The Central Amazon region is characterised by having one dry season (June-October) and one wet season (November-May) each year (Oliveira 1997). At the BDFFP in the continuous forest reserve (Km41), annual rainfall ranges from 1,900 to 3,500 mm, with the driest months averaging 150 mm (Laurance et al. 2003). Thus, strong inter-annual variation occurs in the study area that may affect the timing of dry/wet season. I compared rainfall amount between Colosso (Co 2.5-ha and Co 12-ha fragments) and Km41 field stations, which are 12 km apart (Chapter 2), to characterise the 13-month study period. Here, a month with rainfall between 130-150 mm was considered a dry month (Laurance et al. 2003).

3.2.2 Canopy cover

Canopy cover was estimated in each fragment and in Km41, as an indirect measure of habitat quality. Although other variables, such as biomass and tree size are indicators of habitat quality, canopy cover has a major influence in arboreal species as howlers. In addition, the effects of habitat fragmentation on tree size and biomass have been studied in detail at the BDFFP (Ferreira and Laurance 1997, Laurance et al. 1997).

A spherical crown densiometer was used to estimate forest canopy coverage. Following manufacturer's instructions, four measurements are taken in four different directions (north, south, east, west), at sampling locations in the site, and then averaged. Higher values indicate that more light can penetrate through the forest as a result of a more open canopy. Measurements obtained are given without units. In Km41, 30 quadrats were selected randomly according to the grid system and within the home range of the howler group that resisted habituation (Chapter 2). Subsequently, in each of the 30 selected quadrats, a point was chosen according to the northeast corner position. Data were only recorded in the forest interior, since the home range does not exhibit forest edges. At both fragments, and within the howlers’ home range, 15 points were recorded in edge habitat and 15 in interior forest. According to the grid system of Co 12-ha, quadrats were selected randomly for edge habitat and forest interior, and then a point in each quadrat.
was located in relation to the northeast corner position. In Co 2.5-ha, 30 points (15 for each habitat type) were defined every 20 m. This method was applied in this fragment as a way to avoid dependency between selected points, which could occur due to the small fragment size, and consequently to the low number of quadrats available for selection. In Co 12-ha and Km41, the dependency of points was avoided by selecting first the quadrats and then the points. The different method of selecting points between the small fragment and the medium fragment and continuous forest should not impact upon comparisons across the three sites because, as mentioned before, measurements recorded were independent. Moreover, at a forest site located 140 km from the city of Manaus, the average crown diameter has been estimated in 9.5 m mean which corresponds to 4.5 m radius (Read et al. 2003). This suggests that canopy cover should change every 20 m and that this distance between points is enough to ensure independency of sampling points.

For each site, all measurements were recorded in one clear day. For each fragment, data on both treatments were pooled after no significant differences were found through a student t-test (Co 2.5-ha: F= 0.64, p= 0.43; Co 12-ha: F= 0.03, p= 0.87). Subsequently, canopy cover was compared across the three sites by performing an analysis of variance (ANOVA, Zar 1999).

3.2.3 Resource availability

In this study, I did not attempt to characterise either the seasonal rhythms of the forest at large or of certain food species. My main objective was to assess and compare general patterns of food availability within howlers’ home ranges in the three study sites, to relate them to the feeding behaviour of howlers living in the two forest fragments.

Plot establishment. As the howlers under study showed a difference in home range sizes (Chapters 2 and 5), a different number of plots were established across the study sites. A plot size of 400 m² (20 m x 20 m) was selected according to the grid system of the fragments (Chapter 2). The Co 2.5-ha includes 1 ha plot divided in 20 m x 20 m, with all trees marked and identified by the Phyto-demographic Project of the BDFFP (Gascon and Bierregaard 2001). The total fragment area was used by the study troop and 5 plots were established randomly inside the existing 1 ha plot. For this, each quadrat was
assigned with a number and then a table of random numbers was used to select the plots. The Co 12-ha contains 9 plots of 1 ha also with all trees marked and identified by the above-mentioned project. In this fragment, the home range of the study group was estimated at 6 ha during the pre-sampling period (Chapter 2), and 9 plots were also placed randomly inside the existing 1 ha plots.

A mean home range size of 20 ha was considered for the continuous forest (Km41) on the basis of a previous study within the same forest reserve (Santamaría and Rylands 2003). Sixteen (16) plots were established randomly within the home range of the howler group previously followed for habituation (Chapter 2). The existing grid system of 100 m x 100 m was used and each quadrat located within the howlers’ home range was subdivided in 20 m x 20 m for the plots selection. The area covered by the 400 m² plots across sites represented 8%, 6% and 3.2%, of the howlers’ home range, respectively (Table 3.1).

<table>
<thead>
<tr>
<th>Site</th>
<th>No. plots</th>
<th>No. trees</th>
<th>HR (ha)</th>
<th>HR area sampled (ha)</th>
<th>% HR sampled</th>
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</thead>
<tbody>
<tr>
<td>Co 2.5-ha</td>
<td>5</td>
<td>113</td>
<td>2.5</td>
<td>0.20</td>
<td>8</td>
</tr>
<tr>
<td>Co 12-ha</td>
<td>9</td>
<td>202</td>
<td>6</td>
<td>0.36</td>
<td>6</td>
</tr>
<tr>
<td>Km41</td>
<td>16</td>
<td>334</td>
<td>20</td>
<td>0.64</td>
<td>3.2</td>
</tr>
</tbody>
</table>

Tree surveys. All of the trees in the plots with a diameter at breast height (dbh) > 10 cm and with a height > 6 m were marked and monitored on a monthly basis in the three locations between January 2002 and January 2003. Direct observations for the presence and absence of young leaves (leaf buds), flowers (floral buds) and fruit were recorded for each tree by one or two assistants and myself. A tree was considered as leafing, flowering and fruiting when at least 20% of its crown was carrying young leaves, flowers and fruit, respectively. Monthly monitoring was conducted in fragments during the first week after howler observations and in Km41 during the second week after faeces collection.
Monthly tree surveys were completed within 3-5 days, depending on weather conditions. Ripe and unripe fruits were placed into a single category due to the difficulty in determining the ripeness of some fruits. All relevant categories were noted when a tree exhibited more than one phenophase during a single observation. Trees that died during the survey were excluded from the analysis. Phenological data were recorded for 113 trees in Co 2.5-ha, 202 trees in Co 12-ha and 334 trees in Km41. According to the Phyto-demographic Project database available for the two fragments, trees sampled in the fragments belonged to at least 140 species in 101 genera and 41 families (Figure 3.1). Of this total of genera recorded, 45% at Co 2.5-ha and 61% at Co 12-ha represented food sources for howlers. At Km41, data on the species monitored within the plots are not available, because the Phyto-demographic project has not marked trees in the reserve. Botanical samples were not collected for identification due to logistical reasons. Thus, the percentages of howlers’ food sources represented in the phenological plots at Km41 were not estimated.

![Figure 3.1](chart.png)

**Figure 3.1:** Number of families, genera and species of plots sampled in Co 2.5-ha and Co 12-ha between January 2002 and January 2003. The value in front of the genus bars indicate the percentage of potential genera used by howlers.
Initially, I planned to estimate fruit production by ranking each phenophase in accordance to its abundance relative to the crown volume. The estimates would be assigned a score from 0 to 4: 0% = 0; 1 - 25% = 1; 26 - 50% = 2; 51 - 75% = 3; 76 - 100% = 4, and a general monthly production index (PI) would be calculated following Peres (1991; PI = 100 x sum production scores/No. of trees). During the pre-sampling period (September to December 2001), this method was tested and found inappropriate due to low visibility, owning to the high and close canopy of the forest at the study sites. Thus, inter-observer variability was large, resulting in inaccurate assignments of scores to the crown volume. Consequently, I decided not to quantify fruit production.

**Liana surveys.** Lianas were monitored monthly within the plots by recording plants leafing, flowering and fruiting during the tree observations and by searching for fruit and flowers in the ground. I did not attempt to mark individual lianas, because they can spread over large areas, making individual recognition difficult (Putz 1984, Putz and Windsor 1987). This method, however, produced a low number of monitored lianas: 12 in Co 2.5-ha, 24 in Co 12-ha and 27 in Km41, precluding further analyses of the data.

**Statistical analyses.** For each site, monthly resource availability (fruit, flower and new leaves) was expressed as the proportion of trees in that specific phenophase of all trees sampled in the site. Differences in availability patterns across sites were evaluated using Kolmogorov-Smirnov Z tests (K-S, p< 0.05) (Estabrook et al. 1982, Zar 1999).

### 3.3 RESULTS

**3.3.1 Rainfall variation**

Differences of more than 100 mm of rainfall between the two field stations, Colosso and Km41, were found for three months (February, June, November), indicating that a large variation in the amount of rain may occur among neighbouring areas separated only by 12 km (Figure 3.2). Despite these results, a similar rainfall pattern for the three periods emerged for both areas in 2002:
1. A dry season (< 130-150 mm) from July to September,
2. A dry-wet transition season in October-November (130-150 to 200 mm) and,
3. A rainy season between December-June (> 200 mm).

January 2003 was atypical in its rainfall since < 100 mm of rain was recorded, but it was expected to be a rainy month (>130 mm).

![Figure 3.2: Monthly amount of rainfall between January 2002 and January 2003 between Colosso and Km41 field stations.](image)

### 3.3.2 Canopy cover

Differences in canopy cover were highly significant across the three sites (F= 17.35, p= 0.001). More light penetrated in the small fragment (mean ± SE= 9.8 ± 0.7, N= 30), followed by the medium one (7.5 ± 0.6, N= 30) and finally by the continuous forest reserve (5.1 ± 0.5, N= 30) (Figure 3.3). This result suggests that habitat quality, in terms of canopy cover, is more compromised in the Co 2.5-ha than in Co 12-ha.
Figure 3.3: Comparison of the mean canopy cover (and standard error of the mean) across the three study sites. Canopy cover was estimated in terms of light that penetrates the forest (measurements without unit).

3.3.3 Temporal patterns of trees

The three study sites showed similar leafing and flowering patterns (Figure 3.4 a-c) in the timing of peaks and troughs (Table 3.2). The fruiting pattern only differed significantly between Co 2.5-ha and Km41 (Table 3.2).

Table 3.2: Results of the Kolmogorov-Smirnov for each phenophase between sites (N= 13 for all cases). Significant results are bolded.

<table>
<thead>
<tr>
<th>Phenophase</th>
<th>Pair Sites</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leafing</td>
<td>Co 2.5-ha vs Co 12-ha</td>
<td>0.39</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>Co 2.5-ha vs Km41</td>
<td>0.59</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>Co 12-ha vs Km41</td>
<td>0.59</td>
<td>0.88</td>
</tr>
<tr>
<td>Flowering</td>
<td>Co 2.5-ha vs Co 12-ha</td>
<td>0.78</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>Co 2.5-ha vs Km41</td>
<td>0.59</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>Co 12-ha vs Km41</td>
<td>0.39</td>
<td>1.00</td>
</tr>
<tr>
<td>Fruiting</td>
<td>Co 2.5-ha vs Co 12-ha</td>
<td>0.98</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Co 2.5-ha vs Km41</td>
<td>1.37</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Co 12-ha vs Km41</td>
<td>0.78</td>
<td>0.57</td>
</tr>
</tbody>
</table>
Figure 3.4a-c: Monthly total rainfall and monthly variation in leafing, flowering and fruiting at the three study sites between January 2003 and January 2003.
Leaf flushing increased in June and peaked in the dry season (July to September: 19%-39%). Subsequently, leafing declined steadily in Km41 and sharply in both fragments until the end of the sampling in January 2003 (Figure 3.5a). Despite this peak, new leaves remained available in the forest by a considerable proportion (4%-20%), compared to flowers and fruit. A leafing trough appeared only in March and April (< 4%).

Flowering peaked during the dry-wet transition period (October-December: 4%-13%) and was followed by a decline (Figure 3.5b), but the Co 2.5-ha peak emerged only in December (10%). In contrast to the leafing pattern, and excluding the flowering peak observed, a small proportion of trees produced flowers every month (1%-4%). In Km41 and Co 12-ha, fruiting occurred during the rainy season and reached a peak in March-April (8%-17%; Figure 3.5c). A fruiting trough was observed from May to September. Afterwards, fruit production rose until December, but records were mainly of unripe fruit. It was expected that this increase would persist until January 2003. A drop was detected, however, which could be related to the atypical dryness recorded for this month (< 100 mm).

Co 2.5-ha showed a less distinct fruiting pattern, and the only significant differences were with Km41 (Table 3.2). Fruit availability in this fragment was hardly noticeable, with few trees bearing fruit (2%-6%). A higher proportion of trees fruiting (8%-9%) only appeared in January and February 2002 (Figure 3.5c). Finally, more than half of the trees monitored did not produce flowers or fruit in Co 2.5-ha (68%), Co 12-ha (65%) and Km41 (53%), throughout the sampling period.

3.4 DISCUSSION

3.4.1 Canopy cover

As expected, canopy cover was significantly altered in the two fragments when compared to the continuous forest. Moreover, the effects were more drastic in the Co 2.5-ha than Co 12-ha, since vegetation structure is more impacted in smaller remnants, because they are known to exhibit sharper margins (Laurance et al. 1997). A more open canopy implies changes in the micro-climate of the forest and results in a discontinuous
Figure 3.5a-c: Monthly variation in leafing, flowering and fruiting seasons at the three study sites, between January 2002 and January 2003.
canopy. These alterations may have important consequences for howlers, by affecting their daily movements, their exposure to predators and their thermoregulation (Chapter 5).

3.4.2 Resource availability

There was a marked fluctuation in the availability of food resources that may be related to the rainfall regime. The year can be divided into three distinct periods according to food availability:

1. Fruiting: January-May (rainy season)
2. Leaf flushing: June-September (end wet season and dry season) and,
3. Flowering: October-December (dry-wet transition and beginning of rainy season)

For the small forest fragment (Co 2.5-ha), however, this overall pattern was disrupted for fruit availability, even though significant differences were detected only with Km41.

Fruiting. The fruiting pattern detected in Km41 and Co 12-ha is consistent with those reported for the Manaus region (Brazilian Central Amazon) (Oliveira 1997, Lemos 1999, Naka 2001) and is similar to those documented for other Amazonian regions: western (Peres 1994a), north-western (Stevenson et al. 2000a, Palacios and Rodríguez 2001), French Guiana (Julliot 1992, Zhang and Wang 1995a), and south-western (Terborgh 1986). In this study, a low fruit supply was pronounced during the dry season and the fruiting peak occurred in the middle of the rainy season (March-April). It is suggested that the adaptive significance of this feature could be to decrease seedling mortality by reducing water stress during the critical period of seedling establishment (Garwood 1982, van Schaik et al. 1993, Stevenson 2002). A fruiting rise was also detected between November-December 2002 in Co 12-ha and Km41, which might be a result of combining unripe and ripe fruit into one category, because of the difficulty in determining the ripeness of some fruits. In Co 12-ha, I found that 33% of fruiting trees were from Protium spp. In the Manaus region, this genus produces ripe fruit in January-February, but the ripening period starts in October and lasts three months (M. Santamaria, pers. obs.).
As predicted, fruit availability was lower in Co 2.5-ha. Several factors might explain this finding. Forest fragmentation alters microclimate (Kapos et al. 1997), nutrient cycling (Didham 1998), pollination (Dick 2001), seed dispersal (Chapman and Onderdonk 1998), and seed germination (Bruna 1999). Such changes, as well as edge effects, might alter tree fecundity by increasing or reducing it and, hence, affect the seasonal rhythms of food availability in fragments. At BDFFP, some researchers (Dick 2001, Lepsch-Cunha et al. 2001) reported an increase in fecundity for one tree species and a palm, while Laurance et al. (2003) found that tree reproduction did not increase in forest edges for 12 of the 14 species studied.

Lower fruit availability can also be explained by taking into account that fruiting trees, in comparison to leaves, have patchy spatial and temporal distributions (Milton and May 1976, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000). Thus, fruiting may be significantly altered in a small forest fragment, such as Co 2.5-ha, because fewer trees are available to bear fruit (2-8 trees in 0.2 ha). Consequently, fruit peaks would be more difficult to detect and fruit would be more likely to be scarce throughout the year. In addition, small forest fragments (< 10 ha) are subjected to increased mortality of canopy and emergent trees, especially along forest edges, causing significant vegetation structural changes (Ferreira and Laurance 1997, Laurance et al. 1997). Large trees are often the ones that produce flowers and fruit in tropical forests (Richards 1996), and their decline would mean reduction in fruiting trees available to consumers.

Lower fruit availability may be intensified in central Amazon, an area that has been described as fruit-poor due to very nutrient-poor soils (Chauvel et al. 1987, Laurance et al. 2001). Furthermore, many tropical trees in the Manaus region show supra-annual patterns in fruit production. As recorded in this study, Oliveira (1997) and Naka (2001) also found in the Manaus region that about half the monitored trees did not reproduce during the two and one year sampling, respectively. Oliveira (1997) suggests that supra-annual patterns in this region may be related to uncommon dry years, which result in a higher rate of unripe fruit abortion. Supra-annual patterns have also been detected in other Neotropical forests (Bullock and Solís-Magallanes 1990, Adler and Kiepinski 2000) and African rain forests (Gautier-Hion et al. 1985, Tutin and Fernandez 1993,
Brugière et al. 2002), where long-term studies underline the inter-annual variability in food resource production for primates. Spironello (1999) recorded that only 2 trees/ha of the Sapotaceae family at Km41 reserve of the BDFFP produced fruit annually. This family is known to be highly exploited by howlers in the Manaus region (Andresen 2002a, Santamaría and Rylands 2003, Chapter 4), French Guiana (Julliot and Sabatier 1993) and in Surinam and western Amazon (Peres and van Roosmalen 2002). Thus, fruit disruption should be strong in very small fragments of terra firme forests in Central Amazon and should have important consequences for howlers, because despite being the most folivorous Neotropical primate, they consume a significant amount of fruit (ca 50%), when available in the forest (Julliot and Sabatier 1993, Chapter 4).

Although the fruiting pattern was not altered in Co 12-ha, it is important to note that a forest fragment of this size is not large enough to maintain primates relying mainly on fruit, like black spider monkeys (Ateles paniscus). In fact, only red howlers and golden-handed tamarins survive in fragments of such size, because the former can exploit leaves and the latter forages at forest edges (Rylands and Keuroghlian 1988).

In this study, fruit availability was estimated in terms of the percentage of fruiting trees, whereas fruit production could not be estimated accurately. Both variables, however, are important to understand how primates cope with phenological changes. In this sense, my results on fruit availability are limited. For instance, food choice of howler monkeys cannot be fully understood without measuring both, fruit availability and fruit production, given that choice depends not only on what is available in the forest, but on how large the crop is and how it is depleted over time. Despite this limitation, the general pattern of food availability estimated here helps to understand the feeding and activity responses of howlers living in forest fragments (see chapters 4 and 5).

**Leafing and flowering.** Van Schaik et al. (1993) suggested that leafing and flowering are closely related in time and occur during the dry or early wet seasons, coinciding with the period of greatest solar radiation. Young leaves would be more efficient at photosynthesis and would reduce water loss (through transpiration control) during peak radiation. Subsequently, it would be more efficient to transfer assimilates directly to growing organs (like flowers), instead of storing them for later translocation. In this
study, leafing and flowering patterns were consistent with these predictions. Young leaves emerged during the dry season, as a noticeable and “easy” feature to detect for all sites, even without binoculars. Leafing was followed by flowering one month later. These phenophases were consistent across sites, even though in Co 2.5-ha flowering was two months out of phase (Figure 3.5b).

Peres (1991) reported a bimodal pattern of young leaf production in western Amazon, while Stevenson (2002) recorded a continuous availability of young leaves without a clear peak in north-western Amazon. In this study, however, a distinct leafing peak occurred during the lowest fruit supply (July-September). Despite the differences between these studies, young leaves, compared to flowers and fruit, seem to be available all year round in lowland Amazon forests, even if in low proportions. Consequently the dietary switching of some primates, like howler, and titi monkeys, to a more folivorous diet during fruit scarcity would be in concert with the highest young leaf availability in the forest. In fact, in an earlier study, a group of howlers in Km41 survived on nearly 100% of young leaves during the dry season (July-September 1998) (Santamaría and Rylands 2003).

**Lianas.** Lianas are an important component of tropical forests, yet they are rarely included in phenological studies. Some studies indicated that the reproductive activity of lianas differs from trees. In Panama, Foster (1982) found that lianas fruit continually. In the Manaus region, Lemos (1999) and Naka (2001) reported that, compared to trees, lianas have a bimodal pattern: fruiting during mid-rainy season and dry/wet transition period. Although I was unable to analyse the liana data collected in this study due to small sample size, I suggest that, by increasing the number of plots sampled through the method used in this study, the production of liana-parts could be adequately monitored. This avoids the problem of identifying individual lianas in an area with high plant diversity and also allows to survey fruit, flower and new leaf production. Long phenological transects could also allow systematic records of fruit and flower production of lianas, but not for monitoring new-leaf production. It is important to record this food resource in order to understand the dietary responses of folivorous animals, such as howler monkeys.
3.5 SUMMARY

- Between January 2002 and January 2003, surveys of canopy cover and presence/absence of new leaves, flowers and fruit were conducted in two fragments (Co 2.5-ha, Co 12-ha) and a continuous reserve (Km41) of a *terra firme* forest in Central Brazilian Amazon.

- Canopy cover was significantly affected in both fragments when compared to the continuous forest. More light penetrated through the small fragment than the medium one. A more discontinuous canopy may affect howlers’ daily movements, their exposure to predators and their thermoregulation.

- A strong seasonality in plant-part production was recorded within howlers’ home ranges at the three study sites, showing a period of fruit scarcity for consumers during the dry season (July-September).

- A consistent pattern of leafing, flowering and fruiting was observed at Km41 and Co 12-ha fragment, and this pattern is similar to those reported in other Amazonian regions.

- Low fruit availability was found within the small fragment (Co 2.5-ha), while leafing and flowering were not disrupted.

- This decrease in fruit production is predicted to have important consequences in activity patterns and diet for the howler troop living in this fragment (Chapters 4 and 5).
CHAPTER 4
FEEDING RESPONSES TO HOME RANGE REDUCTION

4.1 INTRODUCTION

Tropical forests display seasonal fluctuations in plant-part supply, and consequently consumers, such as primates, endure periods of food abundance and scarcity (van Schaik et al. 1993, Kaplin et al. 1998, Chapman et al. 1999, McConkey et al. 2003). In order to cope with these food changes, primates are known to shift their diet and foraging behaviour (Chapman 1987, Stevenson et al. 2000a, Palacios and Rodríguez 2001, Brugière et al. 2002). The primates’ ability to respond to a changing habitat has appeared useful when facing drastic forest disturbances, such as habitat fragmentation (Cowlishaw and Dunbar 2000, Norconk and Grafton 2003). While some species are unable to survive in fragments, other primate species remain and adjust to the environmental changes in different ways, such as modifying their dietary strategies (Johns 1986, Tutin 1999, Clarke et al. 2002, Silver and Marsh 2003). Generalisations are difficult, however, given that primates’ responses seem to vary according to species traits (e.g. degree of frugivory), and to local variables (e.g. degree of isolation, availability of food resources) (Saunders et al. 1991, Cowlishaw and Dunbar 2000, Marsh 2003, Chiarello 2003).

Of the large-bodied Neotropical primates, the howler monkey is the only genus that persists in small forest fragments of less than 10 ha (Rylands and Keuroghlian 1988, Crockett 1998). They are extremely tolerant to habitat fragmentation, because of their ability to exploit leaves as dietary items, to have a flexible home range size, and to live in small groups (Rylands and Keuroghlian 1988). The foraging strategies of red howler monkeys, *Alouatta seniculus*, have been well documented in the Amazon region, but mainly in undisturbed habitats (Andresen 1999, Julliot and Sabatier 1993, Queiroz 1995, Stevenson et al. 2000a, Palacios and Rodríguez 2001, Santamaría and Rylands 2003). Feeding data in forest remnants, however, remain scarce for this species, which has been recognised as an efficient seed disperser in Central Amazonia (Andresen 2002a). Since red howlers are the only fruit-eating primates that thrive in small forest patches, their persistence in forest remnants may be relevant to maintain key processes, like seed
dispersal that guarantee the survival of remnants as intact forests (Laurance 1999, Cowlishaw and Dunbar 2000, Laurance et al. 2001).

In this chapter, I investigate modifications of howlers’ feeding behaviour, when home range size is reduced through habitat fragmentation. I compare the diets of two howler groups living in a small (2.5 ha) and a medium (12 ha) forest fragments in Central Amazon, over a 13-month period. The main questions addressed are:

1. What are the seasonal changes in diet composition, richness, and diversity of each howler group?
2. Do temporal dietary variations differ between the two focal groups?
3. Do fluctuations in fruit availability affect the diet composition of the focal groups?

It is expected that, for each study group, diet would display temporal variation, given that howlers are known to eat mainly seasonal foods when they are in greater supply in the forest (Milton 1980). Given that fruit is a food source rich in ready energy, howlers would feed heavily on fruit when available in their home range (Milton 1980). Thus, fruit availability would be positively correlated with fruit consumption and negatively with leaf and flower ingestion. Diet should also be more folivorous for the howler group living in the small fragment (Co 2.5-ha), due to expected low fruit availability. This is because, firstly, fruit compared to leaves shows a clumped distribution in both space and time (Milton and May 1976, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000). Secondly, habitat reduction causes an elevated mortality of large trees (Ferreira and Laurance 1997), which provide more fruit in the forest (Richards 1996). Moreover, since habitat fragmentation reduces plant diversity (Cowlishaw and Dunbar 2000), a corresponding effect is predicted in the array of food species available to howlers. Thus, diet would be less rich and diverse for howlers living in the small fragment.
4.2 METHODS

From January 2002 through January 2003, quantitative data were collected monthly to assess diet composition, richness and diversity. The two focal troops (hereafter Group 1 living in Co 2.5-ha and Group 2 in Co 12-ha) were observed continuously between 0530-0550 and 1730-1820 hours, during four consecutive days every month. For each howler group, the percentage of time allocated to each activity undertaken was estimated by instantaneous scan sampling (hereafter ISS) (Martin and Bateson 1993). The groups were scanned at 10-minute intervals, recording the first activity sustained for at least ten continuous seconds for each individual visible to the observer. A feeding scan was recorded when a group member was inspecting food, bringing it to the mouth, chewing and swallowing it. Observations in each scan are referred to as feeding records. Infants were not included in the sampling.

A strong seasonality in plant-part production was recorded within the howlers’ home ranges at the two forest fragments and at a control site (Km41; see Chapter 3). A pattern of plant-part production was found for all sites, showing three distinct seasons characterised by: a fruiting peak (January-May), a leafing peak (June-September), and a flowering peak (October-December). Only a slightly distinct fruiting pattern was detected for the small fragment (Co 2.5-ha), with few trees recorded bearing fruit, but these differences were not significantly different between fragments.

According to these plant-part availability results, and for comparative purposes, the daily feeding data were pooled into seasonal averages (mean and 95% confidence intervals-CI) or seasonal totals. Thus, dietary analyses within and between focal groups were performed on a seasonal basis, as well as for the annual study (13-months sampling). More details on the focal groups, sampling protocols and descriptions of study sites are found in Chapter 2.

4.2.1 Diet composition

The composition of the diet was estimated for each howler group through the feeding activity recorded during the ISS (Martin and Bateson 1993). At each feeding record, the food category was noted and the food source marked. Food categories were fruit (unripe
and ripe), leaves (leaf buds/young leaves, and mature leaves), flowers (and bud flowers), and “others” (termitaria nest material and water).

In total, 2,340 feeding records (in 570 observation hours) and 3,374 feeding records (in 642 hours) were obtained for Group 1 and Group 2, respectively. Feeding records were analysed by summing the daily records for each food category (fruit, leaves, flowers) and expressing them as percentages of the daily total number of feeding records (N_{Group1}= 47 days and N_{Group2}= 52 days). These percentages were regarded as estimates of the proportion of time spent by each howler group on the different food categories (Martin and Bateson 1993). Seasonal variations in diet composition within each group were assessed using the Kruskal-Wallis test (p< 0.05). If differences were significant, a Mann-Whitney U-test (p< 0.05) was used to contrast the two samples with the highest and lowest sum of ranks (Fowler et al. 1998). Annual and seasonal comparisons of diet composition across groups were performed, using the Mann-Whitney U-test (p< 0.05). The category “others” was not compared in seasonal analyses, because of its low contribution to the total diet (< 1%). Correlations between fruit availability and the proportion of the different food sources in the monkeys’ diet (fruit, leaves and flowers) were analysed by Spearman’s rank correlation coefficient (p< 0.05) (Fowler et al. 1998).

4.2.2 Diet richness

All feeding trees and lianas used by each group during the ISS were marked, numbered and mapped in relation to the grid system of each reserve (Chapter 2). Trees used by howlers were identified through the Phyto-demographic Project database of the Biological Dynamics of Forest Fragments Project (BDFFP). This database comprises a 1 ha plot in Co 2.5-ha and 9 plots of 1 ha in Co 12-ha, with all trees (with a dbh > 10 cm) numbered and identified. In addition, botanical samples of each tree located outside the Phytodemographic plots and each liana exploited were collected and later identified by the specialists at INPA and BDFFP. During the monthly follows, fruit diet was also assessed through direct observations of all fruit feeding events. This method records all fruit trees visited daily, whereas ISS fails to record fruit trees exploited for short periods of time, especially in regions with high plant diversity such as the study area (Chapter 2).
In this way, a complete fruit diet list was built up, also allowing an adequate assessment of howlers’ frugivore behaviour and their seed dispersal role (Chapter 6).

For each focal group, a list of families, genera and species used during the study was obtained, showing the food category ingested (fruit, leaf and flower) and the life habit exploited (tree, liana and hemi-epiphytes). The mean number of species consumed daily was calculated to compare the diet richness between the two howler groups that were not equally sampled ($N_{\text{Group1}} = 47$ days and $N_{\text{Group2}} = 52$ days). Annual and seasonal comparisons on diet richness between groups were conducted for all combined food categories and for each one, through a Mann-Whitney $U$-test ($p< 0.05$). Finally, for each food category and all combined, the dietary overlap rate between groups was estimated through the number of shared species x 100/ total number of species of both groups.

**4.2.3 Diet diversity**

Diet diversity and its seasonal variation were evaluated using the Shannon-Weiner diversity index ($H$), expressed by the formula:

$$H = -\sum p_i \times \ln(p_i)$$

where $p_i$ = proportion of feeding records for the species eaten or the species consumed in each food category. This index varies from 1 to $s$, and a value close to 1 represents a less diverse diet (Krebs 1999). These indices were calculated using the Pcord4 program for windows.

**4.2.4 Diet preferences**

*Main families of plants exploited.* For the annual diet and for each food category, the main families used by each howler group were evaluated by the corresponding proportion of feeding records. The Ivelé’s selection ratio was calculated to compare the relative density of the different families consumed and their proportions in the monkey diet. The relative densities were based on the Phyto-demographic Project database. For Co 2.5-ha, plant family densities were estimated from the 1 ha plot, while for Co 12-ha, family densities were calculated for the six plots of 1 ha that are within the howlers’ home range.
Relative densities were expressed as the number of trees of each family/hectare. The analyses did not include families mainly composed of lianas species, such as Menispermaceae and Convolvulaceae, since the database does not include liana plants. This analysis was performed at the family level and not at the generic or species level, because: (1) information for many genera was not available from the Phyto-demographic database, and (2) plant diversity is very high in the Manaus region, making it difficult to identify all howlers’ food plants at the species level.

The Ivele’s selection ratio was calculated for the entire study as:

\[ Sr = \frac{Frf_i - Drf}{Frf_i + Drf} \]

where \( Frf_i \) = proportion of feeding records of the family \( i \) in the howler diet, and \( Drf_i \) = proportion of the relative density of trees of the family \( i \) in the vegetation plots of the BDFFP. Feeding preferences are defined by a selection ratio between 0 to 1, which means that the family is used more than its relative abundance in the habitat.

Plant species and their frequency of use. The frequency of use of each plant species ingested by both groups was evaluated by its percentage contribution to the total feeding records. Subsequently, the number of species required to make up > 50% of the total diet and for each food category was then estimated. Comparisons were conducted within and between fragments on an annual and seasonal basis.

4.3 RESULTS

4.3.1 Diet composition

The overall diet of each group was composed mainly of leaves (Group 1= 52.7%, Group 2= 57.2%; \( U = 0.64, p= 0.52 \)), and then fruit (32.4% and 34.1%; \( U = 0.50, p= 0.61 \)). Moreover, both groups showed a strong preference for young leaves (46.7% and 56.0%) and ripe fruit (22.8% and 27.3%), rather than mature leaves (6.0% and 1.2%) and unripe fruit (9.6% and 6.8%), respectively. Their diet was complemented with flowers, but Group 1 fed on more flowers than Group 2 (Group 1= 12.6%, Group 2= 6.3%; \( U = 2.04, p= 0.04 \)). Drinking water and eating termitaria nest material (category “others”) were
ininfrequently exploited by both groups, resulting in small variations in the percentages of feeding records (0.4% for both groups; $U = 1.74$, $p = 0.08$) (Figure 4.1). Food category could not be determined in 1.8% of feeding records for Group 1 and in 2.1% for Group 2.

![Figure 4.1: Comparison of annual diet composition between Groups 1 and 2, in terms of percentages of daily feeding records (mean and 95% CI), between January 2002 and January 2003.](image)

The howler groups displayed strong seasonal changes in their diet, varying according to fluctuations of food resources (Table 4.1). During the fruiting season, both groups ate significantly more fruit than leaves, while in the leafing and flowering seasons they fed significantly more on leaves than fruit. In the medium fragment, flower consumption was similar during fruiting and leafing, and increased significantly during the flowering peak. Yet, in this season, leaf ingestion was always greater than flowers (Table 4.1). Although a similar pattern was found in the small fragment, flower intake did not show significant differences due to large variations in flower consumption in each season. (Table 4.1). As a consequence of this result, some significant dietary differences were detected, when comparisons were performed between groups (Table 4.1). During the fruiting season, Group 1 compared to Group 2, ingested more flowers (9.8% and 3.2%) but spent less time to leaves (29.9% and 41.2%) (Table 4.1).
Table 4.1: Seasonal comparisons of diet composition by Groups 1 and 2, between January 2002 and January 2003. Results of Kruskal-Wallis tests (within groups) and Mann-Whitney tests (between groups are presented considering statistical differences at the 5% level. The category “others” and undetermined are not showed in the table.

<table>
<thead>
<tr>
<th>Food categories</th>
<th>SEASONS</th>
<th>Fruiting</th>
<th>Leafing</th>
<th>Flowering</th>
<th>H</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 1</td>
<td>58.8 (± 11.9)</td>
<td>17.3 (± 7.6)</td>
<td>7.5 (± 5.7)</td>
<td>25.8</td>
<td>0.001***</td>
<td></td>
</tr>
<tr>
<td>Group 2</td>
<td>53.3 (± 5.6)</td>
<td>20.3 (± 10.3)</td>
<td>14.1 (± 10.8)</td>
<td>25.3</td>
<td>0.001***</td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>1.19</td>
<td>0.08</td>
<td>0.67</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td>0.23</td>
<td>0.94</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 1</td>
<td>30 (± 10.7)</td>
<td>72.9 (± 7.8)</td>
<td>65.6 (± 13.7)</td>
<td>21.3</td>
<td>0.001***</td>
<td></td>
</tr>
<tr>
<td>Group 2</td>
<td>41.2 (± 6.5)</td>
<td>73 (± 9.8)</td>
<td>68.1 (± 11.8)</td>
<td>20.7</td>
<td>0.001***</td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>2.10</td>
<td>0.08</td>
<td>0.06</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td>0.03*</td>
<td>0.94</td>
<td>0.95</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flower</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Group 1</td>
<td>9.8 (± 5.4)</td>
<td>8.7 (± 6.9)</td>
<td>22.1 (± 10.1)</td>
<td>5.3</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Group 2</td>
<td>3.2 (± 3.5)</td>
<td>3.7 (± 3.7)</td>
<td>15.8 (± 7.3)</td>
<td>17.2</td>
<td>0.001***</td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>2.2</td>
<td>0.97</td>
<td>0.84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td>0.03*</td>
<td>0.33</td>
<td>0.40</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Despite these distinct dietary responses by howlers to food fluctuations, the percentage of trees bearing fruit only explained negatively the variation in the percentage of leaves eaten by Group 1 (leaf: $r^2 = -0.35$, p= 0.03, N= 13). All other correlations performed between trees bearing fruit and the consumption of each food category were not significant for Group 1 (fruit: $r^2 = +0.14$, p= 0.22; flower: $r^2 = +0.11$, p= 0.91; N= 13 in all cases) and Group 2 (fruit: $r^2 = +0.08$, p= 0.36; leaf: $r^2 = -0.003$, p= 0.55; flower: $r^2 = +0.02$, p= 0.62; N= 13 in all cases).

4.3.2 Diet richness

Howlers visited 218 food trees in the small fragment and 384 in the medium fragment. Not all food trees were identified, however, because it was not always possible to localise the feeding lianas or to collect a botanical sample, especially for lianas and for plants used for their leaves. In total, 84.9% and 79.6% of the food plants from each group
respectively, were identified, at least to the genus level. The total number of species identified for each group made up 92.8% and 92.2% of the total feeding time, respectively, while each one of the unidentified food sources accounted for less than 1% of the annual diet.

More tree species were exploited by each group (Group 1: 79.0% ±0.1CI and Group 2: 75.8% ±0.1CI) than were lianas and hemi-epiphyte species (Group 1: 21.0% ±0.1CI and Group 2: 24.2% ±0.1CI). This trend was also observed for leaf and flower sources, but fruit was provided predominantly by trees (> 85%; Figure 4.2).

Overall, Group 2 compared to Group 1 consumed more species (155 vs. 117), belonging to more genera (87 vs. 74) and more families (34 vs. 27) (Table 4.2). When diet was examined across food categories, both groups exploited more species for their leaves, followed by fruit and much fewer species for flowers. More fruit and leaf species, however, were consumed by Group 2, while more flower species were ingested by Group 1 (Table 4.2, appendix 1). In addition, each group ate different food parts from the same plant species at different times of the sampling period (Appendix 1). For instance, both groups exploited Protium altsonii for its young leaves, fruit and flowers. Dietary overlap between the two groups was low for all species combined (22.0%), for fruit (19.7%) and leaf (17.3%) species, and extremely low for flower species (8.3%; Table 4.2).

![Figure 4.2](image-url): Comparisons of plant life habit exploited by Groups 1 (G1) and 2 (G2) in each food category between January 2002 and January 2003.
The number of species eaten on a daily basis showed a similar pattern to the one described above. Daily, Group 2 exploited more species in all food categories combined (38 more species), particularly for fruit and leaf species, while Group 1 consumed more flower species (Table 4.3). Yet, the number of fruit species eaten daily did not differ statistically between groups (Table 4.3). Seasonal differences were only significant during the flowering peak for all species combined and for leaves, as well as in the fruiting season when Group 1 exploited fewer leaf species and more flower species than Group 2 (Table 4.3).

Table 4.2: Comparisons of the total number of species (and genera and families) consumed by Groups 1 and 2, in all food categories combined and in each food category, between January 2002 and 2003. Food plants shared between groups and total number recorded from combined data of both groups are also shown.

<table>
<thead>
<tr>
<th></th>
<th>Group 1</th>
<th>Group 2</th>
<th>In common</th>
<th>Total No. recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Species</td>
<td>117</td>
<td>155</td>
<td>49</td>
<td>223</td>
</tr>
<tr>
<td>Genera</td>
<td>74</td>
<td>87</td>
<td>44</td>
<td>117</td>
</tr>
<tr>
<td>Families</td>
<td>27</td>
<td>34</td>
<td>17</td>
<td>44</td>
</tr>
<tr>
<td>Fruit species</td>
<td>36</td>
<td>43</td>
<td>13</td>
<td>66</td>
</tr>
<tr>
<td>Leaf species</td>
<td>77</td>
<td>120</td>
<td>29</td>
<td>168</td>
</tr>
<tr>
<td>Flower species</td>
<td>25</td>
<td>14</td>
<td>3</td>
<td>36</td>
</tr>
</tbody>
</table>
4.3.3 Diet diversity

Surprisingly, the indices of diversity for each food category and all combined were similarly elevated in both howler groups (Figure 4.3a). Throughout the seasons, fruit and flower diversity indices varied more markedly than leaf diversity indices, and always resulted in higher values in the corresponding peak of availability (Figures 4.3a,b). In the fruiting season, however, major differences between groups emerged for the diversity of flower in the diet, with an index three times higher for Group 1 than for Group 2 (1.8 vs. 0.5).
Figure 4.3a: Comparisons of the diversity indices (Shannon-Weiner) estimated for each and all food categories between Group 1 and Group 2.

Figure 4.3b: Seasonal comparisons of the diversity indices (Shannon-Weiner) estimated for each food category, between Groups 1 (G1) and 2 (G2).
4.3.4 Diet preferences

Main plant families exploited. In terms of percentages of feeding records, the howler groups were consistent in exploiting seven main families: Moraceae, Leguminosae, Sapotaceae, Burseraceae, Lecythidaceae, Chrysobalanaceae, and Malpighiaceae. For each food category, almost all the main families exploited were similar in the two groups, even though the feeding records obtained for each family varied (Figure 4.4a-c), but striking difference between fragments was found in the flower category. Group 1 fed extensively on flowers of one species of Sapotaceae (*Micropholis guyanensis*), while Group 2 was never observed to ingest flowers from that family.

All the main families in the howler diet, except Malpighiaceae, were also the dominant families in terms of their relative density in the fragments (Table 4.4). Howlers ate species belonging to some of the main families, such as Burseraceae, Chrysobalanaceae and Lecythidaceae, in accordance to their abundance (selection ratios between −1 and 0) (Table 4.5). In contrast, howlers of both fragments selected species of Moraceae strongly, followed by species of Leguminosae (selection ratios between 0 and 1). Group 2 also selected the family Malpighiaceae strongly. The family Sapotaceae was only preferred by Group 2 (Table 4.5). Sapotaceae species show supra-annual cycles (Spironello 1999) and red howler monkeys in the area are known to exploit this family heavily (Andresen 2002a, Spironello 1999). Although Group 1 did consume species of this family, few trees were bearing fruit during the fruiting season, explaining the selection ratio between −1 and 0. In fact, this group was repeatedly observed crossing the 50 m secondary vegetation (hereafter gap) towards the continuous forest to eat fruit of different species, in four of the 13 sampled months. Particularly, at the end of the fruiting season (May), they travelled to the continuous forest to consume large amounts of Sapotaceae fruit, which were later recovered in their faeces when the group returned to the fragment.

Although the family Malpighiaceae was highly ranked in the small fragment, selection ratios were not estimated for Group 1, because data for this family were not available from the Phyto-demographic project. *Byrsonima stipulacea* (Malpighiaceae), a species widely exploited for its fruit during the leafing season, grows mainly in forest edges and it is rare in forest interiors. Consequently, this species was not found in the census plots.
Figure 4.4a-c: Comparisons of the main families exploited, in terms of feeding records, for (a) fruit, (b) leaves, and (c) flowers by Groups 1 and 2, between January 2002 and January 2003.
Table 4.4: relative densities (D) of tree families (% of tree/ha) in the small (Co 2.5-ha) and medium (Co 12-ha) forest fragments. Database obtained from the Phyto-demographic project of the BDFFP.

<table>
<thead>
<tr>
<th>Families exploited</th>
<th>Co 2.5-ha D (%)</th>
<th>Co 12-ha D (%)</th>
<th>Families not exploited</th>
<th>Co 2.5-ha D (%)</th>
<th>Co 12-ha D (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lecythidaceae</td>
<td>10,79</td>
<td>14,59</td>
<td>Arecaceae</td>
<td>1,71</td>
<td>1,63</td>
</tr>
<tr>
<td>Leguminosae</td>
<td>13,53</td>
<td>12,67</td>
<td>Boraginaceae</td>
<td>0,17</td>
<td>0,17</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td>13,87</td>
<td>11,84</td>
<td>Caryocaraceae</td>
<td>-</td>
<td>0,17</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>10,10</td>
<td>9,84</td>
<td>Clusiaceae</td>
<td>0,68</td>
<td>0,49</td>
</tr>
<tr>
<td>Lauraceae</td>
<td>4,45</td>
<td>6,64</td>
<td>Ebenaceae</td>
<td>0,34</td>
<td>0,29</td>
</tr>
<tr>
<td>Moraceae</td>
<td>2,91</td>
<td>4,18</td>
<td>Elaeocarpaceae</td>
<td>1,37</td>
<td>0,94</td>
</tr>
<tr>
<td>Chrysobalanaceae</td>
<td>6,16</td>
<td>3,78</td>
<td>Erythroxylaceae</td>
<td>-</td>
<td>0,03</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>5,14</td>
<td>3,78</td>
<td>Icacinaceae</td>
<td>-</td>
<td>0,06</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>4,28</td>
<td>3,23</td>
<td>Lacistemataceae</td>
<td>-</td>
<td>0,17</td>
</tr>
<tr>
<td>Violaceae</td>
<td>1,71</td>
<td>3,09</td>
<td>Meliaceae</td>
<td>1,37</td>
<td>0,94</td>
</tr>
<tr>
<td>Myristicaceae</td>
<td>1,03</td>
<td>2,20</td>
<td>Monimiaceae</td>
<td>-</td>
<td>0,29</td>
</tr>
<tr>
<td>Melastomataceae</td>
<td>2,74</td>
<td>1,97</td>
<td>Nyctaginaceae</td>
<td>0,51</td>
<td>0,57</td>
</tr>
<tr>
<td>Humiriaceae</td>
<td>2,23</td>
<td>1,89</td>
<td>Ochnaceae</td>
<td>0,51</td>
<td>0,17</td>
</tr>
<tr>
<td>Myrtaceae</td>
<td>2,74</td>
<td>1,72</td>
<td>Opiliaceae</td>
<td>-</td>
<td>0,03</td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>1,20</td>
<td>1,49</td>
<td>Polygalaceae</td>
<td>0,34</td>
<td>-</td>
</tr>
<tr>
<td>Cecropiaceae</td>
<td>0,51</td>
<td>1,43</td>
<td>Proteaceae</td>
<td>-</td>
<td>0,03</td>
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<td>1,43</td>
<td>Rhizophoraceae</td>
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<td>0,23</td>
</tr>
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<td>Bombacaceae</td>
<td>0,86</td>
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<td>Rubiaceae</td>
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<td>Rutaceae</td>
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</tr>
<tr>
<td>Malpighiaceae</td>
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<td>Sapindaceae</td>
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<td>0,23</td>
</tr>
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<td>0,49</td>
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<td>0,09</td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td>0,86</td>
<td>0,40</td>
<td>Sterculiaceae</td>
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<td>0,92</td>
</tr>
<tr>
<td>Flacourtiaecae</td>
<td>0,68</td>
<td>0,40</td>
<td>Styracaceae</td>
<td>-</td>
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</tr>
<tr>
<td>Bignoniacae</td>
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<td>0,31</td>
<td>Ulmaceae</td>
<td>-</td>
<td>0,06</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>0,34</td>
<td>0,29</td>
<td></td>
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</tr>
<tr>
<td>Dichapetalaceae</td>
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<tr>
<td>Dukeodendraceae</td>
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<td></td>
</tr>
<tr>
<td>Tiliaceae</td>
<td>0,51</td>
<td>0,23</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Celastraceae</td>
<td>-</td>
<td>0,17</td>
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<tr>
<td><strong>Total no. of Families</strong></td>
<td><strong>27</strong></td>
<td><strong>29</strong></td>
<td><strong>13</strong></td>
<td><strong>23</strong></td>
<td><strong>23</strong></td>
</tr>
</tbody>
</table>
Table 4.5: Selection ratios of families exploited by Group 1 and Group 2. Main families obtained in terms of feeding records are bolded. Ratios were obtained using the Ivelle’s selection ratio (see methods for explanation).

<table>
<thead>
<tr>
<th>Family</th>
<th>INDEX Co 2.5-ha</th>
<th>Family</th>
<th>INDEX Co 12-ha</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Positive selection</strong></td>
<td></td>
<td><strong>Negative selection</strong></td>
<td></td>
</tr>
<tr>
<td>Bignoniaceae</td>
<td>0.82</td>
<td>Malpighiaceae</td>
<td>0.80</td>
</tr>
<tr>
<td>Moraceae</td>
<td>0.78</td>
<td>Bignoniaceae</td>
<td>0.79</td>
</tr>
<tr>
<td>Cecropiaceae</td>
<td>0.74</td>
<td>Moraceae</td>
<td>0.71</td>
</tr>
<tr>
<td>Vochysiaceae</td>
<td>0.60</td>
<td>Duckeodendraceae</td>
<td>0.65</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>0.54</td>
<td>Celastraceae</td>
<td>0.52</td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>0.23</td>
<td>Cecropiaceae</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>Leguminosae</strong></td>
<td>0.16</td>
<td>Leguminosae</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Apocynaceae</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sapotaceae</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dichapetalaceae</td>
<td>0.11</td>
</tr>
<tr>
<td>Chrysobalanaceae</td>
<td>-0.05</td>
<td>Burseraceae</td>
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</tr>
<tr>
<td>Tiliaceae</td>
<td>-0.05</td>
<td>Chrysobalanaceae</td>
<td>-0.23</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td>-0.11</td>
<td>Myristicaceae</td>
<td>-0.25</td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td>-0.12</td>
<td>Anacardiaceae</td>
<td>-0.28</td>
</tr>
<tr>
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<td>-0.51</td>
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<td>-0.40</td>
<td>Lecythidaceae</td>
<td>-0.51</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>-0.41</td>
<td>Melastomataceae</td>
<td>-0.55</td>
</tr>
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<td><strong>Burseraceae</strong></td>
<td>-0.45</td>
<td>Violaceae</td>
<td>-0.60</td>
</tr>
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<td>Euphorbiaceae</td>
<td>-0.52</td>
<td>Vochysiaceae</td>
<td>-0.72</td>
</tr>
<tr>
<td>Olacaceae</td>
<td>-0.54</td>
<td>Euphorbiaceae</td>
<td>-0.72</td>
</tr>
<tr>
<td>Melastomataceae</td>
<td>-0.66</td>
<td>Flacourtaceae</td>
<td>-0.72</td>
</tr>
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<td>Lauraceae</td>
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<td>Annonaceae</td>
<td>-0.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bombacaceae</td>
<td>-0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Myrtaceae</td>
<td>-0.83</td>
</tr>
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<td>Quinaceae</td>
<td>-0.88</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lauraceae</td>
<td>-0.95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Olacaceae</td>
<td>-0.96</td>
</tr>
</tbody>
</table>

* Selection ratios not estimated because Phyto-demographic data on this family was unavailable

located in the interior of the fragment. Nevertheless, I suspect that Group 1 would show a similar selection ratio for this family as Group 2, since both groups displayed similar feeding behaviour during the leafing season. They invested a considerable amount of time eating fruit of *Byrsonima stipulacea* (Group 1: 93.4% and Group 2: 60.7% of the fruit diet).
In addition, the families Apocynaceae, Bignoniaceae and Cecropiaceae were also selected by both groups (Table 4.5). Leaves were mostly exploited from the first two families, whereas fruit were mainly consumed from the last family.

**Frequency of use of plant species.** The overall pattern in the frequency of use of plant species revealed that howlers exploited a few species heavily, while most others were used rarely. In fact, only 15 (from 117) and 14 (from 155) species made up > 50% of the total diet of each group, respectively. In contrast, 86 and 130 species were present in < 1% of feeding records by each group, respectively. The lower availability of fruit in the small fragment was noticed because more main species were exploited for their leaves by Group 1 (10 vs. 4 species), while Group 2 exploited more main species for fruit (10 vs. 5 species) (Appendix 2).

The same frequency pattern was detected for each food category, where 13 and 15 species accounted for > 50% of the leaf diet of each group, 3 and 6 species of the fruit diet and 7 and 5 of the flower diet (Appendix 3). Similar results were found for each food category within seasons, but more plant species were necessary to reach 50% of the diet during the corresponding peak of availability (Figure 4.5a-c). It seems that howlers exploit more food sources, but in lesser amounts, when the choice is larger.

### 4.4 DISCUSSION

#### 4.4.1 Diet composition

Diet composition of each howler group changed according to seasonal fluctuations in food resources, although the only significant correlation was between availability of fruiting trees and leaf consumption for Group 1. Howlers ate more fruit and significantly less leaves during the peak of fruit availability (January-May), and switched to a mainly folivorous diet during the rest of the year. Despite the smaller home ranges, the two howler groups studied here had dietary profiles within the range of howlers observed in undisturbed forest in the Amazon (Mittermeier and van Roosmalen 1981, Andresen 1999, Julliot and Sabatier 1993, Stevenson *et al.* 2000a): howlers are foli-frugivore species (*sensu* Chivers and Hladik 1980) that regularly eat leaves, but consume many fruit whenever available. Their diet is complemented with flowers, which are consumed in
Figure 4.5a-c: Seasonal comparisons of the number of species making up > 50% of the (a) fruit, (b) leaf and (c) flower diets, between Groups 1 and 2.
lesser amount due to their brief periods of availability and small food-patch sizes (Milton 1980).

Thus, my results do not support the prediction that, due to lower fruit availability, howlers in the small fragment would be more folivorous. Both fragments displayed similar seasonal rhythms in food availability, when compared to the control site (Km41), although the small fragment showed a less distinct fruiting pattern, and the peak in fruit availability was hardly noticeable (Chapter 3). Although differences were only significant with the control site, observations recorded in Group 1 suggest that fruit was scarce, in a period of expected abundance. Instead of eating more leaves as was predicted, this group responded to low fruit availability by modifying its feeding behaviour in two different ways:

Firstly, during the fruiting season, they compensated for the lower fruit availability by eating flowers. This is supported by the fact that, during this season, flower intake by Group 1 (9.8%) was significantly higher than for Group 2 (3.2%). Both food types represent a source of ready energy, and flowers are extensively exploited during their brief periods of availability, when fruit is generally scarce. If both food sources are available at the same time, howlers tend to prefer to feed on fruit rather than flowers. For instance, at the control site (Km41), a group of howlers fed intensively on the only edible fruit available (*Goupia glabra*) in their home range, in mid-November 1998. Flowers were available during this period, yet howlers spent more than 50% of their time ingesting fruit, whereas flowers were ignored (Santamaría and Rylands 2003). Moreover, howlers are always reported to eat significantly more fruit than flowers (e.g. Milton 1980, Julliot 1996b), but in this study howlers seem to overcome lower fruit availability by ingesting flowers, a food source that also offers ready energy. In contrast, fruit availability was not disrupted in the medium fragment, where Group 2 fed heavily on fruit during the peak fruiting period and flower consumption was low (3.2%).

Secondly, Group 1 was repeatedly observed crossing the 50 m gap towards the continuous forest to eat fruit in four of the 13 months sampled. Three of these travels took place in the fruiting season (April, May 2002 and January 2003). In April, howlers left and returned to the fragment twice in one week. Seeds from *Helicostylis tomentosa* (Moraceae) were recovered from faeces, and the same species was heavily exploited by
Group 2 within its home range during the same month. From these observations, it is clear that howlers’ ability to cross the gap allowed them to search for other fruit trees and, hence, to cope with low fruit availability in the smaller fragment. Group 2 was never observed leaving the fragment and seemed to be well adjusted to a home range of 7.2 ha (Chapter 5). Moreover, the howlers’ absolute densities were much higher in the small fragment (2.4 individuals/ha) than in Co 12-ha (1 individual/ha) (Chapter 2). This indicates that Group 1 is having a greater impact on the forest area available to them than Group 2. Similar results are reported in Mexico, where a higher mantled howler biomass was recorded (8.0 kg/ha) in a small fragment (3.2 ha) than in a 35 ha (1.1 kg/ha) and 250 ha fragments (0.17 kg/ha) (Juan et al. 2000).

As suggested by other authors (Milton 1980, Julliot 1996b, Silver et al. 1998, Pinto et al. 2003, Pavelka and Houston Knoff 2004) and observed in this study, howlers’ foraging strategy seems to be mainly determined by fruit availability in the forest. In Belize, *Alouatta pigra* has been described as “being as frugivorous as possible (….) and as folivorous as necessary” (Silver et al. 1998: 273), and both groups of *Alouatta seniculus* seemed to behave in this way. Howlers included a large component of leaves in their diet during this study, but their fruit consumption strongly reflected the availability of fruit in the habitat. For instance, trees producing edible fruit out of the peak season were consumed intensively by both groups. Fruits of *Byrsonima stipulacea* and *Ficus* sp. were largely ingested in June –July and August, respectively. For the fig species, Group 1 crossed to the adjacent forest and ingested figs there that were later recovered in the faeces. Thus, howlers seem to be continuously tracking fruit availability in their area. As Milton (1979) pointed out, leaf intake in howlers might be limited by the necessity to acquire food resources rich in ready energy (as sugars), which are essential to perform their daily activities. Young leaves generally contain considerable protein, but are deficient in non-structural carbohydrates and lipids. In contrast, fruit and flowers are rich in non-structural carbohydrates, which represent a source of ready energy.

The responses to habitat reduction by both groups differs drastically to those reported for *A. guariba* in the Brazilian Atlantic forest (Chiarello 1994, Mendes 1989), for *A. seniculus* in a Venezuelan hydroelectric impoundment (Orihuela et al., submitted), and
for *A. palliata* at Los Tuxtlas Mexico (Juan *et al*. 2000). In these studies, howlers switched to a mainly folivorous diet and fruit were barely consumed. In particular, howlers living in extremely small fragments in Mexico (3.2 ha) and Venezuela (0.6 ha) devoted 98% and 97% of their feeding time consuming leaves, respectively, but both studies do not report data on fruit availability. The degree of isolation and habitat disturbance seem to be a more drastic process in these study areas, than at the BDDFP in Brazil. For instance, 92% of the Atlantic forest and 84% of the lowland rainforest in Mexico has already been cut down. In Venezuela, the situation is different since the forest fragments correspond to true islands effectively isolated after an area of 4,300 km² was flooded in 1986. Local conditions influence primates’ responses to fragmentation, making it difficult to generalise. As illustrated by these examples and this study, howlers exhibit a marked behavioural flexibility. In general, they appear to solve the common problem of smaller home ranges in different ways, by eating more leaves, eating more flowers or visiting an adjacent forest (when there is one) by crossing the gap.

A small fragment, such as Co 2.5-ha, does not seem to be large enough for Group 1 to meet their daily basic requirements, and for their long-term survival. Certainly, their persistence in the fragment would be compromised, if the continuous forest was not so close and the howlers could not have the possibility to temporally expand their foraging area. From the history of this fragment, it seems that this group was facing a recent re-isolation process when this study began. The surrounding vegetation mainly composed of trees of *Cecropia* sp. (Cecropiaceae) was tall, resulting in a continuous canopy from fragment to adjacent forest, but the 50 m gap was burnt in September 2000 (Chapter 2). Thus, when this study began, Group 1 was facing a re-isolation and part of its former home range was drastically broken into two. This fact might explain why the howlers were frequently crossing to the adjacent forest. Howlers are known to patrol food trees in order to track food availability (Milton 1980). Facing a fruit shortage, the howlers crossed the gap to check and eat fruit from trees already known by them.

Although howlers are exposing themselves to different risks (e.g. predation, Estrada and Coates-Estrada 1996) by crossing the open vegetation surrounding the fragments, they are known to travel and forage (to eat soil) on the ground (Braza *et al*. 1981, Izawa and Lozano 1990, Gilbert and Stouffer 1989, Estrada and Coates-Estrada 1996, Clarke *et
In a fragmented landscape at Los Tuxtlas Mexico, *Alouatta palliata* moved between isolated forest patches ranging from 10 to 200 m. This behaviour was infrequently observed, suggesting that howlers were limiting their movements between fragments probably as way to avoid potential danger from dogs and humans (Estrada and Coates-Estrada 1996). In Costa Rica, a partial deforestation of the area of a mantled howler group cut off 10% of its former home range. The group travelled across the 50 m felled area, when first cleared, to feed on fruit of *Spondias mombin*, but stopped crossing when a deep canal and two roads effectively isolated the area (Clarke et al. 2002). In my study, Group 1 was always silent and seemed to scan the area (for at least half and hour) before deciding to move out of the small fragment. Although a juvenile (about 1 year old) was seriously injured in his arm, could barely move and died after returning to the fragment in April, howlers continued to visit the adjacent forest. The cause of the injury could not be determined, but seemed to be related to the travel to the adjacent forest.

**4.4.2 Diet richness and diversity**

Diet of howlers from the small fragment consisted of fewer plant species and leaf species exploited on an annual and daily basis, than those living in the medium fragment. As expected, these differences are, at first instance, a result of home range and fragment size. Group 2 lives in a fragment more than five times larger and its home range is more than twice (7.2 ha) the size of Group 1 (2.5 ha) (Chapter 5).

Differences in diet richness of related primate species have been explained by the availability of plants exploited by them. Areas with high plant diversity offer a larger number of potential resources (Maisels and Gautier-Hion 1994, Neves and Rylands 1991). In a fragmented scenario, however, small forest patches (< 10 ha) show an elevated mortality of canopy trees that consequently increases tree-fall gaps (Ferreira and Laurance 1997). Although the fragments of this study are of small and medium size, Co 2.5-ha shows more drastic differences in vegetation structure. Dominant trees were frequently observed falling down, generating large clearings, and thus, leading to a reduction in the number of food trees available for howlers. For instance, canopy cover (in terms of levels of light that can penetrate through the forest) was significantly lower in Co 2.5-ha than in Co 12-ha (Chapter 3). This suggests that vegetation structure, and
thus plant diversity, may be much more altered in the small fragment than in the medium one. Thus, howlers from Group 2 have a larger array of food plants from which to choose than Group 1. Hence, the differences between fragments (size and vegetation quality) were reflected in overall and leaf diet of howlers, with Group 2 having a richer diet.

A drastic effect was expected in the fruit diet due to home range reduction, given that fruiting trees show a clumped distribution in time and space, but my results do not support this prediction. Although Group 2 consumed more fruit species daily than Group 1, differences were not significant. Furthermore, fruit diversity indices were similar (2.5 and 2.8) and, as mentioned earlier, fruit consumption did not show statistical differences (32.4% Group 1 and 34.1% Group 2). Instead a striking difference emerged for the flower diet, with more flower species exploited by Group 1 annually, seasonally and daily. Furthermore, the flower diversity index of this group was particularly high during the fruiting peak. In this period of expected high fruit availability, flower intake, richness and diversity were distinctly greater in the small fragment than in the medium one. Thus, the main differences between the two groups are attributed to fruit ripeness and flower consumption. Although more inter-specific competition may have occurred in Group 2 than in Group 1, this fact should not explain the dietary differences (fruit ripeness and flower consumption) found between groups. Group 1 is the only primate species living in the fragment. Group 2 shares the fragment only with one individual of bearded saki and with one group of golden-handed tamarin, which may not be a permanent resident. In addition, the specialised frugivorous black spider monkey and the omnivorous brown capuchin are absent from the fragment (see Chapters 2 and 5).

It is important to stress that, despite their home range reduction, the two groups still had a rich and diverse diet. Plant diversity is extremely high in the Amazonian, and more specifically in the Manaus region (Oliveira and Daly 1999, Oliveira and Mori 1999), and howlers show a richer diet in this region when compared to other Neotropical sites. For instance, 201 plant species in Manaus at the Km41 reserve of BDFFP (Santamaria and Rylands 2003) and 195 plant species in French Guiana (Julliot 1996b) were recorded in the Amazon region, while 73 were reported in Panama (Milton 1980) and 68 in the Brazilian Atlantic forest (Chiarello 1994). The striking diversity in the Manaus region may clarify why diversity indices between groups estimated in this study were similar. In
addition, the low overlap rate found may reflect the extremely high beta-diversity of the tree flora in the Manaus region, where plots separated by a few hundred metres display different plant assemblages (Oliveira 1997, Laurance 2001).

Finally, both groups exploited, in similar percentages, more trees than lianas and hemi-epiphytes. Similar results were found in Km41 (Santamaría and Rylands 2003), where howlers consumed 67% of their food from trees and 33% from lianas. Thus, this finding is not in accordance with the expected results. A greater proliferation of lianas was expected in the small fragment, due to an increase in treefall gaps, and Group 1 was expected to take advantage of this situation. This result can be related to changes in vegetation cover mentioned above. Indeed, I observed that when a large tree fell down, many lianas were carried with it; perhaps this is why lianas are less abundant in this fragment. Moreover, howlers only exploit certain liana families (e.g. Hippocrateaceae, Menispermaceae), which might not be abundant in the fragment. Lianas are an important component of tropical forests, which reflects the need to monitor lianas in tropical forest, despite the difficulty in sampling them.

4.4.3 Diet Preferences

Both groups converged in most of the dietary choices, with no apparent effect from home range reduction. For instance, howlers normally display a strong preference for Moraceae, a family largely exploited by howlers in areas where it is among the most abundant plants (Milton 1980, Estrada et al. 1999a, Stevenson et al. 2000a). This is not the case for the BDFFP reserves and the two fragments under study, where Sapotaceae is far more abundant than Moraceae (Oliveira 1997). Consequently, Moraceae showed selection ratios between 0 and 1 (Group 1 = 0.78 and Group 2 = 0.71), but few species were exploited (9 by Group 1 and 12 by Group 2). On the other hand, Sapotaceae ratios were lower (Group 1 = -0.11 and Group 2 = 0.13), but the howlers fed on more species (14 by Group 1 and 26 by Group 2) (Appendix 1). Howlers were always observed actively searching for fruit and leaves of these two families. For instance, Andresen (2002a) recovered about 50 fruit species of Sapotaceae from faeces of 5 howler groups in Km41.
It is plausible that Group 2 did not ingest flowers from the Sapotaceae family, because they were just not available in the forest during the sampling period. In fact, howlers at Km41 ate flowers from one Sapotaceae species (Santamaría and Rylands 2003), and Julliot (1992) reported that Micropholis cayennensis was the species most consumed for flowers (26%) in French Guiana. Furthermore, howlers may eat some species intensively that might be ignored in other periods (Julliot 1996b). Some authors pointed out that the availability of the surrounding species might reflect the preference for a certain plant species, which may change when the array of food plants available changes (Gautier-Hion et al. 1985, Julliot 1996b).

The Leguminosae family was also preferred by both groups in terms of number of species and was mainly used for its leaves (30 by Group 1 and 40 by Group 2) (Appendix 1). Yet, these species were not highly exploited in terms of the frequency of feeding records (except for Andira parviflora for Group 1 and Monopteryx inpaee and Dipteryx odorata for Group 2). Leguminosae leaves have high nitrogen content, a variety of secondary compounds, a short life span, and a high substitution rate as mechanisms of defence against herbivore attacks (Maisels and Gautier-Hion 1994). These intrinsic characteristics of the Leguminosae leaves might explain, on the one hand, that the howlers prefer them due to the high nitrogen content, which facilitates the fermentation process (Milton 1998). On the other hand, by consuming only a few leaves of each species, howlers may be avoiding the accumulation of secondary compounds.

Although both groups exploited a small number of species as principal foods, the species used differed between sites. This result is consistent with the low dietary overlap between groups (from 8.3% to 22% for each food category and all combined). The high beta-diversity of the flora in the Manaus region (Oliveira 1997, Laurance 2001) may account for these differences, since plant assemblages vary drastically between areas separated only by a few hundred metres. In this study, a cattle-pasture area of 400 m wide separates the two fragments (Chapter 2, Plate 2.1).

While Julliot and Sabatier (1993) found that > 40 plant species accounted for 50% of the total diet, most studies reported a small number of plant species as principal food sources (8 or less species make up > 50% of the total diet) (Milton 1980, Gaulin and Gaulin 1982, Chiarello 1994, Limeira 1997). Groups 1 and 2 appear to be in the middle,
since 14 and 15 species respectively, made up 50% of the annual diet. Nevertheless, it seems clear that in sites with high plant diversity, howlers feed on more food species, but most of them are exploited less intensely. For instance, more leaf species were necessary to reach 50% of the diet during the peak leafing period, than in the two other seasons.

4.5 SUMMARY

- Between January 2002 and January 2003, I examined the seasonal and spatial variation on the feeding ecology of two howler groups living in a small forest fragment (Co 2.5-ha, Group 1) and a medium (Co 12-ha, Group 2) forest fragment in Central Amazonia.

- Both groups showed a frugi-folivorous diet, with drastic seasonal variations based on plant-part availability (fruit, young leaves and flowers). They ate more fruit and less leaves during the fruiting season (January-May), and switched to a mainly folivorous diet during the rest of the year.

- Group 2 ingested more plant species on an annual and daily basis, and exploited more leaf sources than Group 1. In contrast, the richness and diversity of flowers were distinctly greater for Group 1 than 2.

- Instead of eating more leaves, Group 1 responded to fruit decline (Chapter 3) by eating more flowers and by repeatedly crossing a secondary vegetation-gap (50 m) in order to eat fruit in the adjacent continuous forest.

- These short visits suggest that an area of 2.5 ha is too small for howlers to meet their basic requirements. Moreover, howlers’ foraging strategy seems to be mainly determined by fruit availability in the forest, even though they are the most folivorous Neotropical primates.

- While howlers in the medium fragment behaved similar to those living in undisturbed forests, howlers in the small fragment showed large differences in feeding responses to home range reduction.
CHAPTER 5
USE OF SPACE AND ACTIVITY BUDGETS

5.1 INTRODUCTION

Strong inter-specific differences in the behavioural ecology of Neotropical primates are reported in numerous field studies (Smith 1977, Milton 1980, Terborgh 1983, Chapman 1987, Defler 1995, Passamani 1998, Stevenson et al. 2000a, Di Fiore and Rodman 2001, Palacios and Rodríguez 2001). In particular, the use of space and time allocation to different activities appear to depend on a variety of factors, such as distribution and abundance of food resources, type of diet, body weight and group size (Milton and May 1976, Milton 1980, Crockett and Eisenberg 1986, Terborgh 1983, Neville et al. 1988, Oates 1987, Di Fiore and Rodman 2001). In a fragmented landscape, however, primates are exposed to drastic forest changes and their responses in the face of new ecological conditions are known to vary among species. For instance, their ability to survive in forest remnants is related, to some extent, to species-specific traits, such as degree of frugivory and area requirements (Marsh 2003).

Frugivorous species, like spider monkeys, are unable to persist in small remnants (< 100 ha), because they require larger home ranges to find enough fruit for their survival. They need to allocate a considerable daily time in searching for and consuming fruit, a food resource that is rapidly digested and has a clumped distribution in time and space (Milton and May 1976, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000). By contrast, howlers have the capacity to survive in small forest fragments, because of their ability to exploit leaves, a food resource widely distributed in the forest. As a consequence of their folivory, they allocate long periods to resting (about 60% of the day), in order to concentrate their metabolic activity on processing the leaf material, by caeco-colic fermentation (Milton and May 1976, Milton 1980, Chivers and Hladik 1980, Terborgh 1983, Rylands and Keuroghlian 1988, Crockett 1998). During the fermentation process, resting is required, given that digestion efficiency can be reduced if simultaneous activities are performed (Smith 1977, Gaulin and Gaulin 1982).
The behavioural ecology of red howler monkeys, *Alouatta seniculus*, has been well studied in the Amazon region, but mainly in undisturbed habitats (Milton 1980, Andresen 1999, Julliot and Sabatier 1993, Queiroz 1995, Stevenson et al. 2000a, Palacios and Rodríguez 2001, Santamaría and Rylands 2003). Despite their behavioural plasticity, howler responses to forest reduction have been poorly documented in central Brazilian Amazon, a region where major changes in forest cover have occurred recently because of new intensive development pressures (e.g. extensive soybeans plantations and road constructions; Chapter 1). As howlers’ habitat in this region becomes more and more fragmented, it is important to identify the boundaries of their behavioural flexibility (Estrada et al. 1999a), in order to guarantee their long-term survival.

In this chapter, I describe and compare the use of space and activity budget of two howler groups living in a small (Co 2.5-ha) and a medium (Co 12-ha) forest fragments in Central Amazon. The main questions addressed are:

1. Does the use of space, in terms of habitat types (edges and forest interior), differ between groups?
2. Does the global activity budget of each howler group change among seasons?
3. Are there differences in the activity profiles found between groups?
4. Do fluctuations in fruit availability and dietary changes affect the time allocated to each activity by the focal groups?

The use of space is expected to differ between groups due to differences in fragment size and home range sizes. Edge habitat is expected to be used more in the Co 2.5-ha than in Co 12-ha, since smaller fragments exhibit larger edge:area ratios. Both howler groups, however, would not show any preference for either habitat and thus would use each habitat type according to their proportional availability within the fragment.

For each study group, it is predicted that activity profiles would display seasonal variation, according to fruit availability and dietary changes. The time spent feeding and moving should be greater when there is an increase in energetic food resources, such as fruit and flowers (fruiting and flowering seasons). Howlers are predicted to rest more and move less in the small than in the medium fragment, in order to process a diet that is
expected to be richer in leaves. A more folivorous diet would result from an expected low fruit availability, since fruit is highly aggregated in time and space.

5.2 METHODS

5.2.1 Use of space

From January 2002 through January 2003, daily movements of the groups (hereafter Group 1 living in Co 2.5-ha and Group 2 in Co 12-ha) were marked on available maps of the reserves during four consecutive days every month (Appendix 4 and 5). In Co 2.5-ha, the area is divided in 20 m x 20 m quadrats totalling 1 ha plot, while in Co 12-ha, 9 plots of 1 ha divided almost the whole area into quadrats of the same size (20 m x 20 m). Distances outside the plot system were measured from each external quadrat to the existing fence, and subsequently from it to the forest edges. Thus, both fragments were entirely divided into a grid system.

The location of each group was noted every 30 minutes according to the grid system of each fragment. The activity performed by each group (e.g. resting, feeding) was also recorded (see next section for recording methods of activity). The area enclosing the quadrats used at least by one member of each group was referred to as the home range. Both fragments were divided into two habitat types: forest edge and forest interior. Studies of habitat fragmentation have reported that edge effects, such as micro-climate changes, can penetrate more than 250 m into the forest (Laurance 1997). This is particularly true for organisms sensitive to micro-climatic changes, such as seeds and seedlings, but probably not for howlers. Thus, for the purposes of this study, an edge habitat was defined as a 40 m belt from the margin to the forest interior. For both fragments, this criterion is according to observed changes in vegetation physiognomy (e.g. smaller trees), which are more likely to affect arboreal species like howlers.

A total of 1,070 habitat records for Group 1 and 1,307 for Group 2 were obtained throughout the sampling period ($N_{Group1} = 47$ days and $N_{Group2} = 52$ days). Three seasons (fruiting, leafing and flowering) were considered according to phenological results in Chapter 3. For the entire study and for each season, the use of habitat types within each groups’ home range was analysed as the percentage of frequencies recorded in each habitat type. This analysis was performed at two levels: (1) frequencies obtained for the
combined activities performed by howlers in each habitat type and (2) frequencies recorded for the feeding activity in each habitat type. These two levels of analysis were conducted so as to detect, for instance, if a habitat type was used more for feeding.

Habitat preferences for edge habitat and forest interior were defined as a habitat used above its corresponding availability. Annual and seasonal differences in habitat preferences for each group were assessed using a chi-square test for goodness corrected for ties (p< 0.05) (Zar 1999). Expected results were calculated according to the availability estimated for each habitat type within each howler’s home range. Statistical analyses were only performed within each site and within each season/site, because each group exhibited different size areas for each habitat type and because observed frequencies recorded and thus expected ones varied across each season.

Additionally, the sleeping sites used by each howler groups were recorded during the monthly follows. As previously noted by Julliot (1992), howlers in this study were also observed using several trees within specific areas of the forest. Consequently, a sleeping zone (hereafter SZ) was defined as a 20 m x 20 m area. Two categories were defined as follows: (1) frequent SZ, which correspond to zones used at least twice by each group during the entire study, and (2) occasional SZ were those zones used only once by each group throughout the study. The number and frequency of SZ were obtained for each howler group, and expressed in percentages. Finally, data were supplemented with opportunistic observations of rare events related to habitat use such as inter- and intra-specific encounters and calls.

5.2.2 Activity budgets

The two howler troops were observed continuously from 0520-0550 to 1730-1810 hours during four consecutive days/month. The percentage of time allocated to each activity undertaken by each howler group was estimated using instantaneous scan sampling (Martin and Bateson 1993). Each group was scanned at 10-minute intervals, recording the first activity sustained for at least five continuous seconds of each individual visible to the observer. Observations in each scan are referred as activity records. Infants were not included in the sampling. Based on an ethogram of my own previous study (Santamaría and Rylands 2003), the activities were classified into four
mutually-exclusive categories: resting (sitting, lying or sleeping generally associated to inactivity periods), feeding (searching for and ingestion of, food resources), moving (group progression) and the category “others” (less frequent behaviours such as calls, urination, defaecation and intra- and inter-specific interactions). Data were supplemented with opportunistic observations of rare events such as mating.

A total of 15,643 activity records (in 3,450 scans) for Group 1 and 15,964 activity records (in 3,914 scans) for Group 2 were obtained throughout the sampling period (13-months). Activity records were analysed by summing the daily records of each activity and expressing them as percentages of the daily total number of activity records (N_{Group1}=47 days and N_{Group2}=52 days). This percentage conversion reduces biases arising from unequal samples that resulted from different observations times/day (Defler 1995, Clarke et al. 2002). These percentages were regarded as estimates of the proportion of time spent by each howler group on the different activities.

For comparative purposes, the daily activity data were pooled into seasonal averages, and three seasons (fruiting, leafing and flowering) were considered according to phenological results in Chapter 3. Seasonal variations in each activity within each group were assessed using the Kruskal-Wallis test (p<0.05). If differences were significant, Mann-Whitney tests were used to contrast between pair-seasons/activity. Annual (corresponding to 13-months) and seasonal comparisons on activity budgets across groups were performed, using separate Mann-Whitney tests for each activity (p<0.05). The category “others” was not compared in seasonal analyses, because of its low contribution to the total activity budget (<2.5%). For each howler group, the Spearman rank correlation coefficient (p<0.05) was applied to correlate fruit availability and diet composition (fruit, leaf and flower; Chapter 4) with the proportion of the different activities (Fowler et al. 1998, Zar 1999). For fruit availability vs. activity budget, comparisons were performed monthly, and thus monthly averages were obtained for the activity patterns (N=13 for both groups). Comparisons between diet composition vs. activity budget were conducted with daily averages (Group 1=47 days, Group 2=52 days).
5.3 RESULTS

5.3.1 Use of space

*Home range and habitat availability.* Group 1 moved in the entire fragment, and thus its home range was defined as 2.5 ha. Of this area, 60% (1.5 ha) was composed of edge habitat, while 40% (1 ha) was interior forest. In the medium fragment, home range of Group 2 was estimated in 7.2 ha, of which 26% was edge habitat (1.9 ha) and 74% was interior forest (5.3 ha) (Figure 5.1).

![Home range and habitat availability](image)

**Figure 5.1:** Availability of each type of habitat (interior forest and edge) within the home range of Group 1 (2.5 ha) and Group 2 (7.2 ha).

*Habitat preferences.* Overall, Group 1 compared to Group 2 used more edge habitat to perform all activities combined (61.7% vs. 29.5%) and to feed (56.5% vs. 21.3%) (Figures 5.2a,b). This result is not surprising, since the small fragment encompasses more edge habitat (60%) than the medium fragment (26%). For the entire study and for each season, habitat preferences were detected when analysis were performed within each fragment (Table 5.1). Overall, Group 1 showed no habitat preference to perform all activities combined, but fed significantly more in interior forest. In contrast, Group 2
used edges above their availability to conduct all activities combined, but preferred to feed in interior forest. Seasonal differences within each fragment were not always consistent with this pattern (Table 5.1). For instance, during the flowering season Group 1 preferred interior forest to perform all activities combined but foraged more in edges, and Group 2 foraged preferentially in edge habitat during leafing.

![Figure 5.2](image)

**Figure 5.2:** Comparison of the percentage of habitat records noted in each habitat type (edges and forest interior) between Groups 1 and 2, while performing (a) all activities combined and (b) feeding activity only.
Table 5.1: Statistical results (Chi square for goodness corrected for ties) of habitats used by Groups 1 and 2, to perform all activities combined and feeding activity within each season and for the entire study. E= edge and I= interior forest. Values in bold are statistically different at the 5% level. Letters in parenthesis indicate the preference for that habitat (E= edge, I= interior forest).

<table>
<thead>
<tr>
<th>Seasons</th>
<th>Group 1</th>
<th>p</th>
<th>Group 2</th>
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<td>All activities combined</td>
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<tr>
<td>Fruiting</td>
<td>0.86</td>
<td>&gt;0.05</td>
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<td>Leafing</td>
<td>7.83</td>
<td>&lt;0.05 (E)</td>
<td>32.09</td>
<td>&lt;0.05 (E)</td>
</tr>
<tr>
<td>Flowering</td>
<td>7.35</td>
<td>&lt;0.05 (I)</td>
<td>1.31</td>
<td>&gt;0.05</td>
</tr>
<tr>
<td>All seasons</td>
<td>0.67</td>
<td>&gt;0.05</td>
<td>-</td>
<td>8.04</td>
</tr>
<tr>
<td>Feeding activity only</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fruiting</td>
<td>63.37</td>
<td>&lt;0.05 (I)</td>
<td>43.36</td>
<td>&lt;0.05 (I)</td>
</tr>
<tr>
<td>Leafing</td>
<td>0.19</td>
<td>&gt;0.05</td>
<td>-</td>
<td>4.12</td>
</tr>
<tr>
<td>Flowering</td>
<td>6.01</td>
<td>&lt;0.05 (E)</td>
<td>28.90</td>
<td>&lt;0.05 (I)</td>
</tr>
<tr>
<td>All seasons</td>
<td>16.10</td>
<td>&lt;0.05 (I)</td>
<td>35.89</td>
<td>&lt;0.05 (I)</td>
</tr>
</tbody>
</table>

Sleeping zones and opportunistic observations. Each howler group used 30 sleeping zones throughout the study, of which about 71% were recorded as frequent sleeping zones (Figure 5.3). Observations on intra- and inter-specific interactions and calls suggest that the boundaries of the two howler groups were well defined and confrontations were avoided. Although howls were usually heard at dawn in the area around the camp (at least four groups), both focal groups called rarely (Group 1= 2 calls and Group 2= 4 calls). Interestingly, calls by Group 2 were always produced at the boundary of its home range.

In the small fragment howlers are the only primate species present and, consequently, few intra-specific encounters were observed. Only once did a male howler attempt to visit the fragment from the adjacent continuous forest, but it was chased aggressively by the alpha male. Inter-specific neutral encounters were detected with one group of *Cebus apella* and one of *Saguinus midas*. Both groups visited the fragment briefly in different months.

Group 2 shared the medium fragment with another howler group, but only three neutral encounters were recorded during the pre-sampling (of four months) and sampling periods (of 13 months). On these occasions, both groups called and defaecated, and rapid
movements occurred in the canopy, but without physical aggression. Later, each group moved into its home range area. Hence, the overlapping area was calculated in only 0.04% (two quadrats of 20 m x 20 m), corresponding to less than 1% of overlap for Group 2. Frequent inter-specific encounters were observed monthly, with one to four individuals of bearded saki (*Chiropotes satanas*). The alpha male chased one individual in only two of 58 interactions, when not feeding was occurring. In fact, on many occasions the focal group and one bearded saki were feeding simultaneously in the same tree. Five neutral encounters were also detected with a group of golden-handed tamarin (*Saguinus midas*), which may not be a permanent resident, and one with a pair of white-faced saki (*Pithecia pithecia*) during their short visit in November 2002.

![Figure 5.3](image_url)  
**Figure 5.3**: Comparison of the use of frequent and occasional sleeping zones by Groups 1 and 2 between January 2002 and January 2003.

### 5.3.2 Activity budgets

Both howler groups showed similar annual activity profiles (Figure 5.4). On average, resting was the main activity (Group 1= 70.9%, Group 2= 65.9%), followed by feeding (15.7% and 21.5%), moving (11.0% and 10.7%) and the category “others” (2.4% and 1.9%). Group 1, however, spent significantly more time resting and less time feeding than Group 2 (Resting: $U= 3.42, p= 0.001$; feeding: $U= 4.56, p= 0.001$; moving: $U= 0.31, p= 0.75$; others: $U= 0.06, p= 0.94$).
Time allocation varied seasonally only for resting in Group 1 (Resting: $H' = 10.03$, $p = 0.007$; feeding: $H' = 3.68$, $p = 0.16$; moving: $H' = 5.26$, $p = 0.07$), but for none of the activities in Group 2 (Resting: $H' = 0.66$, $p = 0.72$; feeding: $H' = 2.26$, $p = 0.32$; moving: $H' = 4.02$, $p = 0.13$) (Figure 5.5a,b). In particular, Group 1 spent more time resting during the flowering season, with a corresponding decrease in moving and feeding (Figure 5.5a,b). Some significant differences were detected when seasonal comparisons in the activity profiles were performed between sites (Figures 5.5a,b). Group 1, compared with Group 2, spent more time resting during the flowering season and only approached significant differences in the fruiting season (Table 5.2). Throughout the three seasons, time devoted to feeding was always significantly higher in the medium than in the small fragment (Table 5.2). Finally, neither the percentage of trees bearing fruit, nor diet composition, explained the variation in the activity profiles of each howler group (Table 5.3).

Mating activity between the alpha male and one female was only observed in Group 2 in the October sampling. During this four-days period of sampling, six copulations were recorded, and both the alpha male and the ovulating female performed all the activities in
close proximity of less than 4 m from each other, keeping other members of the group apart (> 10 m).

Figure 5.5: Seasonal activity budgets of (a) Group 1 and (b) Group 2 (mean and 95% CI), between January 2002 and January 2003.
Table 5.2: Statistical results of Mann-Whitney tests comparing seasonal differences in the activity budgets between Groups 1 and 2. Values in bold are statistically significant at the 5% level.

<table>
<thead>
<tr>
<th>Activities</th>
<th>SEASONS</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fruiting</td>
<td>Leafing</td>
<td>Flowering</td>
</tr>
<tr>
<td>Resting</td>
<td>$U$</td>
<td>1.79</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td>0.07</td>
<td>0.50</td>
</tr>
<tr>
<td>Feeding</td>
<td>$U$</td>
<td>2.15</td>
<td>2.23</td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td><em>0.03</em></td>
<td><em>0.03</em></td>
</tr>
<tr>
<td>Moving</td>
<td>$U$</td>
<td>0.27</td>
<td>1.48</td>
</tr>
<tr>
<td></td>
<td>$p$</td>
<td>0.79</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Table 5.3: Results of Spearman rank correlation coefficient ($r$ values) between fruit availability and diet composition vs. the different activities performed by Group 1 and Group 2 between January 2002 and January 2003. N= sample size. P values reported are for all correlations performed (none of them significant).

<table>
<thead>
<tr>
<th>AVAILABILITY OF</th>
<th>DIET COMPOSITION</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit N</td>
<td>Fruit Young leaf Flower N</td>
<td></td>
</tr>
<tr>
<td>Group 1 Resting</td>
<td>-0.33 13</td>
<td>-0.24 0.16 -0.03 47</td>
</tr>
<tr>
<td></td>
<td>0.12 13</td>
<td>0.19 -0.13 0.05 47</td>
</tr>
<tr>
<td></td>
<td>0.17 13</td>
<td>0.10 -0.14 0.13 47</td>
</tr>
<tr>
<td>Group 2 Resting</td>
<td>-0.04 13</td>
<td>0.01 0.01 -0.04 52</td>
</tr>
<tr>
<td></td>
<td>-0.20 13</td>
<td>-0.16 0.21 -0.05 52</td>
</tr>
<tr>
<td></td>
<td>0.22 13</td>
<td>0.07 -0.13 0.09 52</td>
</tr>
</tbody>
</table>
5.4. DISCUSSION

5.4.1 Use of space

*Home range size.* In this study, both howler groups illustrate the extreme flexibility in home range size that characterises the genus *Alouatta*. Clearly, these home ranges sizes are smaller, when compared to a home range of 22 ha recorded for Group 3 in the control site (Chapter 2) and to 21 ha obtained in 1998 for a howler group living in the same control site (Santamaría and Rylands 2003). Thus, according to the assumption at the onset of the study, forest fragmentation has reduced drastically howlers’ home range from about 20 ha at Km41 to 7.2 and 2.5 ha at the fragments. Home range of Group 2 was diminished by 63%, while Group 1 home range was decreased by 88%.

The extreme tolerance of howler monkeys to habitat fragmentation has been attributed mainly to their ability to exploit leaves as dietary items, which in turn results in their capacity to live in small home ranges (Rylands and Keuroghlian 1988). It is important to mention, however, the plausible effect that competition between species, under the “Lotka-Volterra” model (Begon *et al.* 1986), might have on howlers’ home range reduction. In this model, species 1 is a strong interspecific competitor, while species 2 is a weak one. Consequently, species 1 out competes species 2 and attains its own carrying capacity.

A possible scenario in forest fragments would be that due to their ability to live on leaves for long periods of time (Santamaría and Rylands 2003), howler monkeys would be able to out compete, for instance, the specialised frugivorous spider monkey. These two species may have inter-specific competition given that they both ingest fruit and they may overlap in their fruit choice. Whereas spider monkeys would be limited to few fruiting trees available in the forest fragment, howlers would have an alternative food source to exploit, leaves, and thus would satisfied their basic requirements more easily. Consequently, they would be able more fit and consequently they would be able to displace spider monkeys from the few fruit sources, and then from the forest fragments. As a result, howlers would be living in forest fragments with less competition and would be able to satisfy their basic requirements in small home ranges. For instance, in Co 12-ha, less primate species inhabit the fragment compared to the control site, Km41, where six primate species are found. Consequently, less inter-specific competition occurred for
Group 2, resulting in more food available for the group, and from this, its ability to live in a small home range. Nonetheless, it is worthy to note that primates have their own species-specific traits, such as area requirements (Marsh 2003). Spider monkeys are reported to require areas larger than 100 ha (Van Roosmalen 1985, Norconk and Kinsey 1994, Nunes 1998, Stevenson 2002). This competitive scenario may occur, therefore, in forest fragments larger than 100 ha. In fact, data on primates before and after isolation of forest fragments at the BDFFP, showed that black spider monkeys disappeared from two fragments of 10 ha and four of 100 ha, immediately after the isolation process (Rylands and Keuroghlian 1988).

Surprisingly, Group 2 shares the medium fragment of 12 ha with another howler troop of similar size (5-6 members), but ranging in a smaller area (about 5 ha). The home range overlap is extremely low for Group 2, less than 1% (0.04 ha), a fact that is supported by the few confrontations and calls recorded during the study. These observations may imply that both groups do not need to produce frequent calls as a way to avoid encounters, because the boundaries are short. Consequently, borders in this fragment would be easily patrolled compared to undisturbed forest, whereas the home range of a troop usually overlaps with more than one group (Milton 1980, Santamaría and Rylands 2003).

While the medium fragment apparently has the capacity to support at least 12 individuals (1 individual/ha), the small fragment seems to be overloaded by Group 1 (2.4 individuals/ha; Chapter 2) with negative consequences in the howlers’ physical conditions. Although body weight measures were not recorded, howlers in Group 1 seemed in poor body condition and looked extremely thin. As explained below (activity section) and in Chapter 4, Group 2 behaved similar to howlers living in undisturbed forests, while Group 1 exhibited more drastic changes in its dietary and activity patterns. Thus, it appears that Group 1 is presumably at its limits of flexibility, given the environmental changes, and thus the demands are higher in such a small area.

Nonetheless, the small fragment is not effectively isolated, given the repeated travels of Group 1 across the surrounding vegetation to the forest in four of the 13 sampling months, which suggests a larger home range for Group 1. This secondary vegetation
regenerates rapidly (Bierregaard et al. 2001a), but it is cleared about every five years. Thus, this group seems to have faced a re-isolation process since September 2000, when the vegetation around it was cleared (Chapter 2). Hence, it is plausible that the group has suffered several re-isolations, since its first reported presence in 1991-1992 (Gilbert 2003). Despite the temporal expansion of their area, Group 1 lives mainly in the fragment, and it is within the smallest fragments reported for howlers, such as 1.3 ha in Belize (Marsh 1999) and two islands of 0.6 and 0.7 ha in Venezuela (Terborgh et al. 2001). Predation risks and energetic demands of crossing the secondary vegetation should be extremely high, and they may only be fulfilled when rewarding sources, such as fruit, are available. For instance, seeds from plants not available in the fragment were always recovered from the faeces after howlers returned to it (Chapter 6).

**Habitat use.** In terms of habitat quality, smaller home ranges are much more affected than larger ones since they have relatively longer edges. The results reported here provide support for this, since the smaller fragment encompasses more edge habitat (60%) than the medium fragment (26%). Furthermore, vegetation structure and composition changes drastically near the edges as a consequence of habitat fragmentation (Laurance et al. 1997), which in turn may affect the quantity and quality of food available to consumers. Overall, Groups 1 and 2 preferred to forage in the interior of the forest, supporting this notion. Both groups, however, performed all activities combined during the leafing season in edges and Group 2 foraged preferentially in edges only during the same season. This finding is attributed to the fact that both groups ingested considerable amounts of fruit from *Byrsonima stipulacea* (Malpighiaceae) in the leafing season (Group 1: 93.4% and Group 2: 60.7% of the fruit diet; Chapter 6). The Malpighiaceae family has been recognised as a successional family (Laurance et al. 1998b), and I observed that trees of *Byrsonima stipulacea* were located mainly in the edges of the fragments. For example, all 30 trees visited by Group 1 were found in edges, while 12 out of 15 trees exploited by Group 2 were located in edges. Thus, it would be useful to assess differences in howlers’ food plants between edges and interior forests, a parameter that was not estimated in this study.
5.4.2 Activity budgets

Each group displayed different seasonal activity profiles, and both patterns were not related to fluctuations in food resources and diet composition. Each group seemed to adopt different time-allocation decisions that lead to remarkable differences between them. Group 2 exhibited a regular seasonal pattern and resting was always the predominant activity. Milton (1980) suggests that howlers are energy-conservers and Group 2 behaved accordingly. Howlers seem to accumulate energy reserves during the period of high availability of energetic foods, such as fruit and flowers. Later, these reserves may support them during lean periods, when only foliage is available and provide considerably less ready energy. Group 2 ate more fruit during the fruiting peak, switched to a mainly folivorous diet during the rest of the year, but always had regular times of inactivity.

In contrast, a more drastic home range reduction seemed to shape strongly the activities of Group 1. They rested longer, especially during the flowering season, and they spent less time feeding. From these results, it appears that this group was facing a significant decline in food availability, as a direct effect of area reduction. This is supported by Group 2 spending more time feeding and consuming more plant species daily (8.9 vs. 6.9 species; Chapter 4), during the entire study and in each season, in comparison with Group 1.

Alternatively and as already documented in some howler studies (Chivers 1969, Mittermeier 1973, Chiarello 1993, Estrada et al. 1999a), climatic variables such as temperature could also influence activity budgets of Group 1. Edge formation is among the reported effect of habitat fragmentation that modifies microclimatic conditions (e.g. wind penetration and higher temperatures). In turn, tree mortality and canopy-gap formation increases, especially near forest edges (Laurance et al. 1997). In particular, smaller, linear and recently-created remnants display sharper margins. In this study, the small fragment had a canopy significantly more open than the medium one (Chapter 3), suggesting much higher temperatures in the former (no measurements performed). Thus, Group 1 could be forced to limit its energy expenditure in order to reduce thermoregulatory stress, especially during the hottest months of the year (September to November). These months are concentrated mainly during the flowering season, with
values up to 39°C (Laurance 2001), when resting was particularly elevated (77.1%) and feeding was low (13.2%)

As predicted, comparisons between groups revealed remarkable differences in time allocation. Howlers living in the small fragment rested more, especially in the flowering and fruiting peaks, and spent less time feeding consistently throughout the seasons. Yet, these responses were not related to a more folivorous diet as expected. Although fruit depletion was recorded in the small fragment, Group 1 adjusted its diet by consuming more flowers, and by eating fruit during short visits to an adjacent continuous forest in the fruiting peak. The question that follows is why this group allocated longer periods to resting, since its diet was not more folivorous than Group 2. As already noted, an overall decline in food plants is occurring in the fragment, as a consequence of a net effect of area size. Substantial alterations in vegetation structure and composition occur due to habitat fragmentation, leading to a significant loss of biomass (Ferreira and Laurance 1997). As already pointed out by Estrada et al. (1999a) for a group of mantled howlers, the outcome of these vegetation changes would produce not only a further reduction of an already small area, but also a fall in the quantity of actual and potential foods available to the group. Consequently, Group 1 fed significantly less and consumed less food plants than Group 2, simply because there were less food sources to exploit. Subsequently, their daily food energy intake was compromised, and the howlers adopted a more marked energy-conservation strategy than the one already employed by howlers, by resting for even longer periods. For instance, Group 1 showed excessive daily periods of resting that could last 5 hours, while Group 2 never exceeded periods of 4 hours of daily rest. Thus, it appears that a small fragment, such as Co 2.5-ha, does not seem to be large enough for the group to fulfil their daily basic requirements, a balance between energy and nutrients (Milton 1980). Their survival demands seems higher in this more drastically-disturbed fragment than in the medium one, and howlers in Group 1 seemed to be in poor body condition (ribs could be seen).

Surprisingly, the activity profiles reported here for both groups fell within the range observed in different howler species, but some confounding effects may underlie this. Many studies compare howlers’ activity profiles across sites without distinguishing those
conducted in undisturbed forests from those carried out in forest fragments. Furthermore, since howlers are the most inactive species of Neotropical primates, they are always classified as resting for more than 60% of the time. In this study, distinct comparisons were conducted between disturbed and undisturbed habitats. Activity profiles of Group 2 fell within the range of howlers observed in undisturbed forest in the Amazon, where resting account for about 65% of the total time (Table 5.4). In contrast, Group 1 displayed a similar activity pattern to other howler species living in forest remnants, in which resting allocation was up to 75-80% (Table 5.5). In these studies, the activity changes have been related to a forced accentuated folivory (Mendes 1989, Chiarello 1993, Juan et al. 2000) and to the impossibility of expanding their home range (Estrada et al. 1999a, Juan et al. 2000). For example, a mantled howler group living in a 3.2 ha fragment in Mexico displayed extreme folivory, consuming 98% of leaves, and resting 74% of the total time (Juan et al. 2000).

Although Group 2 has suffered reduction of its home range, less primate species inhabit the fragment compared to the control site, Km41, where six primate species are found. Consequently, less intra- and inter-specific competition occurred for Group 2, resulting in more food available for the group. For instance, brown capuchins, *Cebus apella*, are absent in this fragment (Gilbert and Setz 2001), given their home range requirements (up to 800 ha) (Spironello 2001). They are known to deplete faster fruit availability than other consumers, because they live and forage in large group sizes (up to 20 individuals) and they feed intensively in fruiting trees (Spironello 2001). Moreover, this primate species consumed significant amounts of Sapotaceae fruit at the control site (Km41) (Spironello 2001), a family widely exploited for fruit by Group 2 during the fruiting season (Chapter 4).

Finally, it is plausible that resting time was slightly overestimated. Howlers may be classified as resting, while they were actually vigilant. As an effect of habitat fragmentation, howlers were more exposed to predation, given that the canopy was more open. In fact, Group 1 was attacked by an eagle (unidentified species) when feeding in an exposed tree surrounded by gaps. Alpha-males of both groups were occasionally observed scanning the canopy, a behaviour difficult to detect in this high-canopy forest. Gilbert and Setz (2001) indicated that howlers at the BDFFP reserves allocate on average
Table 5.4: Activity budgets (in percentages) reported for the genus *Alouatta* in undisturbed forests (areas > 1000 ha).

<table>
<thead>
<tr>
<th>Species</th>
<th>Country</th>
<th>Forest size (ha)</th>
<th>Home range (ha)</th>
<th>Resting</th>
<th>Feeding</th>
<th>Moving</th>
<th>Others</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alouatta pigra</em></td>
<td>Brazil</td>
<td>7,900</td>
<td>4.5</td>
<td>61</td>
<td>21</td>
<td>14</td>
<td>-</td>
<td>Estrada et al. 1999a</td>
</tr>
<tr>
<td></td>
<td>Brazil</td>
<td>120,000</td>
<td>33</td>
<td>63</td>
<td>17</td>
<td>16</td>
<td>-</td>
<td>Steinmetz 2000*</td>
</tr>
<tr>
<td><em>Alouatta palliata</em></td>
<td>Panama</td>
<td>1,550</td>
<td>32</td>
<td>66</td>
<td>16</td>
<td>10</td>
<td>-</td>
<td>Milton 1980</td>
</tr>
<tr>
<td><em>Alouatta belzebul</em></td>
<td>Brazil</td>
<td>10,000</td>
<td>50</td>
<td>59</td>
<td>20</td>
<td>18</td>
<td>-</td>
<td>Pinto 2002*</td>
</tr>
<tr>
<td><em>Alouatta seniculus</em></td>
<td>French Guiana</td>
<td>100,000</td>
<td>45</td>
<td>65</td>
<td>19</td>
<td>14</td>
<td>-</td>
<td>Julliot 1992</td>
</tr>
<tr>
<td></td>
<td>Brazil</td>
<td>1,000</td>
<td>21</td>
<td>68</td>
<td>22</td>
<td>9</td>
<td>1</td>
<td>Santamaria and Rylands 2003</td>
</tr>
<tr>
<td></td>
<td>Peru</td>
<td>-</td>
<td>25</td>
<td>63</td>
<td>19</td>
<td>11</td>
<td>-</td>
<td>Milton 1980</td>
</tr>
<tr>
<td></td>
<td>Peru</td>
<td>1,841,000</td>
<td>-</td>
<td>63</td>
<td>18</td>
<td>9</td>
<td>-</td>
<td>Andresen 1999</td>
</tr>
<tr>
<td></td>
<td>Colombia</td>
<td>201,875</td>
<td>79</td>
<td>59</td>
<td>23</td>
<td>15</td>
<td>3</td>
<td>Stevenson <em>et al.</em> 2000a</td>
</tr>
<tr>
<td></td>
<td>Colombia</td>
<td>200,000</td>
<td>182</td>
<td>64</td>
<td>18</td>
<td>18</td>
<td>1</td>
<td>Palacios in prep.</td>
</tr>
</tbody>
</table>

* Compiled by Bicca-Marques 2003

Table 5.5: Activity budgets (in percentages) reported for several howler species living in forest remnants of different sizes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Country</th>
<th>Fragment size (ha)</th>
<th>Home range (ha)</th>
<th>Resting</th>
<th>Feeding</th>
<th>Moving</th>
<th>Others</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alouatta palliata</em></td>
<td>Mexico</td>
<td>3.6</td>
<td>3.6</td>
<td>80</td>
<td>17</td>
<td>2</td>
<td>1</td>
<td>Estrada <em>et al.</em> 1999a</td>
</tr>
<tr>
<td></td>
<td>Mexico</td>
<td>3.2</td>
<td>-</td>
<td>74</td>
<td>24</td>
<td>1</td>
<td>1</td>
<td>Juan <em>et al.</em> 2000</td>
</tr>
<tr>
<td></td>
<td>Mexico</td>
<td>35</td>
<td>-</td>
<td>79</td>
<td>16</td>
<td>1</td>
<td>4</td>
<td>Juan <em>et al.</em> 2000</td>
</tr>
<tr>
<td></td>
<td>Mexico</td>
<td>250</td>
<td>-</td>
<td>69</td>
<td>28</td>
<td>2</td>
<td>1</td>
<td>Juan <em>et al.</em> 2000</td>
</tr>
<tr>
<td><em>Alouatta guariba</em></td>
<td>Brazil</td>
<td>250</td>
<td>4.1</td>
<td>64</td>
<td>18</td>
<td>13</td>
<td>5</td>
<td>Chiarello 1993</td>
</tr>
<tr>
<td></td>
<td>Brazil</td>
<td>560</td>
<td>7.9</td>
<td>72</td>
<td>16</td>
<td>10</td>
<td>2</td>
<td>Mendes 1989</td>
</tr>
<tr>
<td><em>Alouatta seniculus</em></td>
<td>Colombia</td>
<td>135</td>
<td>22</td>
<td>79</td>
<td>13</td>
<td>6</td>
<td>3</td>
<td>Gaulin and Gaulin 1982</td>
</tr>
<tr>
<td></td>
<td>Brazil</td>
<td>2.5</td>
<td>2.5</td>
<td>71</td>
<td>16</td>
<td>11</td>
<td>2</td>
<td><em>This study</em></td>
</tr>
<tr>
<td></td>
<td>Brazil</td>
<td>12</td>
<td>7.2</td>
<td>66</td>
<td>22</td>
<td>11</td>
<td>2</td>
<td><em>This study</em></td>
</tr>
</tbody>
</table>
1 to 4% of their time to scanning the area for predators, mainly in the upper canopy. Despite this possible method bias, resting times would be only slightly affected, considering the maximum value of 4% reported for the area by Gilbert and Setz 2001.

5.5 SUMMARY

- Between January 2002 and January 2003, I examined seasonal variation in the activity patterns and habitat use by two howler groups living in a small (Co 2.5-ha, Group 1) and medium (Co 12-ha, Group 2) forest fragments, in Central Amazonia.
- Forest fragmentation reduced drastically howlers’ home range from about 20 ha at Km41 (Chapter 2) to 7.2 and 2.5 ha at the fragments (63% and 88% reduction, respectively).
- Home range comprised 60% of edge habitat for Group 1 and only 26% for Group 2. Strong preferences for foraging in interior forest were found for both groups.
- A more drastic reduction in the home range of Group 1 resulted in a net decline in food plants and, consequently, affected time allocation decisions of this group: howlers living in the small fragment rested more time, especially in the flowering and fruiting peaks, and spent less time feeding consistently throughout the seasons.
- It appears that Group 1 lives in a more demanding environment and is presumably at its limits of flexibility, whereas Group 2 is well adjusted to a less disturbed habitat, given that its activity profile is similar to those reported for undisturbed forests.
CHAPTER 6
FRUGIVORY AND PRIMARY SEED DISPERAL

6.1 INTRODUCTION
Tropical forests are characterised by a myriad of ecological interactions, which contribute to the maintenance of tropical tree diversity (Loiselle and Dirzo 2002). The interactions between fruit plants and their vertebrate consumers have been widely studied for two main reasons. First, many animals rely on fruits for their survival (Bourlière 1985, Chapman and Chapman 1995, Charles-Dominique 1995, Lambert and Garber 1998, Peres and van Roosmalen 2002). Second, the majority of tropical-tree species (> 70%) produce fruits adapted for vertebrate consumption (termed zoochoric fruits) and seem to depend on animal agents to disperse their seeds (Frankie et al. 1974, Howe and Smallwood 1982, Willson et al. 1989, Howe 1990, Jordano 1992).

Seed dispersal is a complex process, because it involves several stages that a seed would have to overcome in order to germinate successfully, grow and, finally reproduce (Fuentes 2000, Wang and Smith 2002). Animals move seeds from zoochoric fruit away from their original source and, in turn, seeds can benefit from this action in four different ways:

(1) Seeds and seedlings may escape from high mortality caused by density and/or distance dependent factors under parental trees (escape hypothesis; Janzen 1970, Connell 1971).

(2) Seeds may land by chance in favourable microsites to germinate and establish such as treefall gaps (colonisation hypothesis; Howe and Smallwood 1982).

(3) Seeds are delivered into specific sites by a particular agent (e.g. mistletoe seeds and passerine birds), and the probability of seed and seedling survival is enhanced in these sites when compared to random sites (direct dispersal; Howe and Smallwood 1982).

(4) Seeds may be deposited beyond the limits of parent patches by animals such as tapirs (Fragoso et al. 2003) and, consequently, seeds are less likely to be attacked by specialised natural enemies (long-dispersal distance; Muller-Landau et al. 2003).
Thus, animals are one of the key elements in the seed dispersal cycle (*sensu* Wang and Smith 2002), and are considered to have an impact on forest heterogeneity and regeneration (Chapman 1995, Fuentes 2000, Wenny 2001, Wang and Smith 2002). Animals, however, vary in their dispersal efficiency owing to differences in their morphology, physiology and behaviour (Howe 1984, Zhang and Wang 1995b, Schupp *et al*. 2002). While some act mainly as seed predators (e.g. parrots, saki monkeys), many other frugivore species may or may not disperse seeds of their food plants successfully (Jordano and Schupp 2000). Their effectiveness, measured as their contribution to plant fitness, depends on the quantity of seeds moved away from parental trees, and on the quality of their dispersal (Schupp 1993). In this last component, seed fate would be determined by factors such as fruit handling, seed processing, location of seeds delivered, seed shadow patterns, and dung characteristics that influence the activity of secondary dispersers and predators (Chapman 1995, Lambert 1999, Jordano and Schupp 2000, McConkey 2000, Andresen 2002b).

In Amazonian rainforest, primates are abundant (Terborgh 1986, Rylands 1987, Peres 1997), and many species include fruit in their diet to a greater or lesser extent (Terborgh 1983, Rylands 1987, Peres 1994b, Julliot and Sabatier 1993, Stevenson *et al*. 2000a, Di Fiore and Rodman 2001). Inadvertently, many of these species provide a dispersal service for many of their food plants (Terborgh 1983, Garber 1986, Stevenson 2000, Peres and van Roosmalen 2002). In contrast to the Cercopithecine primates that disperse most seeds after spitting them out from cheek pouches, Neotropical primates disperse seeds mainly through endozoochory (Chapman 1995), a process in which seeds are swallowed and later discarded unharmed in defaecations. Up to 49% of woody fruit plants at two Amazonian sites in Brazil and Guiana were exploited and dispersed by primates through gut passage (Peres and van Roosmalen 2002). In addition, large-seeded plants relied heavily on large-bodied primates for dispersal because seeds were too large to be swallowed by medium and small-bodied primates (Peres and van Roosmalen 2002).

Because of their arboreal habits, Neotropical primates are seriously threatened by recent changes in land use that have resulted in over-hunting and habitat fragmentation (Peres 1990, Redford 1992, Peres 2000, Chiarello 2003). Their loss as effective

Primate persistence in fragments varies greatly among species and appears to be related to local conditions and species-specific traits (Marsh 2003). At the BDFFP reserves, black spider monkeys (Ateles paniscus), specialised frugivores and seed dispersers, disappeared in forest fragments of 10 ha after isolation in the 1980s (Rylands and Keuroghlian 1988). Because fruit distribution tends to be patchy in time and space (Van Schaik et al. 1993, Janson and Chapman 1999), this primate species (Ateles paniscus) requires larger areas in order to find enough fruit for its survival, a requirement not fulfilled in such small forest remnants. In contrast, red howler monkeys were the only large-bodied primate species remaining and establishing permanent resident groups in 10 ha forest patches (Gilbert and Setz 2001, Gilbert 2003). They are tolerant of habitat fragmentation, because of their ability to consume leaves, to have a flexible home range size, and to live in small groups (Rylands and Keuroghlian 1988).

Howlers may contribute to maintaining the regeneration ability of small forest remnants through several attributes. Although howlers are the most folivorous primates in the Neotropics, they consume large amounts of fruit when available in the forest (Milton 1980, Julliot and Sabatier 1993). Howlers are recognised as primary seed dispersers that swallow most of their seeds without damaging them (Julliot 1996a, Andresen 2002a). Moreover, howlers are the only large-bodied frugivore capable of surviving in fragments of less than 10 ha, and are the only fruit-eater remaining and able to disperse large seeds (> 25 mm long) in such small patches (Andresen 2002a, Marsh and Loiselle 2003). In addition, red howler monkeys were described recently as prevalent and efficient seed dispersers in an undisturbed forest in Central Amazonia (Andresen 2001, 2002a). On the one hand, howlers swallowed and dispersed a high number of 137 different seed species.
On the other hand, seeds in large faecal clumps, such as those produced by howlers, had a higher probability to be buried by dung beetles than seeds in small clumps, and thereby compensating the negative effects of high seed density. In this way, seeds buried had a higher chance of escaping predation by rodents on the ground surface (which are also attracted to howler depositions), and eventually recruiting as seedlings and saplings (Andresen 2001, 2002a).

In small fragments, howlers are known to modify their behaviour in order to cope with forest changes and new ecological conditions (Juan et al. 2000, Clarke et al. 2002, Silver and Marsh 2003, this study: Chapters 4 and 5). Because the behaviour of fruit-eating animals and their dispersal efficiency are strongly interrelated (Schupp 1993), the role of howlers as seed dispersers may be altered in forest fragments. Few attempts have been made, however, to assess possible changes in their dispersal role in forest fragments (Estrada et al. 1999b, Serio-Silva and Rico-Gray 2002, Marsh and Loiselle 2003).

In this, and the following chapters, I evaluate how reduction in howlers’ home range alters some aspects of their seed dispersal role. Here, I specifically compare the two focal groups in their frugivorous behaviour, fruit consumption and some components of seed dispersal. In particular, I provide information on howlers’ handling behaviour, seed processing, defaecation rhythm, seed retention times, dispersal distances, and effect of endozoochory on seed germination success. In the next chapter, I compare, through faecal analyses, seed dispersal patterns produced by howlers across the small fragment (2.5 ha), the medium fragment (12 ha) and the continuous forest reserve (Km41).

The following questions are addressed in this chapter:

1. Do focal groups differ in their fruit-eating behaviour and fruit processing?
2. Does defaecation rhythm (time and number of depositions) vary between focal groups?
3. Are retention times of ingested seeds different between groups?
4. Are both focal groups dispersing seeds away from the parental plants at each fragment?
5. What is the effect of endozoochory on seed germination success?
In this chapter, expected results are discussed according to results obtained in previous chapters, because, as mentioned above, changes in howlers’ behaviour may affect their role as seed dispersers. For instance, a more folivorous diet was predicted for Group 1 living in a small fragment than Group 2 living in the medium one, but in Chapter 5, both groups showed similar percentages of fruit intake, despite a lower fruit supply recorded at the small fragment. Here, more detailed information on fruit-eating behaviour is assessed in order to determine if more subtle changes in their fruit-eating behaviour are occurring. For example, included are data on number of trees used and visits recorded daily.

It is expected that Group 1 would exploit fewer species and individual trees fruiting, given that there should be less fruit trees available in its home range, an area less than half the size used by Group 2 (7.2 ha). Howlers swallow the seeds of most fruit eaten (Julliot 1996a) and, therefore, it is predicted that both groups would swallow and disperse the seeds of the majority of fruit ingested.

According to the results obtained in previous chapters, defaecation rhythms should show differences between groups, because Group 1 spent significantly more time resting and less time feeding than Group 2 (Chapter 4). In particular, fewer faeces should be produced by Group 1 daily, given that they were devoting less time to feeding and consequently should have less food material to process. Large variations have been observed in the time that howlers defaecate (Julliot 1992), so it is difficult to predict if the daytime at which howlers defaecate would differ between groups. Morning and afternoon peaks are expected, however, given that howlers defaecate before starting their early activities and after long resting periods in the afternoon (Milton 1980, Julliot 1992, Andresen 2002a).

Compared to other Neotropical primates, howlers show long seed retention times of about 21 hours (Julliot 1996a, Yumoto et al. 1999), which are related directly to their digestive system adapted for leaf fermentation (Milton 1980). Because both groups showed similar fruit and leaf intake during this study, no changes are expected in gut passage times between them.

Seed-dispersal distances are a result of seed-transit times and animal-movement patterns (Garber 1986, Zang and Wang 1995b), but movement patterns are difficult to
predict, because monkeys have circuitous routes (Stevenson 2000). Even if passage rates are long, as is the case in howlers, seeds may be dropped under the parental tree crown, if the group returns to feed on the same tree in the following days. Group 1, however, forages and moves in an area (2.5 ha) less than half the size used by Group 2 (7.2 ha), and consequently Group 2 should be delivering seeds at greater distances than Group 1. Moreover, it is expected that Group 2 would be more effective at dispersing seeds away from their parental tree than Group 1. Circuitous movements would be more frequent in Group 1 because of the smaller home range, which would result in higher chances for seeds to land close to their parental tree.

Seed passage through howlers digestive tract may enhance, decrease or not affect germination rates and latency periods, and thus appear to be specific to fruit species physiology (Julliot 1996a, Stevenson et al. 2002). Germination trials could not be compared across groups, because the howlers did not disperse seeds of the same species sufficiently to set-up the experiments. Instead, comparisons were performed between seeds defaecated and seeds recovered from fruits found in the forest ground. In this experiment, germination rates and latency periods are expected to vary among seed species.

6.2 METHODS

6.2.1 Fruit diet, seed handling and seed fate

Fruit diet. From January 2002 to January 2003, and during monthly follows of four-days, the fruit diet of each howler group was assessed through direct observations of all occurrences of fruit-eating events. This method was applied to analyse the fruit-eating behaviour, instead of the instantaneous scan sampling (ISS) used to assess diet profiles and activity budgets in Chapters 4 and 5. The former method allows an adequate assessment of the impact of howlers’ fruit-eating behaviour on seed dispersal, by recording all fruiting trees visited daily and the exact time of consumption. In contrast, the latter, ISS, fails to record fruit trees exploited for short periods of time, especially in regions with high plant diversity such as the study area (Chapter 2).

A fruit-eating event was defined as the time elapsed between the first individual beginning to eat at a particular tree, until the last monkey of the group left that food
source. Because howlers perform most activities together (Milton 1980, Julliot and Sabatier 1993), the time of entry and exit to a tree varied only up to 3 minutes between individuals of the group, reducing a possible overestimation of the time spent eating fruit. Fruit were not divided into unripe and ripe due to the difficulty in determining the ripeness, since fruit development is a gradual process (Waterman 1984, N. Dominy pers. comm.). Feeding trees were identified later through the Phyto-demographic Project database of the BDFFP and through botanical samples (see Chapter 5 for details).

For each group, the number of fruit species exploited, the number of trees visited, the daily time spent eating fruit, the daily visit rate and the mean time length/each visit were obtained. For the last three variables, differences between groups were evaluated by Mann-Whitney U-tests (p< 0.05) (Fowler et al. 1998). Finally, the time spent feeding on each fruit species was also obtained for the entire sampling period. Species exploited more than 1% of the total time were included in the analysis.

**Seed handling and seed fate.** Seed handling for each species consumed was noted and classified as swallowed (pulp and seed ingested), chewed (seeds eaten), and dropped or spat (seeds drop/spat beneath the parental tree). Seed size (length, width, depth) was measured for 50 species (N= 1364 seeds) that were recovered in howler faeces at the two fragments and at the control site, Km41 (see Chapter 7 for details). Seed fate was determined by combining handling behaviour data with faeces collection (section 6.2.3).

**6.2.2 Defaecation rhythm**

During the daily follows of each group, the hour and number of individuals defaecating were noted. Howlers are known to defaecate more or less simultaneously from lower branches and in areas free of underlying vegetation (Julliot 1992, Gilbert 1997, Andresen 2002a), but one or two individuals would occasionally defaecate on their own at a different time of the day. Thus, I divided and compared “group defaecations” (hereafter GD; figure 6.1) and “individual defaecations” (hereafter ID), throughout the study period. Group defaecations were defined as those in which at least 3 members of the group (without including infants) were defaecating more or less at the same time, while single
ones corresponded to one or two individuals defaecating separately in time from group defaecations.

The defaecation rhythm of howlers was analysed first in terms of the daily hour that group defaecations occurred. The day was divided in one hour-intervals from 0600 to 1700 hours, totalling 12 intervals. Faecal events earlier than 0600 and later than 1800 hours were added to the nearest interval. Deposition times were expressed as the percentage of faecal events occurring at each hour-interval. Second, the frequency of daily defaecations was compared between the two howler groups through the mean number of faeces produced daily, both by GD and ID. Data were normally distributed and thus statistical differences were analysed by student $t$-tests ($p<0.05$) (Fowler et al. 1998).

6.2.3 Seed retention time and dispersal distance

Faecal samples were collected during daily group observations and later analysed for the identification of seeds, which had passed undamaged through the digestive tract of the howlers (Figure 6.2). Seeds $>3$ mm were retrieved with brass sieves of 1 mm mesh and later morphotyped, counted and measured. The number of small seeds ($<3$ mm) such as *Ficus* sp., were estimated by weighed sub-samples from collected faeces. Here, a faecal sample represents all dung produced after a single defaecation event of the whole group (GD) or one-two individuals (ID). For each group, seed-retention times and dispersal distances were obtained by combining records from direct fruit-feeding observations with subsequent collection of faecal samples.

Seed-retention times were estimated as the time elapsed between the beginning of ingestion of fruit and the first time of appearance of seeds in faeces. This rate was only estimated for those species in which no consumption of the same species occurs within two days. This is because previous studies on howler monkeys report a mean time of first seed appearance of about 21 hours that ranges from 15 to 22 hours (Estrada and Coates-Estrada 1984, Milton 1984, Julliot 1996a, Yumoto et al. 1999). Thus, gut passage times estimated here came mainly from fruit species infrequently consumed. Median retention times of first appearance of seeds were compared between groups by a Mann-Whitney $U$-tests ($p<0.05$) (Fowler et al. 1998).
Figure 6.1: Three members of the group defaecating synchronously.

Figure 6.2: Seeds embedded in howlers faeces.
Seed-dispersal distances were determined by measuring the direct distances between trees exploited and defaecation sites. A distance was estimated for those fruit species in which only one fruit tree was visited by howlers throughout the monthly follows. As explained in Chapter 4, both fragments are completely divided into a grid system of 20 m x 20 m. Thus, the exact location of all fruiting trees and defaecations sites were determined in each fragment by measuring their coordinates (x, y) in relation to the grid system. Later, this information was mapped using Arc View version 3.2. Through this computer program, I measured distances between fruiting tree and different defaecation sites where seeds belonging to that tree were delivered. Then, a range of dispersal distances was estimated for a particular tree. In addition, buffers zones of 10 m and 3 m radius were created for feeding trees and depositions sites, respectively. Buffer values were defined according to data available from the literature (Andresen 2002a, Read et al. 2003). At a forest site located 140 km from the city of Manaus, the average crown diameter was estimated in 9.5 m mean, which corresponds to 4.5 m radius (Read et al. 2003). Based on this result, I used a 10 m radius as the buffer tree value, because seed predation is higher not only beneath a tree crown, but also close to it for some species (Howe 1984). At Km41 reserve, Andresen (2002a) estimated that the median forest area of a howler faecal sample (produced by synchronous group droppings) was 17 m$^2$. This value corresponds to 1.8 m of radius, if the deposition area is assumed to be a circle. I conservatively defined a 3 m radius as the buffer value for depositions sites (Figure 6.3).

Differences in the median distance of dispersal were compared between groups, using a Mann-Whitney $U$-test (p< 0.05) (Fowler et al. 1998). For each group, the effectiveness of dispersal was assessed and compared by estimating the percentage of faecal samples whose seeds were deposited away from the buffer zone of the corresponding seed source.

### 6.2.4 Germination tests

Germination trials were conducted only for those species with a minimum of 90 seeds dispersed by howlers. Only eight species fulfilled this requirement of which one was a liana (Table 6.1). Five species were retrieved from faeces produced by Group 2 living in the medium fragment, whereas three species were retrieved from depositions of Group 3
Figure 6.3: Example of a direct dispersal distance measured with the Arc view programme.
Two seed treatments were compared: (a) dispersed seeds by howlers and recovered in faeces, and (b) non-dispersed seeds, referred to as control seeds that were collected under the crowns of trees visited by Group 2 and from fruiting trees found opportunistically in KmA. Fruit pulp was manually removed from control seeds and both control and dispersed seeds were washed. It has been stated that fruit under the canopy represent those fruits rejected by frugivores and that, in order to represent a true control, seeds should be collected directly from the trees. Here, seeds were not recovered from trees, because of the difficulty to collect them, especially from high trees, and because fruit on the ground do not necessarily represent fruit discarded by frugivores. Nonetheless, seeds recovered under the canopy were always carefully inspected for insect predation, so as to avoid unviable seeds.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Life habit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annonaceae</td>
<td>Bocageopsis multiflora</td>
<td>Tree</td>
<td>Group 2</td>
</tr>
<tr>
<td>Cecropiaceae</td>
<td>Pourouma villosa</td>
<td>Tree</td>
<td>Group 2</td>
</tr>
<tr>
<td>Hippocrateaceae</td>
<td>Cheiloclinium hippocrateoides</td>
<td>Liana</td>
<td>Group 3</td>
</tr>
<tr>
<td>Malpighiaceae</td>
<td>Byrsonima stipulacea</td>
<td>Tree</td>
<td>Group 2</td>
</tr>
<tr>
<td>Moraceae</td>
<td>Clarisia racemosa</td>
<td>Tree</td>
<td>Group 3</td>
</tr>
<tr>
<td>Moraceae</td>
<td>Heliocystis tomentosa</td>
<td>Tree</td>
<td>Group 2</td>
</tr>
<tr>
<td>Myristicaceae</td>
<td>Osteophloeum platyspermum</td>
<td>Tree</td>
<td>Group 2</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td>Pouteria engleri</td>
<td>Tree</td>
<td>Group 3</td>
</tr>
</tbody>
</table>

For each species, treatments were set-up only when 90 seeds recovered from faeces were completed, and this could take up to four days. Seeds were placed for germination in a wooden greenhouse of 2 m x 6 m, raised 60 cm above the ground and covered with a white nylon netting to avoid the action of predators and herbivores. The greenhouse was located in a shaded old gap at KmA field station (Figure 6.4). Each 90-seed treatment comprised three replications of 30 seeds each. Seeds were planted individually in perforated plastic cups, filled with washed sand and covered with vermiculite. This is a neutral inorganic compound with a high capacity of water absorption and retention, and
Figure 6.4: Germination greenhouse where trials were set up and a seed germinating in a plastic cups covered with vermiculite.
prevents contamination by microorganisms. Seeds were watered as necessary to maintain a humid soil. Each seed planted was monitored weekly, and it was considered to have germinated when the seed radicle emerged.

Germination rates and latency periods were estimated for each treatment of each species. Germination rates were estimated as the percentage of the number of seeds germinated divided by the total number of seeds planted. For each species treatment, a mean was obtained from the three replications. Subsequently, differences in germination rates between treatments of each species were detected by Mann-Whitney U-tests (p<0.05) (Fowler et al. 1998).

A latency period refers to the number of days that a seed requires to germinate from planting. These data result in a distribution in which the number of germinated seeds varied across time (in days). For each species treatment, mean number of seeds germinated was estimated from the three replications, at each time interval. Differences on the distribution of latency periods were evaluated by Kolmogorov-Smirnov tests (p<0.05) (Zar 1999, Fowler et al. 1998).

6.3 RESULTS

6.3.1 Fruit diet, seed handling and seed fate

Fruit diet. Throughout the study period (13 months), 128 fruit feeding events (in 47 observation days) and 201 fruit feeding events (in 52 observation days) were obtained for Group 1 and Group 2, respectively. Overall, Group 2 exploited more species (43 vs. 36) and visited more trees (72 vs. 45) than Group 1, whereas both groups spent similar times eating fruit each day (U= 1.37, p= 0.17), exploited similar number of trees daily (U= 1.34, p= 0.18) and visited each tree for similar durations (U= 0.04, p= 0.97) (Table 6.2).

Seventeen fruit species in Group 1, and 14 in Group 2, were consumed for more than 1% of the total feeding time (Figure 6.5). Moreover, Group 2 showed a more even distribution in the time spent consuming the 14 fruit species, whereas Group 1 exploited heavily two fruit species that accounted for 51.4% of the total feeding time. These species were Clarisia racemosa (Moraceae) and Byrsonima stipulacea (Malpighiaceae).
Table 6.2: Comparisons of fruit diet between Groups 1 and 2, including the number of species and trees exploited, mean of daily feeding time, mean visit rate per day and visit length. N= sampling size and a= number of fruit feeding events.

<table>
<thead>
<tr>
<th></th>
<th>Group 1</th>
<th>Group 2</th>
<th>(N_{G1}) (days)</th>
<th>(N_{G2}) (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fruit species consumed</td>
<td>36</td>
<td>43</td>
<td>47</td>
<td>52</td>
</tr>
<tr>
<td>No. fruiting trees visited</td>
<td>45</td>
<td>72</td>
<td>47</td>
<td>52</td>
</tr>
<tr>
<td>Mean visit rate per day</td>
<td>2.8 (±0.6)</td>
<td>3.7 (±0.8)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean of daily feeding time (min.)</td>
<td>35.6 (± 8.1)</td>
<td>46.4 (± 9.2)</td>
<td>47</td>
<td>52</td>
</tr>
<tr>
<td>Mean visit length (min.)</td>
<td>11.8 (± 1.7)</td>
<td>12.8 (± 1.6)</td>
<td>(128^a)</td>
<td>(201^a)</td>
</tr>
</tbody>
</table>

Figure 6.5: Percentage of the feeding time spent on each fruit species consumed in more than 1% of the feeding time for (a) Group 1 and (b) Group 2, throughout the study period.
Seed handling and seed fate. For the whole study, both groups were observed exploiting 66 fruit species, and most of seeds of these species were swallowed: 33 out of 36 by Group 1 (91.7%) and 38 out of 43 by Group 2 (86%). Excluding seeds < 3 mm, swallowed seed sizes ranged between 5.8 x 5.0 x 3.9 mm (length, width, depth) and 33.2 x 16.8 x 15.2 mm (mean: length= 15.7 mm ± 0.8CI, width= 9.9 mm ± 0.2CI, depth= 8.1 mm ± 0.2CI, N_{species}= 50).

Four different categories that resulted from combining handling behaviour with seed fate are collated in Table 6.3: (1) swallowed - successfully dispersed, (2) swallowed – predated, (3) chewed – predated, (4) spit or dropped – not dispersed. Swallowed seeds were mainly retrieved undamaged from faeces, but some were not recovered and thus these seed species were considered predated. Seeds chewed or masticated resulted in predation, whereas seeds spit or dropped under the parental tree were considered as not dispersed.

Table 6.3: Comparisons on the handling behaviour and seed fate between Group 1 (G1) and Group 2 (G2) in terms of the number and percentage of species exploited, and percentage of feeding time.

| Handling      | Seed fate          | No. of species |  | % of species |  | % of feeding time |  |
|---------------|--------------------|----------------|--------------------------|--------------------------|--------------------------|--------------------------|
|               |                    | G1      G2    | G1           G2    | G1           G2    | G1           G2    |
| Swallowed     | Successfully dispersed | 26 33  | 72.2 76.7 | 87.2 80.6 |
| Swallowed     | Predated           | 7 4     | 19.4 19.3 | 10.8 8.5 |
| Chewed        | Predated           | 0 1     | 0 2.3    | 0 0.2 |
| Dropped       | Not dispersed      | 3 2     | 8.3 4.7  | 2.0 9.8 |
| Unknown       | Unknown            | 0 3     | 0 7.0    | 0 0.9 |

Overall, Group 2 dispersed successfully more species (33) than Group 1 (26), but these differences disappeared when the percentage of dispersed species were estimated for each Group (Group 1= 72.2%, Group 2= 76.7%). Moreover, both groups invested similar percentages of time exploiting fruit species successfully dispersed (Group 1= 87.2%, Group 2= 80.6%). Group 2 invested more time feeding on fruit species that were dropped in comparison to Group 1 (Group 2= 9.8%, Group 1= 2.0%). This result is mainly attributed to the fact that fruits of Protium altsonii (Bursaraceae) were consumed heavily by Group 2 in May (9.6% of annual fruit feeding time), and their seeds were dropped/spat after discarding the seeds from the pulp, which was easily separated. Only Group 2 was
observed eating one species, *Stryphnodendrom pulcherrimum* (Leguminosae), and handling and fate of three species could not be identified for the same group. Finally, the analysis of faecal samples added new fruit species that were swallowed and dispersed by each group, but were not detected during direct observations of the howlers: eight for Group 1 and four for Group 2.

### 6.3.2 Defaecation rhythm

In total, 95 defaecation events (in 47 days) for Group 1 and 154 (in 52 days) for Group 2 were recorded throughout the study. Overall, 78% and 77% of all faecal events for Groups 1 and 2 respectively were recorded as Group defaecations (GD), while the remaining depositions were classified as individual defaecations (ID).

The frequency of faeces produced daily during GD, however, differed significantly between groups. Group 2 defaecated significantly more times each day (2.3 ± 0.2 CI) than Group 1 (1.8 ± 0.2 CI) \((T= 3.66, p= 0.001)\). No differences were found for ID (Group 1 = 1.3 ± 0.2 CI; Group 2 = 1.4 ± 0.3 CI; \(T= 0.47, p= 0.64\)).

Defaecations of both groups occurred in each time interval, but showed a bimodal pattern. A marked peak was found for both groups in early morning and a slight one in early afternoon (Figure 6.6). Group 1 showed a peak between 0600-0800 hours (16.2% for each interval) and 1200-1400 hours (10.8 and 12.2% for each interval), and Group 2 between 0600-0700 hours (23.5%) and 1300-1500 hours (9.2% and 8.4%, respectively) (Figure 6.6).

### 6.3.3 Seed retention time and dispersal distance

In total, 93 faecal samples for Group 1 and 146 for Group 2 were collected throughout the study. Gut passage times were calculated in only 18 cases out of 329 visits recorded, because some tree species were frequently revisited within each monthly sample. Seed retention times were estimated for 8 fruit species consumption events of Group 1 and 10 of Group 2 (Table 6.4). Median retention times of first appearance of seeds in faeces were similar between groups (Group 1= 20.2 hours; Group 2=19.5; \(U= 0.14, p= 0.16\)), and varied from 15.3 to 25.3 hours. For six species, maximum retention time could be estimated. For instance, seeds of *Batocarpus amazonicus* (Moraceae) were retrieved first
at 16.8 hours, but appeared in the following five faeces collected with a maximum retention time of 64 hours (Table 6.4).

**Figure 6.6**: Comparison on the percentage of group faecal events obtained for each time interval of the day between Group 1 and Group 2, throughout the study period.

**Table 6.4**: Retention times for first appearance of seeds for Groups 1 and 2, including some values for maximum retention times, with number of seeds counted in minimum retention times.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Retention times (hour.min)</th>
<th>Minimum</th>
<th>Maximum</th>
<th>No. seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Duguetia chrysea</td>
<td></td>
<td>22,7</td>
<td>-</td>
<td>15</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>Protium apiculatum</td>
<td></td>
<td>23,7</td>
<td>-</td>
<td>12</td>
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<tr>
<td>Cecropiaceae</td>
<td>Pourouma sp.</td>
<td></td>
<td>23,2</td>
<td>-</td>
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<td>Leguminosae</td>
<td>Eperua glabriflora</td>
<td></td>
<td>22,2</td>
<td>-</td>
<td>2</td>
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<tr>
<td>Leguminosae</td>
<td>Inga sp.</td>
<td></td>
<td>21,8</td>
<td>-</td>
<td>6</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td>Manilkara bidentata</td>
<td></td>
<td>16,3</td>
<td>-</td>
<td>17</td>
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<tr>
<td>Sapotaceae</td>
<td>Sarcaulus brasiliesis</td>
<td></td>
<td>21,5</td>
<td>-</td>
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<tr>
<td>Sapotaceae</td>
<td>Pouteria jariensis</td>
<td></td>
<td>19,5</td>
<td>24,5</td>
<td>5</td>
</tr>
<tr>
<td><strong>Group 2</strong></td>
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<td></td>
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<tr>
<td>Bignonieae</td>
<td>Anemopaegma sp.</td>
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<td>Burseraceae</td>
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<td>Cecropiaceae</td>
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<td>42,7</td>
<td>21</td>
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<td>Hippocrateaceae</td>
<td>Cheiloclinium hippocrateoides</td>
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<tr>
<td>Moraceae</td>
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<td>16,8</td>
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<tr>
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<td>22,8</td>
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<td>1</td>
</tr>
<tr>
<td>Sapotaceae</td>
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<td></td>
<td>18,7</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td>Elaeoluma nuda</td>
<td></td>
<td>25,3</td>
<td>-</td>
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</tr>
<tr>
<td>Sapotaceae</td>
<td>Chrysophyllum wilsonii</td>
<td></td>
<td>19,7</td>
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<tr>
<td>Violaceae</td>
<td>Rinorea sp.</td>
<td></td>
<td>18,3</td>
<td>22,3</td>
<td>50</td>
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</table>
Direct dispersal distances were estimated for those species for which only one tree was visited during the monthly-follows. In total, 67 cases belonging to 20 species for Group 1 and 138 cases of 25 species for Group 2 were obtained. Dispersal distance showed a high variation within and between seed species, and ranged from 0 to 148 m for Group 1 and from 3 to 322 m for Group 2 (Table 6.5). Consequently, on average seeds were dispersed significantly further by Group 2 (median= 114 m) than Group 1 (median= 63 m; $U= 3.84$, $p= 0.001$, $N= 205$), suggesting that home range reduction of howlers decreases the distance at which seeds are delivered. Despite these differences, however, almost all seeds were moved away from the corresponding parental tree crown (Group 1= 93%, Group 2 = 91%; Figure 6.7).

![Figure 6.7](image)

**Figure 6.7:** Comparison of the distribution frequency of defaecation sites and the direct dispersal distance from parental trees, between Group 1 and Group 2.
Table 6.5: Minimum and maximum dispersal distance estimated from fruit species of trees/lianas and recovered seeds in faeces. a= number of dispersal distances events recorded.

<table>
<thead>
<tr>
<th>Groups</th>
<th>Family</th>
<th>Species</th>
<th>Minimum</th>
<th>Maximum</th>
<th>N&lt;sup&gt;a&lt;/sup&gt;</th>
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<td></td>
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<td><strong>Dispersal distance (m)</strong></td>
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<td></td>
<td></td>
<td><em>Guatteria olivacea</em></td>
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<td>Apocynaceae</td>
<td><em>Geissospermum urceolatum</em></td>
<td>106</td>
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<td></td>
<td>Burseraceae</td>
<td><em>Protium apiculatum</em></td>
<td>21</td>
<td>134</td>
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<tr>
<td></td>
<td></td>
<td><em>Protium guianense</em></td>
<td>34</td>
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<td></td>
<td><em>Protium tenuifolium</em></td>
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<td></td>
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<td>Euphorbiaceae</td>
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<td></td>
<td></td>
<td><em>Pouteria engleri</em></td>
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<td></td>
<td></td>
<td><em>Pouteria reticulata</em></td>
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<td></td>
<td>TOTAL</td>
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<td>167</td>
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<td></td>
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<td></td>
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<td></td>
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<td><em>Micropholis guayanensis</em></td>
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<tr>
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<td></td>
<td><em>Pouteria engleri</em></td>
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<tr>
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<td></td>
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<tr>
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<td>TOTAL</td>
<td></td>
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<td></td>
<td><strong>138</strong></td>
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</table>
6.3.4 Germination tests

Three out of eight species planted for germination trials could not be analysed statistically, because only a few seeds germinated (< 5%). These species were *Helicostylis tomentosa*, *Bocageopsis multiflora* and *Byrsonima stipulacea*. The first species exhibits long periods of dormancy (Z.E. Camargo, pers. comm.), while the other two species have a hard coat that was probably not weakened sufficiently by passage through the howlers’ gut.

Overall, seeds recovered from faeces had a higher germination rate than control seeds (Figure 6.8). All but one showed significant differences: *Pourouma villosa* ($U = 1.99$, $p = 0.04$), *Clarisia racemosa* ($U = 2.03$, $p = 0.04$), *Cheiloclinium hippocrateoides* ($U = 1.99$, $p = 0.04$) and *Osteoploeum platyspermum* ($U = 1.99$, $p = 0.04$). Germination rates were not statistically different for *Pouteria engleri* ($U = 0.88$, $p = 0.38$).

By contrast, germination delays were similar between treatments for the five species analysed (Figure 6.9): *Pourouma villosa* ($Z = 0.25$, $p = 1.00$), *Clarisia racemosa* ($Z = 0.24$, $p = 1.00$), *Cheiloclinium hippocrateoides* ($Z = 0.35$, $p = 1.00$), *Osteoploeum platyspermum* ($Z = 1.54$, $p = 1.00$) and *Pouteria engleri* ($Z = 0.75$, $p = 0.63$). A high variation was detected among species, and the time for first seed to germinate ranged between seven days in *Clarisia racemosa* and 151 days for *Helicostylis tomentosa*.

![Figure 6.8](image-url)  
*Figure 6.8*: Comparison of germination rates between faeces and control treatments, for five fruit species dispersed by red howler monkeys.
Figure 6.9: Comparison of germination delays between faeces and control treatments for five fruit species dispersed by howler monkeys. a= axis has a longer time interval than the other four figures.
6.4 DISCUSSION

6.4.1 Fruit diet, seed handling and seed fate

Fruit diet. A marked difference between Groups 1 and 2 was expected in relation to the number of fruit species exploited and the time spent eating fruit, but Group 2 ate only seven fruit species more than Group 1. Furthermore, differences in the time spent eating fruit daily were not significant between groups, even though Group 2 devoted more time to fruit ingestion. These results are in accordance to those recorded and reported in Chapter 5 through a different method, the instantaneous scan sampling (ISS; Martin and Bateson 1993). Thus, it is clear that fruit consumption and fruit species exploited by both howler groups were not altered by the reduction of their home ranges. These are unexpected results given that, first, a lower fruit supply was found in the small fragment when compared to Km41, the control site and, second, Group 1 has a home range less than one third of Group 2.

Plant diversity is extremely high in the Manaus region (Oliveira and Daly 1999, Oliveira and Mori 1999), and this may clarify partially why the number of fruit species exploited by the two study groups was similar, despite the reduction in home range size caused by habitat fragmentation. Nevertheless, differences in the number of fruit species used are conspicuous when comparisons are performed between both focal groups and a howler group living in 45 ha of an undisturbed French Guiana forest with high plant diversity (Julliot and Sabatier 1993). During 19 months sampling, this group consumed 97 fruit species, while Groups 1 and 2 fed on 36 and 43 fruit species, respectively. Furthermore, Andresen (2002a) reported 137 fruit species recovered from faeces of howlers in Km41 during a 25-month study period. This number reflects the diet of five groups and may be an overestimated for comparisons with the two focal groups of this study. In fact, large differences in diet are found between howlers groups within the same habitat (Julliot and Sabatier 1993), but fruit species consumed by Groups 1 and 2 tend to decrease when forest is fragmented and their home range size is reduced.

The intensity of fruit species used by each group also gives a clue to understanding the similar result obtained for fruit consumption. Howlers live in cohesive groups and exploit fruiting trees with larger crops than can feed the whole troop (Andresen 1999, Wehncke et al. 2004). Of the species used in more than 1% of the feeding time, Group 2 exploited
fruit species in an even fashion, but Group 1 displayed a clumped consumption, whereby two species represented 51.4% of the total feeding time (Figure 6.5). Although fruit production was not estimated here, these differences in fruit species intake suggest that fruit crops were larger in the medium fragment than in the small one.

A closer analysis of the frugivorous behaviour of both groups revealed differences in the number of trees visited. As predicted, Group 2 used 27 more fruit trees/lianas than Group 1, a result that may be related to home range size. In absolute values, more adult trees are found within the home range of Group 2 (7.2 ha) than Group 1 (2.5 ha), simply because the former area is larger. I calculated the differences between tree numbers in each group’s home range, using a mean of 23 trees per 20 m x 20 m plot, which was obtained from the number of trees sampled in the phenological plots in each fragment (Chapter 3). The home range of Group 2 includes 3,937 trees, nearly three times more trees than in Group 1’s home range, with 1,350 trees. According to this, plus the fact that howlers patrol their home range to monitor fruit availability (Milton 1980), it can be assumed that Group 1 visited less fruiting trees than Group 2, simply because there were less trees bearing fruit.

I discussed previously (Chapters 4 and 5) that Group 1 was facing a fruit shortage and that the group adjusted to this lack of sources in ready energy by resting more and feeding less, by eating flowers and by crossing the 50 m gap to obtain fruit from the continuous forest. Here, another behavioural adjustment seems to occur in Group 1 due to the low fruit supply, and this is related to fruit edibility. Fruit development involves several stages through which, for instance, colour, size, astringency, levels of tannins and sugar concentration are modified gradually (Waterman 1984, Maisels et al. 1994, Waterman and Kool 1994). Edibility refers to certain fruit traits that make the fruit desirable by consumers (e.g. higher sugar concentration and less tannins), whereas the traditional division of ripe and unripe fruit is a more abstract categorisation that corresponds mainly to fruit colour, but it is not necessarily associated to other important fruit characteristics (N. Dominy pers. comm.). The ability to exploit edible fruit seems to vary through primate species, and what is edible for one species may not be for another. For instance, spider monkeys are able to exploit a smaller range of edible fruit when compared to howler monkeys (N. Dominy, unpubl. data). During direct feeding
observations, it is difficult to recognize if a fruit consumed is within the edible range. In this study, individuals of Group 1 were observed with their mouths covered by white latex, after ingesting fruit of a Sapotaceae tree in February 2002 (18% of monthly feeding time). Levels of latex are known to decrease as fruit develops (Subramaniam 1981). According to this, I suggest that Group 1 seems to extend its range of fruit exploitation towards less edible fruit because more edible fruit are unavailable or in lower supply within its home range. In contrast, Group 2 was never observed with their mouths covered by latex, since fruiting trees contained enough edible fruit to feed the whole group. Further research in this direction is required to confirm this observation. For this, nutrient analyses of fruit exploited by howlers need to be performed, so as to determine the range of edibility of fruit for howlers in forest fragments.

Thus, Group 1 seems to live in an overall period of lean fruit supply, because of the small size of its home range. Large crops of specific trees may help to secure their intake of ready energy for short periods, as was the case of *Clarisia racemosa* and *Byrsonima stipulacea* that accounted for 51.4% of the total fruit feeding time. When large crops are depleted, however, Group 1 exploits less edible fruit and travels to the adjacent continuous forest so as to fulfil the energetic requirements of the whole group.

*Seed handling and seed fate.* Small to large seeds (range: 0.1 mm to 33 mm long) of fruit species exploited by howlers in this study were mainly swallowed (Group 1 = 72.2% and Group 2 = 76.7%), as has been reported in other howler studies (Julliot 1996a, Andresen 2002a, Stevenson et al. 2002, Peres and van Roosmalen 2002). Seed size varies greatly in tropical forest plant (Foster and Janson 1985, Gautier-Hion et al. 1985), and this seed trait is known to determine if a seed is swallowed or not by a particular primate species (Peres and van Roosmalen 2002). Seed swallowing is found in small and large-bodied primates of the Old and New world (Lambert 2002), but large-seeded species (> 25 mm long) are mainly dispersed by large arboreal vertebrates (Peres and van Roosmalen 2002). For instance, large-seeded plants of woody fruit plants at two Amazonian sites in Brazil and Guiana relied heavily for dispersal on large-bodied primates, which included spider, woolly and howler monkeys. Seeds were too large to be swallowed by medium and small-bodied primates (Peres and van Roosmalen 2002). In
In this study, one species, *Duckeodendron cetroides* (Duckeodendraceae) exploited by Group 2 was discarded, probably because the seed was too long (ca. 40 mm) to be swallowed by the howlers.

In contrast, seeds of *Protium altsonii* were always dropped under the tree because the pulp was easily detached from the seed. Furthermore, seeds of Sapotaceae were mainly swallowed and dispersed, but some seeds could also be discarded during a single feeding bout. In this case, seeds that fell into the ground were not quantified, because the high canopy of the study site made it difficult to estimate fruit consumption rates. Many seeds are swallowed because the pulp adheres strongly to the seed with nutrients that are more efficiently removed by the action of digestive enzymes (Lambert 1999). Thus, the results on seed handling in this study indicate that, when possible, howlers avoid carrying the extra weight of the seed. The dropping/spit behaviour has been reported in *Alouatta palliata* (Estrada 1984, Estrada and Coates-Estrada 1984) and *Alouatta pigra* (Ponce et al. 2004), but rarely described and quantified in other studies of howlers. For instance, *Alouatta pigra* dropped seeds of *Brosimum alicastrum*, which was the most important food plant for the howlers in the Tikal National Park in Guatemala (Ponce et al. 2004).

Howlers are known to swallow fruit rapidly without dental processing, and teeth are rarely used to chew seeds. Thus, seed damage is generally accidental (Julliot 1996a, Andresen 2002a, Stevenson et al. 2002). In French Guiana, for instance, a howler group living in an undisturbed forest chewed only one seed species of 97 fruit species (Julliot 1996a). In this study, up to 91% of fruit species exploited by both groups were swallowed and successfully dispersed. Yet, some seed species (Group 1= 7, Group 2= 4) were swallowed, but were not recovered later in the faeces, indicating than both pulp and seeds were used as a food source. It is possible that some of these swallowed/predated seeds were accidentally destroyed, because the seeds were not completely developed. In fact, four out of the seven species swallowed - predated by Group 1 were dispersed by Group 2. Moreover, only one seed species, *Stryphnodendron pulcherrimum* (Leguminosae) was chewed by Group 2.
In the medium fragment, a previous study reported that seeds accounted for 27% of the diet of a howler group during five months of sampling (Neves and Rylands 1991). In this study, Group 2 was never observed eating and chewing seeds directly from the fruit, a behaviour easily detected in several individuals of *Chiropotes satanas* living in the same fragment. Two possible explanations may clarify the marked differences between studies. Firstly, the group observed by Neves and Rylands (1991) was studied after 4-5 years of the first isolation of the fragment, and drastic changes in forest production may have occurred affecting food availability and influencing howler feeding behaviour. Secondly, and a more plausible explanation, unripe fruit was considered as analogous to seeds. Unfortunately, the authors did not provide any explanations in relation to this issue. *Alouatta seniculus* has been observed eating young seeds in a *terra firme* forest during low fruit availability, but seed intake was not quantified (Peres 1997).

### 6.4.2 Defaecation rhythm

My results show that members within each group defaecated more often in synchrony (ca 80%), than they did separately. The contribution of individual defaecations to the overall pattern of seed deposition, however, should not be ignored, because about 20% of all deposition events were individual defaecations.

Andresen (2002a) reported that 75% of howler depositions are produced by the whole group synchronously. She inferred this value from faeces collected and not from direct howler observations. Interestingly, my results obtained through direct howler observations give similar values to the ones reported by Andresen (2002a). Thus, it appears that the defaecation behaviour of the two focal groups was not affected by the reduction of home range size. This behaviour should respond to howlers’ behaviour and physiological traits and, consequently, should not be altered by extrinsic factors such as home range reduction.

Howlers are reported to show a bimodal deposition rhythm in which the group defaecates in the morning before beginning their daily activities and again in the afternoon after long periods of resting (Milton 1980, Gaulin and Gaulin 1982, Julliot 1996a, Andresen 2002a). In this study, both groups showed one marked defaecation peak in the morning and a slight one in the afternoon, even though depositions were recorded
at all time intervals, except after 1700 hours in Group 1. Despite this bimodal defaecation
rhythm, the number of faeces produced through group defaecations differed significantly
between focal groups. Group 1 defaecated on average less than twice a day (mean= 1.8
faeces of group defaecations), but faecal samples produced daily ranged from 1 to 3. By
contrast, Group 2 produced on average more than two faecal samples/day (mean= 2.4
faeces of group defaecations), ranging from 2 to 4 daily samples. Thus, it appears that
home range reduction affected the defaecation rhythm of Group 1. These differences
between groups may be related to changes in activity patterns found in Chapter 4. As a
direct effect of home range size and in order to cope with low food availability, Group 1
rested significantly more and fed less than Group 2. These activity adjustments may
explain the lower number of faeces produced daily by Group 1, because a lower food
intake should result in less food material to process and consequently in less defaecations.

6.4.3 Seed retention time and dispersal distance

Seed retention time. Few studies report seed retention times for free-ranging howlers,
because of the difficulty to measure them in the field. Howlers tend to visit a single or
several trees of the same species repeatedly during its fruiting period, especially preferred
fruit species (M. Santamaría, pers. obs.). Seed passage rates, measured as the first time of
appearance and mean passage time, have been obtained for two free-ranging groups of
Alouatta seniculus (Yumoto et al. 1999, Julliot 1996a), and for captive howlers of
Alouatta palliata (Milton 1984, Estrada and Coates-Estrada 1984). All values reported in
these studies ranged from 15 to 22 hours with a maximum seed passage time of 70 hours.
In this study, seed retention times were similar between the two focal groups and within
the range reported in the four studies mentioned above. Time elapsed between fruit
ingestion and first seed to appear varied between 15.2 hours for Anemopaegna sp.
(Bignoniaceae) and 25.2 hours for Elaeomuda nuda (Sapotaceae) (Table 6.4).

Among large-bodied Neotropical primates, howlers show the slowest rate of seed
passage time (Milton 1984, Estrada and Coates-Estrada 1984). Given that there is a link
between digestive physiology and feeding ecology, howlers’ long retention times have
been associated to their reliance on leaves. In order to process sufficient quantities of
food to fulfil their nutritional requirements, howlers retain food as long as possible in
their digestive tract. In this way, howlers extract and absorb leaf nutrients efficiently whereby bacteria have more time to ferment leaves (Lambert 1998, Milton 1998). Some seeds may be trapped in this fermentation process and consequently are delivered later on. In fact, some seed species may continue to appear in faeces 70 hours after their initial consumption. Further research is necessary in order to assess variation in the distribution of retention times across different plant species and according to howlers’ diet. For instance, first time of appearance of seeds may be longer with a folivorous diet than with a frugi-folivore diet. These studies may need to be conducted with captive animals due to the necessity of separating feeding bouts for each plant species.

The effect of seed size on seed retention times needs also to be explored, because howlers ingest a wide range of seed sizes (range: 1-33 mm in this study). In fact, a modest positive correlation (sensu Fowler et al. 1998) was found between retention time and seed length using a Spearman’s rank correlation ($r^2= 0.4$, $p= 0.39$, $N=12$). Seed length was unavailable for six species and thus only 12 species were considered in this analysis, with seed lengths between 8.6 and 23.1 mm. The significant correlation indicates that smaller seeds tend to appear first in faeces than larger ones, but seed size only explains 40% of the variation in retention times. Moreover, seeds smaller than 3 mm may behave differently (T. Yumoto, pers. comm.). In fact, Levey (1986) found that small seeds passed at a slower rate through the bird gut than larger ones. Instead of a linear relationship, passage rate in howlers and seed length may exhibit a U-shaped relation, but more data are required to explore this issue.

**Dispersal distance.** As expected, Group 2 deposited seeds at significantly longer distances (median= 114 m) from parental trees than Group 1 (median= 63 m). This result is not surprising given that Group 1 lives in a much smaller home range than Group 2, and thus there is a limit to the distance at which seeds can be dropped. Nonetheless, Group 1 played an unexpected dispersal service by moving seeds from the continuous forests to the fragment. The dispersal distances were not measured, because howlers could not be followed during these short travels. It can be inferred, however, that because Group 1 slept in the adjacent continuous forest and they always defaecate in the morning, some seeds coming from the fragment were also deposited in the forest. Similar results
on dispersal distances were found between a disturbed site (40 ha) and a well-preserved site (600 ha) for *Alouatta palliata* in Mexico (Serio-Silva and Rico-Gray 2002). Mean dispersal distances for two fig species were significantly greater at the preserved site (173 m and 248 m for each fig species) where each one of the eight howler troops have a home range of ca 75 ha, than at the disturbed site (73 m and 57 m for each fig species) with each of the four howler troops living in a home range of ca 10 ha.

Thus, differences in dispersal distances seem to vary according to howlers’ home range size, especially for maximum distances that a seed can reach. For instance, a group of red howlers ranging in 25 ha in Colombian Amazon moved seeds at a mean distance of 317 m with a maximum distance of 637 m (Yumoto et al. 1999). In French Guiana, a group of red howlers, with a home range of 45 ha, dispersed seeds from 0 to 550 m with a mean of 255 m (Julliot 1996a). In Mexico, Estrada and Estrada-Coates (1984) reported a low mean of 112 m for five species dispersed by a group of *Alouatta palliata* ranging in 60 ha, but with a maximum distance of 811 m.

According to the escape hypothesis (Janzen 1970, Connell 1971), seeds transported at even short distances may enhance seed and seedling survival and, thus, sapling recruitment (Augspurger 1983, Howe et al. 1985). In this study, despite the small home ranges of the two focal groups, up to 93% of the seeds were moved at least some meters away from the parental crown (Table 6.5). Similar results are reported in Argentina, where seed dispersal of three seed species by *Alouatta caraya*, living in a 10 ha forest fragment, always resulted in seeds being moved away from the seed source (Bravo and Zunino 2000). Dispersal distance is only one of many factors influencing the quality of a disperser and, in this context, the dispersal quality of both howler groups are not affected by the reduction of their home ranges. Under the long-dispersal distance model (Muller-Landau et al. 2003), however, howlers are not able to disperse seeds as far as tapirs do (> 1000 m; Fragoso et al. 2003). This is simply because their home range sizes never exceed about 80 ha, except in Caparu station where red howlers range in unusual large home ranges (182 ha; Palacios and Rodríguez 2001). In this context, howlers’ dispersal distance is low.
Red howler monkeys have been shown to spend longer periods of time in fruiting trees than sympatric species, such as spider and woolly monkeys (Andresen 1999, Yumoto et al. 1999). Consequently, they have been stated to be less efficient dispersers, in terms of moving less seeds away from the parental tree crown (Andresen 1999, Yumoto et al. 1999, Schupp et al. 2002). These findings were conducted mainly during low fruit availability (Andresen 1999) and during short periods of time (two months for Yumoto et al. 1999). Thus, they should be interpreted with caution, as howlers’ behaviour is flexible. Indeed, my results do not support those findings, because up to 93% of seeds were dispersed away from the seed sources and because mean duration of visits to fruiting trees was short (less than 13 minutes, table 6.2). Moreover, the time spent in a tree should not be relevant for howlers, given their bimodal pattern of defaecation and the low chance of seeds been deposited under parental trees. What appears more relevant is whether there are few fruit sources within the howlers’ home range, so that they return regularly day after day.

Some specific traits of howlers behaviour may also elucidate the differences found here in relation to these studies (Andresen 1999, Yumoto et al. 1999). On one hand, Gilbert (1997) found that red howlers at the BDFFP defaecate from sites with specific characteristics and not at random sites in the forest. Before defaecating, howlers move from the resting tree to horizontal branches that correspond to areas free of underlying foliage. Both focal groups living in fragments and howlers at Km41 (Santamaría and Rylands 2003, this study) exhibited this behaviour. This characteristic mode of howlers defaecation plus the bimodal rhythm of deposition may decrease, therefore, the probability of seeds being delivered under the original feeding sources. For individual depositions, however, howlers seem to defaecate in sites that are not free of underlying vegetation (Gilbert 1997), but I never observed a member of the group eating fruit and then defaecating at the same spot. They always left the tree and then discharged. For instance, the same support was used at least seven times within four days by Group 2, and this branch was located on the travel route between two feeding trees.

On the other hand, fruit-eating behaviour has been noted to vary in some frugivorous animals during lean periods (Terborgh 1986, Zhang and Wang 1995b, Santamaría and Franco 2000). Some tree species, producing fruit asynchronously and in large crops, may
act as keystone species (e.g. *Ficus* sp.), because they support a large number of fruit-
eating animals during the periods of low food availability (Leighton and Leighton 1983,
Howe 1984, Terborgh 1986, Peres 1994a). Sometimes, there is only one tree offering a
large crop within the animals’ home range and consequently the tree is visited frequently
(Santamaría and Franco 2000, Santamaría and Rylands 2003). In this situation, some
species (e.g. Salvin’s curassow) remain for large periods of time in the fruiting tree,
eating, resting and sleeping, a behaviour that has been described as “stationary feeding”
(*sensu* Zhang and Wang 1995b). In contrast, other species (e.g. capuchin monkeys)
follow a ”moving-foraging” pattern (*sensu* Zhang and Wang 1995b), in which short visits
are made to the tree (Zhang and Wang 1995b, M. Santamaría pers. obs.). It is only in this
situation that howlers spent longer times in feeding trees that in turn resulted in seeds
being deposited beneath the parental tree or in close proximity. For instance, a howler
group observed in Km41 displayed a stationary behaviour when a fruit tree of *Goupia
glabra* was the only fruit source in the forest (Santamaría and Rylands 2003). Feeding
sessions lasted up to three hours and howlers rested and slept in the three or in close
proximity. Consequently, faeces were dropped between 0 and 30 m from the fruit source
(unpubl. data). In this study, only Group 2 exhibited this behaviour during one sampling-
month when one fig tree produced a large fruit crop during fruit scarcity. Indeed, the
longest visit was recorded at that tree in which Group 2 spent 75 minutes ingesting fruit.
It contrasts with maximum visit length obtained for the fruiting season, where Group 1
ingested fruit of *Clarisia racemosa* and Group 2 fed on *Micropholis guyanensis* for about
50 minutes.

6.4.4 Germination tests

In this study, a distinct pattern of howlers’ gut treatment was not found for the eight
seed species set up for germination trials. Three species germinated at low percentages,
indicating that dormancy was not broken by howlers’ digestive tract. For the other five
species analysed, latency periods were not affected by passing through howlers’ gut.
Germination, in contrast, improved significantly by gut passage in four out of five
species. It is important to note that all eight seed species dispersed were viable and thus
howlers did not harm their germination power.
My results are according to those reported for howlers and other Neotropical primates, for whom the effect of endozoochory on germination success was variable and, consequently, a pattern was not found (Estrada and Coates Estrada 1984, Garber 1986, Zhang and Wang 1995b, Julliot 1996a, Bravo and Zunino 2000, Serio-Silva and Rico-Gray 2002, Stevenson et al. 2002). For instance, red howlers at Tinigua National Park tended to increase the germination rate, but to delay the time of germination (Stevenson et al. 2002). In French Guiana, Julliot (1996a) found that red howlers enhanced, decreased or did not affect germination for seventeen seed species.

Generalisations to gut treatment are difficult to draw because seed germination responses depend on intrinsic traits of seeds and fruit-eating animals (Traveset and Verdú 2002). Seed morphology and physiology is heterogeneous (Waterman 1984), and seed-coat traits, such as the permeability of the coat to water and gases, may or may not be affected by the animals’ digestive tracts (Traveset and Verdú 2002). Moreover, animals fed on different food sources and they exhibit different physiological and morphological traits that, in turn, have a different effect on germination success. Nevertheless, seed ingestion rarely reduces germination success (Stevenson et al. 2002, Traveset and Verdú 2002), and pulp removal alone seems beneficial for seeds (Wenny 2000). In fact, Wenny (2000) demonstrated that seeds in intact fruits of a Neotropical montane tree failed to germinate when compared to seeds cleaned by hand or regurgitated by birds.

6.5 SUMMARY

- Between January 2002 and January 2003, I compared the two focal groups in their fruit-eating behaviour, seed handling and processing, defaecation rhythm, seed retention times and dispersal distances. The effect of howlers’ endozoochory on seed germination success was also assessed but not compared between groups.
- Fruit intake and fruit species exploited were similar between groups, but Group 2 visited more fruiting trees than Group 1 in their larger home range.
- Both groups swallowed the majority of fruit seed species exploited (up to 91%), yet some of these species were digested during gut passage (Group 1= 19.4% and Group 2= 9.3%).
• Members within each group defaecated more often in synchrony (ca 80%) than they did separately, but home range reduction affected the bimodal defaecation rhythm of Group 1 that defaecated significantly less than Group 2. These differences seem related to activity adjustments of Group 1, which rested more and fed less than Group 2.

• Group 2 deposited seeds at significantly longer distances from parental trees than Group 1, due to a smaller home range size of the latter. Nonetheless, and despite the small home ranges of the two focal groups, about 90% of the seeds were moved away from the parental crown (> 10 m). Moreover, Group 1 played an unexpected dispersal service by moving seeds from the continuous forests to the fragment.

• Howlers’ gut treatment had a positive or neutral effect on germination success, suggesting that responses depend on intrinsic traits of seed species.
CHAPTER 7
THE EFFECT OF HOME RANGE REDUCTION ON SEED DISPERsal PATTERNS OF RED HOWLER MONKEYS

7.1 INTRODUCTION

Although seeds can be moved away from parental trees by natural agents, such as water and wind (Van der Pijl 1982), seed dispersal by animals is the predominant form of dissemination in tropical forests (Frankie et al. 1974, Howe 1990, Jordano 1992). In fact, more than 70% of trees exhibit fleshy fruits to attract fruit-eating vertebrates and depend on animals to disperse their seeds (Frankie et al. 1974, Julliot 1992, Peres and van Roosmalen 2002). Because plants are unable to control where their seeds are deposited (Garber and Lambert 1998), primary, but also secondary, animal dispersers influence profoundly the distribution of seeds and seedlings on the forest ground (Howe 1990, Forget 1996, Wenny 2000, Andresen 2002b, Wang and Smith 2002, Wehncke et al. 2003).

High seed densities are frequently associated with fruiting trees and accordingly seed dispersal patterns are often addressed in relation to dispersal distances from seed sources (Schupp et al. 2002). Many animal species, however, deliver and accumulate seeds in a heterogeneous manner on the forest ground, owing to specific behavioural traits (Condit et al. 2000, Wenny 2001, Schupp et al. 2002). For instance, bats produce seed-clumps below feeding roosts and tapirs defaecate in latrines, and both sites are located away from fruiting trees (Romo et al. 2004, Fragosco 1997). Thus, contagious seed dispersal seems to be common and more widespread, as previously recognised (Wenny 2001, Schupp et al. 2002).

Among different contagious dispersal categories identified, howler monkeys have been classified as dispersers to sleeping sites (Wenny 2001, Schupp et al. 2002). This is because they use certain sleeping areas in the forest regularly, and they usually defaecate before beginning their daily movements to food sources (Milton 1978, Julliot 1996a, Gilbert 1997, Andresen 1999, Andresen 2002a, this study: Chapters 4 and 6). In addition, all members of a howler troop usually defaecate synchronously. Consequently, each
sleeping area in the forest displays a number of deposition sites with high seed-density (Julliot 1996a).

The poor dispersal quality of howlers has usually been evaluated according to these commonly-recorded defaecation and dispersal patterns (Chapman 1989, Wehncke et al. 2003, Peres and van Roosmalen 2002), which have been observed in free-ranging howlers living mainly in undisturbed forests (Estrada and Coates-Estrada 1984, 1991, Chapman 1989, Julliot 1996a, 1997, Andresen 1999, 2002a, Wehncke et al. 2004). Yet, primate behaviour is flexible and subtle variations in their behaviour may occur. Indeed, contagious dispersal categories are non-mutually exclusive (Schupp et al. 2002), and howlers appear to display several modes of deposition that have been poorly documented. For instance, howlers do not always defaecate in sleeping areas of the forest, a fact commonly ignored. Moreover, they can also deposit seeds *en route* (*sensu* Schupp et al. 2002), when travelling and foraging (Gilbert 1997), and I observed that these depositions were produced by the whole group or by one or two individuals. This behaviour means that parts of the howler seed shadow have a low density, with potentially positive effects on seed survival. Furthermore, howlers not only defaecate synchronously, but they can also re-use exactly the same supports, and the grounds under these supports are generally free of underlying vegetation (Gilbert 1997, M. Santamaría pers. obs.). These combined behaviours may result, on the one hand, in the formation of latrines, which are specific sites in the forest that receive an irregular seed income over time. On the other hand, it results in seeds being deposited randomly in the forest ground. Thus, a more detailed picture of the seed shadow produced by howlers is necessary to give a proper evaluation of their dispersal effectiveness.

Some authors have stressed the lack of data on dispersal patterns by a particular disperser, as well as the necessity to characterise natural seed shadows in detail (Wenny 2000, 2001, Schupp et al. 2002). Behaviour plasticity among howler species is a widespread feature (Estrada et al. 1999a) that has helped them to tolerate habitat fragmentation and to survive in particularly small forest fragments (Juan et al. 2000, Clarke et al. 2002, Silver and Marsh 2003, this study: Chapters 4 and 5). Such behavioural modifications may alter howlers’ seed-dispersal patterns, and these plausible changes have rarely been assessed (Marsh and Loiselle 2003, Estrada et al. 1999b). This
is pertinent, given that the loss of alternative seed dispersers in forest remnants may disrupt dispersal services that in turn may alter the structure and dynamics of tropical forest (Andresen 2000, Onderdonk and Chapman 2000, Bruna 2003, Peres and van Roosmalen 2002, Andresen 2003).

In this chapter, I evaluate how reduction in howlers’ home range alters seed dispersal patterns and the natural seed shadow created by them. Subsequently, I assess seedling survival in some of the natural howlers’ deposition sites. For this, seed dispersal patterns are evaluated across the three sites under study: a small fragment (Co 2.5-ha), a medium one (Co 12-ha) and a continuous forest (Km41) functioning as a control area. Specific questions addressed in this chapter are:

1) How many species do howlers disperse, and are these numbers affected by howlers’ home range reduction?

2) Are howlers generating different deposition patterns (latrines vs. random sites) when their home range size is reduced through habitat fragmentation?

3) Are the characteristics (seed richness and density) of deposition sites (latrines vs. random sites) altered by howlers’ home range reduction?

4) How are howler seed shadows dispersed spatially and are there differences in their distribution due to home range reduction?

5) Are there variations in seedling survival in natural seed shadows produced by howlers living at the three study sites?

Because fruit sources, compared to leaves, show a clumped distribution in both space and time (Milton and May 1976, van Schaik et al. 1993, Janson and Chapman 1999, Cowlishaw and Dunbar 2000, Onderdonk and Chapman 2000), it is expected that reduction of howlers’ home range would decrease the number of species dispersed by them. A larger number of fruit species should be available in larger home ranges and accordingly howlers should consume and disperse more seed species at Km41 than in the fragments. These differences should be more drastic during the fruiting season, when howlers ingest more fruit species in accordance with their availability in the forest.
During lean fruit periods (leafing and flowering seasons), howlers feed mainly on young leaves and thus differences across sites should be diffuse.

At the BDFFP, howlers use specific sites for defaecations, but also drop faeces at random, when foraging, resting and travelling throughout their ranging area (Gilbert 1997, M. Santamaría pers. obs.). Accordingly, I classified these sites as latrines and random sites. Overall, more seeds should be deposited in latrines than at random sites, due to the prevailing behaviour of howlers to move and defaecate from specific supports. The tendency to defaecate in latrines, however, should be more extreme in fragments, since they have a smaller area in which to forage and this would result in major re-use of specific supports. The effect of home range reduction will be more drastic in the small than in the medium fragment.

Latrines are predicted to show a higher seed species richness, and density than random sites, given that latrines are used repeatedly and would receive an irregular input of seeds. In contrast, random sites would be the result of one defaecation event and thus would only receive one seed income. Given the patchy distribution of fruit resources in the forest, however, the richness of both latrines and random sites are expected to be lower with howlers' home range reduction.

A clumped distribution is expected for seed shadows generated by howlers across sites, according to howler behaviour: (a) synchronous defaecations (ca 80%, Chapter 6); (b) defaecations performed from specific supports that produce latrines (c) use of sleeping areas plus bimodal rhythm of deposition that leads to high concentration of faeces around sleeping sites. An effect of home range size, however, is predicted in the degree of seed shadow patchiness. At Km41, seed shadow should be patchier than in fragments, because more areas of the forest ground would fail to receive seeds in larger than in smaller home ranges.

At the three sites, seedling survival was assessed for a sample of the natural seed shadow produced by howlers. It is difficult to make predictions because comparisons were performed at the community level and species-specific traits may be a confounding effect. Yet, if seed predation is density-dependent, it is expected that seed predation increases with seed density of deposition sites.
7.2 METHODS

7.2.1 Species dispersed and seed size

Between January 2002 and January 2003, faecal samples were gathered from three howler groups having adjacent home ranges and living around the Km41 field station (hereafter Groups 3, 4 and 5). During one week each month, howlers were located in the early morning through their characteristic dawn calls, and faeces were recovered later once the group had defaecated. Howler groups were not followed in this site. In addition, specific searches for depositions were carried out within the troops’ home ranges, roughly defined during the pre-sampling period but refined during the sampling period. During these searches, two field assistants and myself independently looked for faeces in marked latrines and searched for new defaecation sites using olfactory cues. Monthly sampling effort was 50 search-hours/person. In both forest fragments, and for the same sampling period, faecal samples were collected only during the follows of the two focal groups (four days/month).

Identical protocols for dung collection and analysis were used across the three study sites. As defined in the previous chapter, a faecal sample represents all dung produced after a single defaecation event of the whole group (GD) or one-two individuals (ID). All faecal material and seeds separated from the dung when falling to the ground were collected in plastic bags. At the field stations, the total fresh weight of each faecal sample (dung and seeds combined) and the weight of seeds were recorded. Afterwards, faeces were washed and seeds > 3 mm long were retrieved through brass sieves of 1 mm mesh. All seeds removed were morphotyped, counted, and, for seeds with more than ten seeds, measured (length, width, depth and weight). The numbers of small seeds (< 3 mm) were estimated through counts of weighed faecal sub-samples (e.g., *Ficus* sp., *Goupia glabra*, *Coussapoa* sp. and *Cecropia sciadophylla*). Quantities of seeds belonging to the Melastomataceae family were not estimated, because seeds were extremely small and difficult to separate from dung without a stereoscope, and because both groups consumed them infrequently.

Seed samples were stored in plastic bags with small quantities of mothballs, labelled and used as a comparative collection across sites. In the fragments, identification of dispersed seed species came mainly through direct observations of the feeding trees.
exploited by the focal groups. As mentioned in Chapter 5, trees used by howlers were identified mainly through the Phyto-demographic Project database of the BDFFP, but also through botanical samples collected and identified later. At Km41, some seed species were identified based on the seed collection and on fruits recovered from the ground that were later checked in several fruit and plant guides (van Roosmalen 1985, Ribeiro et al. 1999, Stevenson et al. 2000b). Some seeds of the Sapotaceae family were identified by W. Spironello from the Department of Silviculture at INPA (National Institute for Amazon Research).

The mean of total fresh dung weight (including seeds)/faecal sample was estimated for Groups 1 and 2 living in the fragments and for all groups combined from Km41. At this latter site, data were pooled after finding no significant differences among groups ($H = 3.37, p = 0.19$). Given that the amount of dung produced varies according to the type of defaecation event (group depositions-GD; individual depositions-ID, Chapter 6), this analysis was conducted only for group defaecation events. These are defined as those in which at least 3 members of the group defaecates synchronously, whereas ID correspond to one or two individuals defaecating separately in time from the rest of the group. Yet, this information on type of defaecation event was available only for howlers living in the fragments. The mean value obtained for ID was $107.8 \text{ g} (\pm 21.1 \text{ g CI}; N = 31)$ for Group 1 and $98.8 \text{ g} (\pm 17.1 \text{ g}, N = 33)$ for Group 2. According to these values, only faeces with a weight above 150 g were included in the analysis. Sixty-one faecal samples produced through group defaecations were obtained for Group 1, 100 for Group 2 and 70 for Groups at Km41. Differences in faecal samples weight were assessed across sites using a Kruskal-Wallis test ($p < 0.05$) (Fowler et al. 1998).

The total numbers of species and seeds dispersed were estimated for the entire study and for the fruiting and leafing/flowering season, separately. The leafing and flowering seasons (hereafter non-fruiting season) were pooled, because both periods represent low fruit supply in the forest. Mean seed size were estimated for all seed samples measured independently of collection site. Seeds were grouped in three length size categories: small ($< 10 \text{ mm}$), medium (10-25 mm) and large ($> 25 \text{ mm}$). Large seeds were defined according to Peres and van Roosmalen (2002). Six more species with less than 6
seeds/species were included only for this analysis. Then, the percentage of seed species dispersed in each category was estimated.

7.2.2 Deposition patterns: latrines and random sites

The exact location of all depositions were marked carefully in the forest and recorded on maps. As mentioned in Chapter 6, howlers living in the fragments showed group and individual defaecations events. During group defaecations, I also observed that, despite faeces being produced at the same time, they did not always land in close proximity to each other. For instance, four individuals could defaecate from the same branch of a tree, while a fifth member dropped faeces at a distance > 5 m away from the main group deposition. Thus, faeces produced synchronously, but distributed in different areas of the forest ground, were collected in separate plastic bags. The same protocol was applied for individual defaecation events. Thus, a defaecation event could often result in several deposition sites in the forest ground.

Subsequently, all deposition sites obtained for each group were mapped using Arc View version 3.2. Their coordinates (X, Y) were measured in relation to the grid system, as explained in the previous chapter (see section 6.2.3). Buffers of 3 m radius were created for each deposition site. This buffer value is according to deposition patterns reported by Andresen (2002a). At Km41, she estimated that the median forest area of a howler faecal sample (produced by synchronous group droppings) was 17 m², which corresponds to a 1.8 m radius of a circle area. In order to be conservative, a buffer zone of 3 m radius was used for each deposition site. Afterwards, overlapping deposition sites were grouped as a single site. This procedure was applied for two reasons. First, subjectivity was avoided through this method when determining if deposition sites were closer enough to be considered one single deposition site or far enough to produce two different deposition sites. Second, some seeds were returned to the deposition sites for germination experiments, and thus the exact area where seeds were delivered by howlers needed to be defined (section 7.2.4).

Deposition sites were divided in latrines and random sites according to the following criteria. Sites that received a seed income at least twice during the sampling period were classified as latrines, while others were considered as “random sites” (hereafter RS). This
information was complemented with opportunistic data collected during bi-weekly seed germination controls in howlers’ deposition sites (see below, section 7.2.4). For each howler group, the occurrence of depositions produced in latrines and RS were estimated for the entire study. Since sample sizes were small, especially for latrines for Groups 4 and 5 in Km41, all analysis in this and the following sections were conducted only across Groups 1, 2 and 3. Group 5 ranged in a rugged terrain, making it difficult to search for faeces properly.

Comparisons on seed richness and seed density in latrines and RS were performed within and across groups. Again, only Groups 1, 2 and 3 were considered and faeces without seeds were removed from the dataset. Large quantities of seeds were recovered from *Byrsonima stipulacea* in fragments (Group 1= 5035, Group 2= 5040). In order to avoid an overestimation of seeds dispersed, this species, as well as species with seeds < 3 mm long, were not included in the density analysis.

For each group, the number of seeds dispersed/group/day were estimated combined the number of depositions produced each day (Chapter 6) in latrines and RS, multiplied by the median obtained in latrines and RS. In average, Group 1 produced 1.8 defaecations/day, whereas Group 2 defaecated 2.3/day

An additional analysis was performed between Groups 1 and 2, in order to determine if individual and group defaecations tended to be produced in latrines and/or RS. Although faecal samples that weighed < 150 g could be associated to individual defaecations at Km41, it was not uncommon to recover faeces several hours later after deposition (> 3 hours). Faeces found more than five hours after deposition were usually heavily modified by dung beetle activity. Hence, faecal samples weighing < 150 g that were found some hours after deposition could not be reliably assigned as a GD or ID event.

### 7.2.3 Spatial distribution of seed shadows

A seed shadow is the spatial pattern of seeds produced by a seed disperser during the process of seed dispersal (Jordano and Godoy 2002). The seeds shadows generated by Groups 1, 2 and 3 was evaluated using the coefficient of dispersion (Fowler *et al.* 1998). This coefficient is defined as follows:

$$CD = \frac{\text{variance}}{\text{mean}}$$
The number of deposition sites (latrines and RS) was counted by using the maps produced through Arc view. In fragments, counts were conducted in quadrats of 20 m x 20 m, following the grid system. At Km41, the home range of Group 3 was estimated at 22 ha (see chapter 2), and counts were performed within this home range using a superimposed grid of 20 m x 20 m over the original grid system of 100 m x 100 m (Chapter 2). For latrines, counts also included their frequency of use. For instance, a quadrat with one RS and one latrine used five times throughout the study would result in six counts. Subsequently, mean and variance of deposition sites counts/quadrat were calculated for each group, and then the coefficient of dispersion was estimated. A ratio close to 1 indicates that deposition sites are randomly distributed, whereas ratios above 1 represent a clumped or contagious distribution and below 1 yield to a regular distribution (Fowler et al. 1998).

In addition, the occurrence of latrines and random sites in and outside sleeping zones (Chapter 4) and fruiting trees were calculated only for howlers living in fragments. Even though latrines could be associated with sleeping zones at Km41, this information was not recorded systematically and hence was not analysed. In Chapter 4, sleeping zones of Groups 1 and 2 were defined as a 20 m x 20 m quadrat. Both sleeping zones and fruiting trees were mapped using Arc View version 3.2 (Chapters 4 and 6). A buffer zone of 10 m of radius was defined for fruiting trees according to the average crown diameter estimated by Read et al. (2003, Chapter 6). Finally, the percentage of latrines and RS found in sleeping zones as well as in fruiting trees was estimated. Once again, the number of deposition sites included the frequency of use of latrines.

7.2.4 Seed and seedling survival in deposition sites
At each site, seed and seedling survival at the community level were estimated for part of the seed shadow created by howlers. Seeds were returned and planted without dung, at the original deposition sites. At Km41, defaecation sites recorded for the three howler groups were pooled, since what is relevant here is the post-dispersal fate of dispersed seeds and not who generated the seed shadow. Seed location was marked with a number on a stake. The number of seeds of a single species varied strongly among faecal samples, ranging from 1 to 529 seeds. When large seed numbers of a particular species were
recovered in a latrine or RS, up to 100 seeds of that species were planted at that deposition site. Seeds were monitored bi-weekly for germination and predation/removal. Monitoring began in April – May 2002 at both sites and November 2002 (five deposition sites in Km41) and continued until February 2003.

Germination was defined as the emergence of the seed radicle. Predated seeds were considered as those partially eaten and those removed from the deposition sites. Here, all seeds removed/predated would be included in the predation category. Although secondary dispersers, such as dung beetles, could relocate seeds, this was improbable because seeds were sown without dung, the olfactory clue that attracts them. It is important to note, however, that dung is a factor that sometimes influences the seed predation rate of rodents (Chapman 1989, Andresen 2001, Feer and Forget 2002). Thus, predation rates may be underestimated. Yet, the effect decreases over time (Chapman 1989, Andresen 1999), because dung is removed rapidly by dung beetles (ca 24 hours; Feer and Forget 2002), by rain during the rainy season (Andresen 2001) or because dung dries out and loses its odour faster during the dry season (M. Santamaría, pers. obs.). Finally, seedlings were monitored for irreversible damage such as herbivory, desiccation, and cotyledon predation. Seedlings, whose seeds were damaged, but resprouted, were classified as alive.

Intensity of predation and germination were calculated as the number of seeds predated/germinated, divided by the total number of seeds planted. (i.e., percentage of seeds in each category). Both predation and germination were estimated for each site and compared across them. Differences were not made between latrines and RS, because sample size was small and could not be controlled throughout the study. Indeed, deposition sites could only be classified as latrines or RS after the end of the study.

Seedling survival corresponds to those seedlings remaining alive throughout the study period (9-10 months). Survival was a result of the number of seeds germinated minus seeds predated minus seedling irreversible damaged. Seedling survival rate was then estimated as the proportion of seedlings alive per site at the end of the sampling period from the total seeds that germinated (February 2003). In order to test if seed predation increases with seed density, a Spearman rank correlation coefficient (p< 0.05, Fowler et
al. 1998) was performed at each site between the number of seeds planted (density) vs. the number of seeds predated in each deposition site.

7.3 RESULTS

7.3.1 Species dispersed and seed size

Overall, 342 faecal samples were recovered from the five howler groups, and 80% of these samples contained seeds (Table 7.1). Mean weight of faecal samples produced through group defaecations was similar across sites ($F = 0.63, p= 0.53$), and averages ranged between 408 g in Km41 and 418 g in Co12-ha (Table 7.2). Seeds greater than 3 mm accounted for a mean of 14% total faecal weight ($\pm 1.9$ CI), but ranged from 0.1% to 57%.

Table 7.1: Number of species and seeds recovered in faeces collected from two howler groups in Colosso fragments and three groups in Km41 continuous forest between January 2002 - January 2003.

<table>
<thead>
<tr>
<th>Groups</th>
<th>Fragments 1</th>
<th>Fragments 2</th>
<th>Undisturbed forest (Km41)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. species dispersed</td>
<td>40</td>
<td>41</td>
<td>68</td>
</tr>
<tr>
<td>No. seeds dispersed</td>
<td>6,372</td>
<td>7,645</td>
<td>3,038</td>
</tr>
<tr>
<td>No. seeds dispersed without B. stipulacea</td>
<td>1,337</td>
<td>2,605</td>
<td>3,038</td>
</tr>
<tr>
<td>No. faeces collected</td>
<td>87</td>
<td>142</td>
<td>58</td>
</tr>
<tr>
<td>No. faeces with seeds only</td>
<td>66</td>
<td>120</td>
<td>38</td>
</tr>
</tbody>
</table>

Table 7.2: Mean weight of fresh dung produced through defaecations (weight $> 150$ g), 95% confidence intervals (CI), and sample size (N) across sites between January 2003-January 2003. a= data pooled for Groups 3, 4 and 5 (See methods for explanation).

<table>
<thead>
<tr>
<th>Site/Group</th>
<th>Faecal weight (Mean)</th>
<th>CI</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1</td>
<td>408.6</td>
<td>33.1</td>
<td>61</td>
</tr>
<tr>
<td>Group 2</td>
<td>417.9</td>
<td>24.4</td>
<td>100</td>
</tr>
<tr>
<td>Km 41 a</td>
<td>407.9</td>
<td>25.4</td>
<td>70</td>
</tr>
</tbody>
</table>
In total, 146 species, including seeds < 3 mm, were dispersed by howlers living in the fragments and Km41 (Figure 7.1). Group 3 (Km41) dispersed the highest number of seeds and species among the five groups. The number of species dispersed varied markedly between fruiting and non-fruiting seasons (Figure 7.2). As expected, howler groups dispersed more fruit species during the fruiting peak (range: 18 to 59), and much fewer species in non-fruiting season (range: 5-9). Once again, Group 3 delivered the seeds of 59 fruit species during the fruiting peak, a much higher number than the other four groups (Figure 7.2).

![Figure 7.2: Number of seeds dispersed during the fruiting and non-fruiting seasons by Groups 1 and 2 living in the forest fragments and Groups 3 to 5 in Km41, between January 2002 and January 2003.](image)

Group 1 living in the small fragment, dispersed seeds from the adjacent forest into the fragment. This group was observed repeatedly crossing the 50 m gap towards the continuous forest, to eat fruit in four of the 13 months sampled. Seeds from four species that were unavailable in the fragment were recovered in faeces. These species included *Helicostylis tomentosa* (Moraceae) consumed in April 2002, *Ficus* sp. (Moraceae) exploited in August 2002, and two species belonging to the Sapotaceae and Moraceae families ingested in May 2002 and January 2003 respectively.

Excluding seeds < 3 mm, the mean seed size of dispersed species was 15.7 ± 0.8 mm in length, 9.9 ± 0.2 mm in width, 8.1 ± 0.2 mm in depth and 1.0 ± 0.02 mm in weight, $N_{\text{species}} = 50$ and $N_{\text{seeds}} = 1344$) (Appendix 6). Seeds dispersed fall mainly in the medium
(a) Combretaceae

(b) Protium apiculatum (Burseraceae)

(c) Pouteria engleri (Sapotaceae)

(d) Cheiloclinium hippocrateoides (Hippocrateaceae)

**Figure 7.1**: Fruit consumed by red howler monkeys whose seeds were dispersed.
length category with 39 species, whereas five species were large seeds and 12 were small. Large seeds belonged to the Sapotaceae (3 species), Myristicaceae (1 species) and Euphorbiaceae (1 species) families, with a maximum length of 33.2 mm, width of 16.8 mm and height of 15.2 mm.

7.3.2 Deposition patterns: latrines and random sites

A similar deposition pattern was found across the three study groups (Figure 7.3). More deposition sites were generated at latrines (Group 1 = 66%, Group 2 = 61% and Group 3 = 61%) than at random sites (Group 1 = 34%, Group 2 and 3 = 39%), even though the absolute number of latrines was less than the number of random sites (Latrines vs. RS: Group 1 = 26 vs. 38, Group 2 = 37 vs. 77, Group 3 = 17 vs. 30).

Figure 7.3: Comparisons of deposition sites (in %) produced in latrines and random sites (RS) by Groups 1, 2 and 3.

Large variations were found in the number of seed species found in latrines and RS. Species numbers ranged from 1 to 9 in RS and from 1 to 13 in latrines (cumulative values), with an outlier value of 24 species recovered in a latrine used five times by Group 3. For each group, more seed species were delivered by howlers in latrines.
(Median\textsubscript{Group1} = 4, median\textsubscript{Group2} = 4, median\textsubscript{Group3} = 5) than in random sites (Groups 1, 2, 3 = 2). Yet, these differences were statistically significant in both fragments (Group 1: $U$ = 3.08, $p = 0.002$, $N$ = 42; Group 2: $U = 3.25$, $p = 0.001$, $N = 83$), but not in Km41 ($U = 0.78$, $p = 0.43$, $N = 36$). Moreover, comparisons performed across sites revealed no significant differences in the median seed species deposited by each howler group in latrines ($K = 0.72$, $p = 0.69$, $N = 74$) as well as in RS ($K = 2.17$, $p = 0.34$, $N = 87$), even though overall Group 3 dispersed more species than Groups 1 and 2.

Results on seed density in several deposition sites are presented in Table 7.3. Both latrines and RS received a similar number of seeds dropped by howlers of Groups 1 and 2. Yet, Group 3 deposited more seeds in latrines (Median = 64) than RS (Median = 19), even though differences were only at the limit of significance ($U = 1.8$, $p = 0.07$, $N = 32$). When comparisons were performed across sites, Group 3 delivered significantly more seeds in latrines than groups living in fragments ($K = 8.6$, $p = 0.01$, $N = 68$), whereas similar median seed numbers were found for RS across groups ($K = 0.12$, $p = 0.94$, $N = 51$).

In fragments, group and individual defaecations (GD and ID respectively) were produced both at latrines and random sites. Moreover, both group and individual defaecations were more likely to occur in latrines (GD: Group 1 = 56%, Group 2 = 49%; ID: Group 1 = 14%, Group 2 = 12%) than at random sites (GD: Group 1 = 26%, Group 2 = 31%; ID: Group 1 = 4%, Group 2 = 7%) (Figure 7.4). These figures were combined with the median number of seeds deposited in latrines and RS (Table 7.3) and with the number of faeces produced each day through group defaecations (GD) and individual defaecations (ID) (Group 1 = 3.1, Group 2 = 3.7; Chapter 6), in order to estimate the number of seeds deposited each day and each year (Table 7.4). Group 1 dispersed 56 seeds/day and 28,586 seeds/year, whereas Group 2 delivered 75 seeds/day and 27,339 seeds/year.
### Table 7.3: Medians of seed species and seed densities delivered in latrines and random sites (RS) by each howler group. P values are shown for analysis performed (a) within groups and (b) between groups. Significant results are bolded.

<table>
<thead>
<tr>
<th>Site</th>
<th>Group</th>
<th>N</th>
<th>Latrine</th>
<th>RS</th>
<th>M-W test&lt;sup&gt;a&lt;/sup&gt; (p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Richness</td>
<td>Co 2.5-ha</td>
<td>1</td>
<td>42</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Co 12-ha</td>
<td>2</td>
<td>83</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Km41</td>
<td>3</td>
<td>36</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>M-W test&lt;sup&gt;b&lt;/sup&gt; (p)</td>
<td></td>
<td></td>
<td>0.69</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td>Density (No. seeds/deposition site)</td>
<td>Co 2.5-ha</td>
<td>1</td>
<td>25</td>
<td>17</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Co 12-ha</td>
<td>2</td>
<td>62</td>
<td>21</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Km41</td>
<td>3</td>
<td>32</td>
<td>64</td>
<td>19</td>
</tr>
<tr>
<td>M-W test&lt;sup&gt;b&lt;/sup&gt; (p)</td>
<td></td>
<td></td>
<td>0.01**</td>
<td>0.94</td>
<td></td>
</tr>
</tbody>
</table>

### Table 7.4: Estimations of the numbers of seeds delivered per deposition site daily and yearly.

<table>
<thead>
<tr>
<th>Deposition site</th>
<th>Group 1 (seeds/deposition/day)</th>
<th>Group 2 (seeds/deposition/year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group defaecation</td>
<td>Latrine</td>
<td>%d</td>
</tr>
<tr>
<td></td>
<td>Random site</td>
<td>18.4</td>
</tr>
<tr>
<td>Individual defaecation</td>
<td>Latrine</td>
<td>6.8</td>
</tr>
<tr>
<td></td>
<td>Random site</td>
<td>2.3</td>
</tr>
<tr>
<td>Total no. seeds dispersed</td>
<td>56</td>
<td>75</td>
</tr>
</tbody>
</table>
7.3.3 Spatial distribution of seed shadows

Seed shadows produced by the three howler groups displayed a clumped distribution (Figure 7.5a-c) that ranged from 0 to 11 deposition sites/quadrat (20 m x 20 m). The degree of patchiness was slightly higher for Group 2 (CD = 3.5) than Groups 1 and 3, for which values were similar (CD = 2.7 and 2.6 respectively). Many quadrats within the home ranges of the three howler groups failed to receive faeces: 44 out of 90 quadrats of Group 1 (49%), 142 out of 228 of Group 2 (62%) and 42 out of 650 of Group 3 (6%) (Figure 7.5a-b).

More deposition sites were produced within sleeping zones by Group 1 (62% of total recorded) than by Group 2 (44%) (Figure 7.6). Moreover, latrines were not always associated to sleeping zones, since 26% of latrines for Group 1 and 28% for Group 2 were located outside them (Figure 7.6). Finally, drastic differences between Groups 1 and 2 were found in relation to feeding trees, and more deposition sites were found under fruiting trees in the small (79%) than in the medium fragment (40%) (Figure 7.7).
Figure 75a: Location of fruiting trees, sleeping zones (frequent and occasional) and defaecations sites within the home range of Group 1.
Figure 75b: Location of fruiting trees, sleeping zones (frequent and occasional) and defaecations sites within the home range of Group 2.
Figure 75c: Location of defaecations sites within the home range of Group 3.
Figure 7.6: Comparisons of deposition sites (in %) produced in and out of sleeping zones by Groups 1 and 2, and that occurred in latrines and random sites (RS). Values in boxes are in percentages.

Figure 7.7: Comparisons of deposition sites (%) produced in and out of feeding trees by Groups 1 and 2.
7.3.4 Seed and seedling survival in deposition sites

In total 424, 912 and 996 seeds of Co 2.5-ha, Co 12-ha and Km41 were returned and planted in 12, 26 and 25 deposition sites, respectively (Figure 7.8a-c). These seeds belonged to 18 species in each fragment and to 26 species in Km41 (Appendix 7). Medians of the number of species and seeds planted are shown in Table 7.5. Many seeds from different species failed to germinate or remained dormant throughout the 9-10 months of monitoring: 78% in Co 2.5-ha, 89% in Co 12-ha and 67% in Km41). Seeds in the category predated were both removed or eaten in situ since the seed coat remained in the deposition site. Predation by insects was not observed.

Table 7.5: Medians of the number of species and seeds planted in howlers’ deposition sites at the three study areas.

<table>
<thead>
<tr>
<th>Site</th>
<th>N</th>
<th>No. species/deposition site</th>
<th>No. seeds/deposition site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Median</td>
<td>Range</td>
</tr>
<tr>
<td>Co 2.5-ha</td>
<td>12</td>
<td>3</td>
<td>2 - 6</td>
</tr>
<tr>
<td>Co 12-ha</td>
<td>26</td>
<td>3</td>
<td>2 - 7</td>
</tr>
<tr>
<td>Km41</td>
<td>25</td>
<td>3</td>
<td>1 - 10</td>
</tr>
</tbody>
</table>

The total percentage of seeds predated was similar in Km41 and in the small fragment (15%), but was much lower in the medium fragment (3%). By contrast, seeds germinated at a higher rate in Km41 (33%), whereas germination was lower in the small fragment (22%), and strongly reduced in the medium fragment (11%) (Figure 7.9). As a result of these differences between germination and predation, seedling survival was similar and two-folds higher at Km41 and Co 12-ha (51% and 50% respectively) than at Co 2.5-ha (23%) (Figure 7.9).

At Km41, seed predation in defaecation sites increased significantly with seed density ($r^2=0.8; p=0.001, n= 16$) (Figure 7.10), but was only at the significance limit in Co 12-ha ($r^2=0.4, p=0.07, n= 10$), and not correlated in Co 2.5-ha ($r^2=0.2, p=0.24, n= 8$). At Km41, latrines had higher seed densities than RS and they showed a tendency to have higher predation than RS (Figure 7.10).
Figure 7.8a: Latrine produced by Group 3 living in Km41.

Figure 7.8b: Seeds planted in a deposition site of Km41.

Figure 7.8c: Seedlings in a latrine in Km41.
Figure 7.9: Comparisons of predation, germination and seedling survival across the three study sites: the small fragment (Co 2.5-ha), the medium fragment (Co 12-ha) and the continuous forest (Km41).

Figure 7.10: Effect of seed density on the number of seeds predated at Km41.
7.4 DISCUSSION

7.4.1 Species dispersed and seed size

In this study, two methods were used to collect howler faeces, which accounts for the large differences in sample sizes obtained for the five focal howler groups. Faeces gathered during monthly-follows of Groups 1 and 2 resulted in larger samples sizes than those obtained through monthly searches on the ground in Km41 (Table 7.1). In particular, fewer faecal samples were recovered from Groups 4 (35) and 5 (20), resulting in less species recovered, especially for Group 5 (Group 4= 40 species, Group 5= 28 species). As mentioned before, this last group ranges in a rugged terrain, making it difficult to search for faeces properly.

Despite these sample size differences, the number of species dispersed by Group 4 and 5 (40 and 29 respectively) remained similar to the two groups living in the fragments (Group 1= 40 species, Group 2= 41 species). Thus, it appears that a sample size effect rather than a similar fruit diet explains these unexpected results. In contrast, Group 3 showed the highest number of seed species dispersed (68), indicating that as predicted, home range reduction decreased the number of seed species disseminated by howlers. In terms of dispersal quantity, howlers dispersed a large number of seeds throughout the sampling period and these results are in accordance to other howler studies (Milton 1980, Julliot 1996a, Estrada and Coates-Estrada 1984, 1991, Andresen 2002a). If seeds of Byrsonima are not included, and although size of faecal samples was two to three times smaller, Group 3 also dispersed a much higher number of seeds (3,038) than Groups 1 and 2 (1,337 and 2,605 respectively). In terms of seeds dispersed daily and yearly, Group 2 dispersed a higher number of seeds than Group 1. Although these estimates could not be obtained for Group 3, more seeds are expected to be delivered by this group in comparison to howlers living in the two fragments.

In this study, howlers dispersed large number of fruit species mainly during the fruiting season. This result accords with diet profiles reported for Groups 1 and 2 in Chapter 5. As expected, differences between sites were more conspicuous during the fruiting season. Whereas other Ateline species, such as Ateles spp., forage in larger areas during lean periods in order to find fruit and other sources (Andresen 1999, Stevenson et al. 2000a), howlers switch to a more folivorous diet, minimising its energy expenditure and
consuming fruit only when available in large crops (Milton 1980). Thus, faeces without seeds were not uncommon (20% for all groups), and appear to reflect low fruit availability in the forest, rather than non-fruit consumption, as already pointed out by Andresen (2002a). If a fruiting tree or trees appear to fruit during the fruit scarcity period, however, they do exploit fruit intensively and disperse their seeds. This was the case of *Byrsonima stipulacea*, a pioneer species widely exploited by Groups 1 and 2 during the leafing period. More than 5,000 seeds were dispersed by each group in three sample-months. Seeds from this species were recovered also in Km41, but in lower amounts, because trees of this species appear to be less abundant in interior forests (M. Santamaría, pers. obs.).

At Km41, Andresen (2002a) searched and recovered faeces on the forest ground from five howler groups and found that they dispersed 137 seed species over 25 months of sampling. My results show that the three howler groups in Km41 dispersed 99 different species over 13 months and this lower value is attributed to the shorter sampling period. Many tropical trees in the Manaus region show supra-annual patterns in fruit production and consequently fruit availability displays a high inter-annual variability (Oliveira 1997, Naka 2001, Spironello 1999). As a result, fruit consumption by howlers fluctuates widely between years. For instance, Andresen (2002a) recorded 47 species dispersed during the first year of sampling and 90 different species were added in the second year. Thus, she stressed the importance of recording seed dispersal during more than one year.

Nonetheless, in this study conducted for 13 months, 147 seed species were recovered from faeces from the five howler groups living in fragments and the continuous forest. Thus, this result supports Andresen’s conclusion that howlers in Central Amazon are highly prevalent as seed dispersers. Two facts may explain howlers’ prevalence in Central Amazonia. First, beta-diversity is extremely high in the Manaus region (Oliveira 1997, Laurance 2001) and accordingly, each howler group is dispersing different fruit species. For instance, a low overlap in the fruit diet was found between Groups 1 and 2 (Chapter 5). Second, howlers may be able to exploit a larger number of fruit species in the study area, compared to other Amazonian sites, due to lower inter-specific competition. A specialised frugivore, such as *Ateles paniscus* is found in lower densities
at the study site and is absent in small fragments (Rylands and Keuroghlian 1988), while other fruit-eating primates, such as *Lagothrix* spp. do not occur in the area. In the north-western Amazon, for example, *Lagothrix lagothricha* and *Ateles belzebuth* were potential dispersers of a higher number of species (85%) than red howlers (53% species; Stevenson *et al.* 2002). This may be, because of food partitioning among the three primates, with howlers being less frugivorous and usually displaced by the other two species.

At present, around 1250 tree species (including morpho-species) have been identified at the BDFFP reserves, of which only 12% are common (Laurance 2001). Yet, the number of species that depend on animal agents to disperse their seeds has not been estimated, as well as the number of seed species that rely only on primate dispersal. In French Guiana and Western Amazon, Peres and van Roosmalen (2002) documented that about 85% of woody plants were zoochorous and of this total, around 45% were ingested and dispersed by primates. They showed that larger seeds (> 25 mm long) were exclusively dispersed by three large-bodied primates: *Ateles*, *Lagothrix* and *Alouatta* spp., constituting a “large-fruit primate syndrome” (*sensu* Peres and van Roosmalen 2002). The morphological traits of this syndrome correspond to large seeds of indehiscent husks that are swallowed by a small guild of dispersers. They found, however, that *Ateles* and *Lagothrix* disperse a larger number of large species than *Alouatta*. In this study, the howler groups dispersed mainly medium size seed species (39), and disseminated few large seeds (five species). Howlers in French Guiana dispersed seeds as large as 40 mm long (Julliot 1996a), but the number of species/seed size categories were not reported. Here, the low number obtained for large seeds may be underestimated, because, firstly, not all species dispersed by howlers were measured because of the small sample sizes. Secondly, fruits of Sapotaceae that are close or may fall in the “large-fruit primate syndrome”, were not ingested, simply because such fruit were not available. In fact, this family shows supra-annual patterns in fruit production (Spironello 1999), and howlers are known to exploit a large number of their fruit species at BDFFP (Spironello 1999, Andresen 2002a, Chapter 5), French Guiana (Julliot 1996a), Surinam and Western Brazilian Amazon (Peres and van Roosmalen 2002). At these four sites, this family is among the dominant woody plant families (Julliot 1996a, Oliveira 1997, Laurance 2001, Peres and van Roosmalen 2002).
In conclusion, Groups 1 and 2 ingested and dispersed a large number of fruit species with small, medium and large sized seeds, even though these numbers were reduced through habitat fragmentation. Both groups are the only large arboreal mammals capable of dispersing large seeds in the fragments, because *Ateles paniscus*, which also swallows large seeds, cannot survive in fragments of these sizes (Rylands and Keuroghlian 1988). Finally, the ability of howlers’ in Group 1 to cross a gap enriches the small fragment with seeds brought from the adjacent forest. While some primates cannot persist in small fragments and small-bodied primates disperse mainly seeds less than 20 mm long (Garber 1986, Oliveira and Ferrari 2000, Peres and van Roosmalen 2002), howlers have the ability of coping with habitat fragmentation and dispersing large seeds. According to all these factors, howlers may be a key element to be considered during restoration and management programmes because they can provide a dispersal service and maintain fruit plant-howlers interactions. In a hunting scenario, however, howlers may vanish from small areas. Nonetheless, as pointed out by Peres and van Roosmalen (2002), howlers can also be more resilient to hunting pressure than *Ateles* and *Lagothrix* spp. The former has the ability to become behaviourally inconspicuous, whereas the latter are preferred preys of hunters.

**7.4.2 Deposition patterns and spatial distribution of seed shadows**

Howlers are generally regarded as low-quality dispersers when compared to other medium- and large-bodied Neotropical primates (Chapman 1989, Peres and van Roosmalen 2002, Wehncke et al. 2003). This is because howlers tend to produce large faecal clumps with high seed aggregation. Consequently, it has been stated that the same density-dependent mortality factors that occur under parental trees, are also found in howler defaecation sites (Howe 1980, Chapman 1989). Yet, this study shows that this is not always the case and indicates how difficult it is to generalise about the effectiveness of a disperser. Regardless of home range size, deposition patterns and spatial distribution of deposition sites by howlers illustrate three main points:

(1) Howlers dispersed seeds in both latrines and random sites, but more often in the former (up to 66%),
In latrines, howlers deposited more seed species than in random sites, and this patchiness was associated not only to sleeping zones, but to latrines located outside them.

In the following sections, these points are discussed and similarities and differences found across the three study sites are stressed.

**Deposition patterns.** Howlers’ deposition patterns have generally been related to their bimodal rhythm of defaecation that results in a high number of faeces, and thus seeds, being deposited around sleeping trees (> 60%, Julliot 1996a), which in turn are associated with high density-dependent mortality. Yet, howler deposition patterns have rarely been related to two other factors that can influence seed fate. Firstly, about 20% of depositions are produced by only one or two individuals of a group (Chapter 6). These individual defaecations produce smaller faecal clumps weighing less than 150 g and I found that these depositions occur at both latrines and random sites by howlers living in the fragments. Secondly, although howlers tend to use latrines most often, some defaecations are deposited at random sites. At random sites, particularly where only one or two individuals have defaecated, smaller seed aggregations should result in higher survival rates, assuming that seed and seedling mortality are frequently dependent on seed density (Janzen 1970, Connell 1971). It follows, therefore, that howlers’ dispersal quality varies, taking into account that seed and seedling survival depend on deposition characteristics (Schupp 1993). This fact indicates that defining a species as “good disperser” or “bad disperser” is wrong (Lambert and Kaplin 2001).

In the continuous forest (Km41), the characteristics of deposition sites varied between latrines and random sites as was expected. Group 3 deposited significantly more seeds at latrines than at random sites and displayed a similar trend for seed species (Table 7.3). For instance, 415 seeds of 24 species were recorded in a latrine used five times. Thus, seeds accumulated gradually at latrines and predation should be higher at these sites than at random ones, but this pattern was modified partly by the reduction of howlers’ home
range. While Groups 1 and 2 delivered more species in latrines than at random sites, similar amounts of seeds were deposited at both defaecation sites (Table 7.3).

The consequences of these modifications are difficult to determine, because seedling survival could not be systematically compared between latrines and random sites. Yet, in Km41, an effect of seed density was found on predation, and seeds in latrines had higher predation than in random sites. Generalisations on seed fate are difficult, however, because other factors come into play in this interactive system of howlers-dung-seed shadows. Howlers’ faeces attract rodents and dung beetles (Estrada and Coates-Estrada 1991, Andresen 2002b). Rodents act mainly as seed predators, but are also associated to scatterhoarding through which survival of unretrieved seeds may be enhanced by avoiding other predation factors (Forget 1996, Feer and Forget 2002). Dung beetles are attracted more strongly to large faecal clumps than small ones, and act inadvertently as secondary dispersers when seeds are rapidly buried with the dung balls. In this relation, the effects of predation may be compensated by secondary dispersal (Andresen 2002a, but see Wehncke et al. 2004). In addition, latrines may exhibit abiotic conditions favouring germination. These sites are generally free of underlying vegetation and may be subjected to more light, less foliage in the soil and additional fertilisation provided by faecal material. Moreover, high seedling competition in latrines may be reduced due to differences in the latency periods among species (Chapter 6). Finally, faeces deposited in latrines do not always contain seeds, especially during fruit lean periods, suggesting high variations in seed income over time. All these factors need to be assessed in detail in order to determine howlers’ influence in forest structure.

Spatial distribution of seed shadows. As predicted, seed shadows produced by howlers at the three study sites exhibited a clumped distribution, but the degree of patchiness was not higher at the continuous forest than in the fragments, as expected. This result may be attributed again to differences in sample sizes, which are accounted for the different sampling methods applied. I suspect that more faecal samples would have been collected through systematic follows for Group 3, increasing the number of random sites and latrines, but also the frequency of use of latrines. This would result in a more clumped distribution. For instance, during my observations in 1998 (Santamaría and Rylands
2003), 103 faecal samples were collected for a howler group at Km41, during 530 observation hours (44 days in six months). This group ranged in 21 ha and was observed using regularly five well-defined sleeping zones, where faeces were frequently found in recognised latrines. In north-western Colombian Amazon, a red howler group followed for more than 10 years was easily located at dawn in recognised sleeping trees (H. Lozano, pers. comm.). It appears, therefore that direct observations of howlers provide more detailed information and more faecal samples, than through searching for faeces on the ground. Yet, this last method has the advantage of providing information on several groups and consequently has a population approach.

The clumped distribution pattern produced by howlers monkeys has been related to the use of sleeping zones and to the characteristic behaviour of defaecating before starting the daily activities (Milton 1980, Julliot 1996a, Bravo and Zunino 2000, Schupp et al. 2002). In this sense, my results are in accord, given that 56% of deposition sites of Groups 1 and 44% of Group 2 were produced in sleeping zones. In this study, however, patchiness appears to be also related to the use of latrines, because they are not always located in sleeping zones (Figure 7.6). About 30% of latrines of both groups were found outside sleeping zones (Figure 7.6) and howlers’ deposition sites are produced frequently in latrines (ca 60-65%). For instance, some latrines were located along travel routes and used regularly by Group 2 when passing by.

The effect of home range reduction on deposition sites produced at sleeping zones and fruiting trees is difficult to assess here because data are not available for Group 3. It is clear, however, that Group 1 is producing more deposition sites in sleeping zones and especially under fruiting trees than Group 2, and that these results are related to home range size. In fact, the chances of faeces and seeds to be dropped under fruiting trees by Group 1 are increased in an area about three times smaller (2.5 ha) than the one used by Group 2 (7.2 ha), but both groups dispersed most seeds away from the plant source. Thus, most of the seed shadows produced under fruiting trees are composed of foreign seeds and, in this sense, the quality of dispersal of howlers is not affected by habitat reduction. Interestingly, this result confirms the expectations of Schupp et al. (2002), in which seeds
defaecated by howlers beneath fruiting trees should be from other fruit sources, due to their long gut-transit times.

Few studies have estimated the percentage of defaecations associated with sleeping sites. In French Guiana, Julliot (1996a) reported that 60% of howler group faeces were located within 20 m of sleeping trees, whereas in Argentina, 91% of defaecations were produced at dormitories by a black howler group living in a 10 ha fragment (Bravo and Zunino 2000). Comparisons are difficult to perform with my study, because, on the one hand, Julliot limited defaecation counts in an area < 20 m around the sleeping trees (about 40 m x 40 m), and this area is larger than the one defined here (20 m x 20 m). On the other hand, the size of sleeping zones is not reported in Bravo and Zunino’s study. Certainly, depositions produced by howlers are strongly related to sleeping sites, simply because they always defaecate before starting their activities. Yet, the distance at which seeds are deposited varies in relation to the sleeping zone. For example, it was common to observe howlers moving more than 20 m before defaecating. In addition, sub-adult males sometimes moved in the morning without defaecating before the whole group, did and later dropped faeces somewhere outside the sleeping zone.

7.4.3 Seed and Seedling survival in deposition sites

In this study, the fate of seeds delivered in howlers’ multi-species deposition sites varied greatly and appeared to be related to seed species at all sites and to seed-density at Km41. A high percentage of seedlings survived after about ten months of seed deposition on the ground (Co 2.5-ha= 23%, Co 12-ha= 50%, Km41- 51%), yet seedlings need to be monitored over longer periods until they become saplings. Seedling survival was highest at Km41 and Co 12-ha (ca 50%) and much lower at Co 2.5-ha (23%). Post-dispersal seed fate was related to seed germination and predation that displayed large variations within and between sites. Here, natural, and not experimental, deposition sites were monitored, and the marked differences on germination and predation appeared to be related to the large variation in the number and species planted in each deposition site.

At Km41, seed predation depended on seed density because a strong positive correlation was found. In this correlation, latrines tended to display higher seed densities with consequently higher predation than random sites (Figure 7.10). These results
suggest, firstly, that not all deposition sites produced by howlers exhibit high seed density and thus many seeds escape predation. Secondly, seeds deposited at random sites may have more chance to establish as seedlings, because of lower seed densities. In the fragments, by contrast, only weak and absent correlations were found for Co 12-ha and Co 2.5-ha, respectively. Moreover, predation was very low at the medium fragment (3%) compared to the small fragment (15%) and Km41 (15%). Thus, these results indicate that factors (e.g. seed availability, undiscovered clumps of seeds) other than seed density may influence also seed predation. Little consistency has been found on the effect of seed density on seed predation rates (Andresen 2002a, Feer and Forget 2002, Romo et al. 2004, see review Hammond and Brown 1998). For instance, reduced seed removal by rodents from howler dung has been reported during periods of fruit abundance when alternative resources are available in the forest, resulting in rapid rodent satiation (Feer and Forget 2002, Chauvet et al. 2004).

Differences in predation may also be accounted to seed species planted in the deposition sites. Rodents are known to show preferences for some seed species, and Sapotaceae seeds are among these (Spironello 1999). For example, red-rumped agoutis in an Amazonian forest relied heavily on seeds of two Sapotaceae species (50%, Silvius and Fragoso 2003). I observed that in a multi-species deposition site, rodents ate seeds from Sapotaceae and ignored other species, suggesting that Sapotaceae seeds could be predated (including removed) by rodents. At Km41, Spironello (1999) found heavy predation of Sapotaceae seeds that were embedded in howlers’ faeces. Here, more Sapotaceae seeds were planted at Km41 (244) and Co 2.5-ha (164) than at Co 12-ha (74), and seed predation varied accordingly. For instance, 62 out of 65 seeds predated at the small fragment were Sapotaceae seeds. Thus, the low seed survival obtained in the small fragment may be explained because, firstly, many Sapotaceae seed were planted (162 out of 424) and, secondly, these seeds suffered high predation (62 out of 162 – 38%). By contrast, in the medium fragment, only 67 out of 912 seeds planted were from the Sapotaceae family. Moreover, seeds planted were largely from seed species of Bocageopsis multiflora, Byrsonima stipulacea and Helicostylis tomentosa (654 seeds in total) that were rarely predated (only 7 seeds of H. tomentosa) and seem not to be species exploited by rodents.
Different seed survival found between fragments is also related to germination, which in turn was associated again to seed species planted. This is because morphological and physiological seed-traits influence germination (Vásquez-Yanes and Orozco-Segovia 1990). Small seeds with a hard coat generally show dormancy periods, whereas large seeds tend to germinate quickly (Vásquez-Yanes and Orozco-Segovia 1990). In this study, seed germination rates were particularly low at the medium fragment (11%), than at the other two sites (Co 2.5-ha= 22%, Km41= 33%). At Co 12-ha, many seeds of several species planted showed dormancy. This was the case again of *Byrsonima stipulacea*, *Bocageopsis multiflora* and *Helicostylis tomentosa* (Appendix 7), which revealed long periods of latency during the greenhouse trials (Chapter 6). Differential germination rates among seed species may have implications for multi-species seed shadows, because inter-specific competition between seeds and seedling can be reduced or avoided.

### 7.5 SUMMARY

- Between January 2002 and January 2003, I evaluated seed-dispersal patterns produced by howlers living in three study sites: a small fragment (Co 2.5-ha), a medium one (Co 12-ha) and a continuous forest (Km41).
- Home range reduction decreased the number of seed species disseminated by howlers from 68 species by Group 3 living in the continuous forest to about 40 species in each fragment.
- In terms of dispersal quantity, howlers dispersed large amounts of seeds in all sites, especially during the fruiting season. When seeds of *Byrsonima stipulacea* were not included in the analysis, an effect of home range size was recorded on the number of dispersed seeds (> 3 mm long), being lower at the fragments.
- At the three sites, howlers dispersed mainly medium-sized seed species, but they also delivered small seeds and large ones that were up to 33 mm long.
• Three main points emerged from this study in terms of deposition patterns, indicating that the view of categorising a species as a “good disperser” or a “bad disperser” is misguided:

(1) Howlers dispersed seeds in both latrines and random sites, but more often in the former (up to 66%),

(2) In latrines, howlers deposited more seeds of more species than in random sites, but at both fragments seed densities are similar between defaecation sites,

(3) Deposition sites displayed a spatially-clumped distribution and this patchiness was associated not only to sleeping zones, but to latrines located outside dormitories.

• The fate of seeds delivered in howlers’ multi-species seed shadows varied greatly and were related to seed species at all sites and to seed density at Km41. After nearly one year, seedling survival was higher at Km41 and Co 12-ha (ca 50%) and lower at Co 2.5-ha (26%). Despite these differences, howlers seem to contribute to the forest regeneration at the continuous forest and at the two forest fragments.
CHAPTER 8
CONCLUDING DISCUSSION

8.1 OVERVIEW

Amazonian rainforests constitute the largest area of tropical forest remaining on earth, but, like other tropical forests, they are seriously affected by deforestation. The accelerating pace of land-use change in recent decades is transforming Amazonian forests into a fragmented landscape dominated by human activities (Gascon et al. 2001; Figure 8.1). As a result, many wildlife species, including Amazonian primates, are being forced to live in forest fragments. Yet, not all primate species can cope and adjust to the environmental changes occurring in the forest fragments. Furthermore, as many primate species disperse seeds for many of their fruit plants, their absence from fragments may disrupt dispersal services that in turn would alter forest regeneration. In many regions where deforestation has removed the majority of the forest cover, the protection, management and restoration of remaining forest fragments are essential to the long-term conservation of biodiversity. It is necessary to conserve forest remnants with on-going ecological processes, such as seed dispersal. In order to make conservation recommendations, baseline information on how animals respond and adjust in disturbed habitats is required.

Information has been provided on the ecological responses of red howler monkey to home range reduction and the subsequent effects on their seed dispersal role in central Amazonia. Among Neotropical primates, howler species (Alouatta spp.) have been widely studied, and Alouatta seniculus, the species of this study is not an exception. Compared to other medium-sized primates, howler monkeys are extremely tolerant of habitat fragmentation, because of their ability to consume leaves, to have a flexible home range size, and to live in small groups (Rylands and Keuroghlian 1988). Despite their behavioural plasticity and the role they may play in forest regeneration in remnants, howlers’ responses to forest reduction are poorly documented in the central Brazilian Amazon. As howlers’ habitat in this region becomes more and more fragmented, it is important to identify the boundaries of their behavioural flexibility (Estrada et al. 1999a).
In this study, habitat fragmentation significantly diminished howlers’ home range, from about 20 ha in the continuous forest (Km41) to 7.2 ha in the medium fragment (Co 12-ha) and to 2.5 ha in the small fragment (Co 2.5-ha). In spite of this, howler group size was not affected, maintaining between 5 to 6 individuals/group. The effect of home range reduction was assessed, firstly, in terms of the changes on the behavioural ecology of howlers living in the small fragment (Group 1, Co 2.5-ha) and in the medium fragment (Group 2, Co 12-ha) and, secondly, how these changes modified their defaecation patterns and thus influenced their role as seed dispersers.

A more drastic reduction in the home range of Group 1 resulted in low fruit availability and in a net decline in food plants, affecting diet and time allocation decisions. Overall, Group 1 ate more flowers, left the fragment temporarily to obtain fruit from an adjacent continuous forest, rested more and fed less, in comparison to Group 2. Despite these differences, both howler groups ate more fruit and less leaves during the fruiting season (January-May), and switched to a mainly folivorous diet during the rest of the year.

Although the reduction of howlers’ home range decreases the number of species and seeds dispersed, howlers were effective dispersers for many species they consumed at the three study sites. In fragments, up to 77% of small to large seeds of fruit species exploited by Groups 1 and 2 were dispersed by endozoochory, and howlers’ gut treatment, lasting about 20 hours, had a positive or neutral effect on germination success. Despite that, Group 1 deposited seeds at shorter distances from fruit sources than Group 2, and up to 93% of seeds were moved away from the parental crown by both groups.

Howlers are generally regarded as low-quality dispersers, because they produce large faecal clumps with high seed aggregation. This defaecation pattern is considered disadvantageous, because, similar to seeds that fall under the parental tree, dispersed seeds may suffer high seed and seedling mortality (Andresen 2000). Yet, in this study, howlers did not always deliver seeds in this way. Five main points emerged in terms of defaecation patterns, which emphasize that the view of categorising a species as a “good or bad” disperser is misguided:

1. Howlers defaecated mainly in synchrony (ca 80%, group defaecations), but also separately (individual defaecations),
(2) In both defaecation types, howlers dispersed seeds in latrines and random sites in the forest, but more often in the former (up to 66%),

(3) Seed deposition displayed a spatially-clumped distribution and this patchiness was associated not only to sleeping areas but to latrines located outside them.

(4) In latrines, howlers deposited more seeds of more species than in random sites, but at both fragments seed densities were similar between defaecation sites.

(5) The fate of seeds delivered in howlers’ multi-species seed depositions varied greatly, according to seed species at all sites and to seed-density at Km41. Nonetheless, after nearly one year, seedlings survived at about 50% in the continuous forest and the medium fragment and 26% in the small fragment.

8.2 LIMITATIONS OF THIS STUDY

My study had some limitations that were mainly related to the sampling design. Habituation and systematic observation of long-lived primate species are always difficult and time consuming. Consequently, studies researching long-lived organisms cannot use replicas in the same way as studies working on smaller, shorter and/or sessile organisms. The lack of replicas on my study design reflects these logistical difficulties. In addition, funding was limited because howler monkeys have been widely studied and, in particular, *Alouatta seniculus* is not an endangered species. As a result, fewer howler groups could be followed and observed than the four groups previously planned. Consequently, my discussions and conclusions on feeding behaviour, use of space and activity budgets in fragments are based mainly on the two focal groups and in this sense, they may be restricted. Yet, primates’ responses to forest reduction depend not only on species-specific traits, but also on the local environmental conditions which are found in fragments. Thus, my research represents a study case in which particular fragmentation conditions are occurring, and the responses of howlers are evaluated in this context.

The responses of howler monkeys to habitat fragmentation as well as their impact on forest integrity can be assessed through different study designs. In my study, I planned to compare howlers living in the two fragments (Co 2.5-ha and Co 12-ha) with howlers living in the control site (Km41). The unexpected disappearance of the howler group
previously observed in 1998 in Km41 (Santamaría and Rylands 2003) and then the impossibility of habituating a new group, resulted in a lack of a howler control group. When possible, however, results obtained for the howlers in fragments were compared with information recorded in 1998 (Santamaría and Rylands 2003) and with other howler studies conducted in undisturbed forests of the Amazonian basin (e.g. Julliot 1992).

A different and ideal approach to understanding the relationship between howlers and forest fragmentation, to the one used in this study, would be a comparison between forest fragments with and without howlers. In this way, a macro approach would be achieved compared to the more micro approach that I used. Such an ideal scenario, however, is difficult to find. For instance, Marsh and Loiselle (2003) studied the relative recruitment of fruiting trees dispersed by howlers in Belize, comparing six fragments inhabited by howlers with only one fragment without them, since they could not find empty fragments. Moreover, variables such as fragment size, topography, plant composition among others, should be ideally controlled, but this is not always possible.

8.3 IMPLICATIONS FOR CONSERVATION

This study was conducted in a particular fragmentation scenario. The BDFFP is an experimental project and therefore has many research advantages. Firstly, and most importantly, pre-fragmentation censuses for many species of plants and animals were undertaken. Secondly, the project has been able to control several and often confounding variables: such as the patch shape and human intervention (e.g. hunting). Hence, the effects of fragmentation on howler behaviour and diet, without the frequently-added problems of hunting, can be discerned. Although my results may be conservative compared to unmanaged fragmented landscapes, such as Brazilian Atlantic forests where fragmentation is older, more extensive and where many anthropogenic factors are in play, the findings of my study have several implications for the conservation of howlers in a fragmented landscape:

(1) Close adjacent forests assist howlers’ movements in inhabiting fragments. Howlers do cope with the loss of forest area. Yet, while Group 2 residing in the medium fragment is well adjusted to a less-disturbed habitat and behaves similar to howlers living
in continuous forests, Group 1 inhabiting the small fragment lives in a more demanding environment and is presumably at its limits of flexibility. Its persistence in the fragment would be compromised, if the continuous forest was not so close and the howlers could not have the possibility to temporally expand their foraging area. This is supported by the repeated travels that Group 1 made to obtain fruit from the adjacent continuous forest. In contrast, Group 2 never travelled to the adjacent forest, but an adult male left the group and seemed to have abandoned the fragment. Howlers’ dispersal ability through open areas is reported to be limited to distances of about 200 m (Estrada et al. 2002). Moreover, the absence of Alouatta palliata groups in forest remnants in Mexico was negatively correlated with the distance to the nearest forest (Estrada and Coates-Estrada 1996). Thus, short distances facilitate inter-fragment forest movements and, consequently, are important for the survival of howlers living in very small forest remnants, such as 2.5 ha.

(2) Forest corridors are necessary for howlers’ long-term survival. From a landscape perspective, the degree of isolation of forest fragments varies greatly according to the nature of the fragmentation process. Long distances are limiting howlers’ dispersal between patches and large forest areas. The creation and maintenance of forest corridors, such as live fences and windbreaks would enhance the dispersal opportunities of howlers by establishing and improving connectivity between fragments, and between fragments and continuous forests. In addition, both forest corridors and active management of the matrix would promote movement of seed dispersers, such as howlers.

Inter-fragment and forest movements are important to the long term-survival of howlers for several reasons. Firstly, genetic flux is promoted between individuals of the howler population, and thus helping to maintain viable populations in the long term. Secondly, howlers can re-colonise regenerating forest areas and/or forest patches, increasing their population size. In Costa Rica, for example, the population of Alouatta palliata expanded to a new protected area by a substantial increase in size via the formation of new groups, over a time period of 28 years (Fedigan and Jack 2001). Thirdly, pressures derived from area loss, such as food stress and parasitic infestation, may be alleviated, especially for howlers living in very small fragments that would be able to establish home ranges.
according to their requirements. As shown in this study, Group 2 is well adjusted to a home range of about 7 ha and shares the 12 ha fragment with another howler group. By contrast, Group 1 is struggling in a home range nearly one third the size of Group 2. Finally, the risks (e.g. predation or accident) associated with crossing opening areas are diminished. In Mexico, groups of *Alouatta palliata* moved more frequently across riparian forest strips than through open areas (Estrada and Coates-Estrada 1996). A red howler male was killed by a car when crossing the main highway of the State (BR 174) of 50-80 m in width, which links the city of Manaus to Venezuela in the north (F. Pinto, pers. comm.; Figure 8.2).

**Better small forest fragments with howlers, rather than without them.** Although home range reduction affected some seed dispersal components (e.g. number of species and seeds dispersed, and low seedling survival in Co 2.5-ha), howlers living in fragments were efficient seed dispersers for many fruit plants consumed that ranged from small to large-seeded species. More frugivorous primates such as spider monkeys have disappeared from the forest fragments that were studied here, but they are also absent in other small and medium fragments of the BDFFP (Gilbert and Setz 2001). Consequently, howlers appear to be the only fruit-eating arboreal mammal dispersing large-seeded species that persists in small forest fragments, and in this way, they may be reducing the risk of local extinction for some plant species. Thus, both howler groups are providing a crucial seed dispersal service that is contributing to the regeneration ability of forest remnants. From a conservation and restoration perspective, small forest remnants with howlers are a better choice than small fragments without them, because seed dispersal is not disrupted. Howlers should be considered as essential elements during management and restoration programmes of fragmented landscapes, especially composed of small fragments, given that they have several key attributes. Firstly, howlers have a remarkable flexibility to survive in extremely small fragments as shown in this study, and thus are reinforcing the conservation value of small forest fragments (Turner and Corlett 1996). Secondly, they are fruit-eaters of a large number of plant species and their diet includes a considerable proportion of fruit. In fact, howlers are “as frugivorous as possible and as folivorous as necessary” (Silver *et al.* 1998: 273). Finally, howlers appear to be the main
efficient seed disperser of many species in small and medium forest patches. In this study, Group 1 played an additional ecological service by enriching the small fragment with seeds coming from the continuous forest and thus promoting the genetic flux between adjacent areas.

In conclusion, an ideal conservation strategy for a fragmented landscape would include remnants with howlers and would establish vegetation corridors enhancing the inter-fragments and forest movements of this seed disperser. Howlers would rapidly colonise fragments empty of other howlers, and in this way, corridors would be promoting the genetic flux of howlers and of their food plants. This strategy would ensure that seed dispersal for a considerable number of fruit plants would be maintained and that trees would be effectively recruiting in the forest remnants.

Currently, red howler monkeys are usually ignored, because they are not an endangered species and because they are one of the most well-studied genera of Neotropical primate. Few research projects have focused, however, on their dispersal efficiency and in their interactions with fruit plants in forest fragments (but see Estrada et al. 1999b, Marsh and Loiselle 2003). Yet, the conservation value of red howler monkeys lies in their ecological seed-dispersal role. As pointed out by Andresen (2000), it is essential to conserve the diversity of ecological interactions and processes, rather than individual components (e.g. the plants or the animals), in order to avoid an “empty forest” (sensu Redford 1992).
Figure 8.1: Recent deforestation close to the city of Manaus (source: BDFFP).

Figure 8.2: Red howler monkey killed by a car when he was crossing the main highway that links Manaus and Venezuela (photo by: Marcos Amend©).
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