# ECOLOGIA COGNITIVA E FORRAGEAMENTO DE *Alouatta guariba clamitans* CABRERA, 1940: OS BUGIOS-RUIVOS POSSUEM MAPAS MENTAIS?

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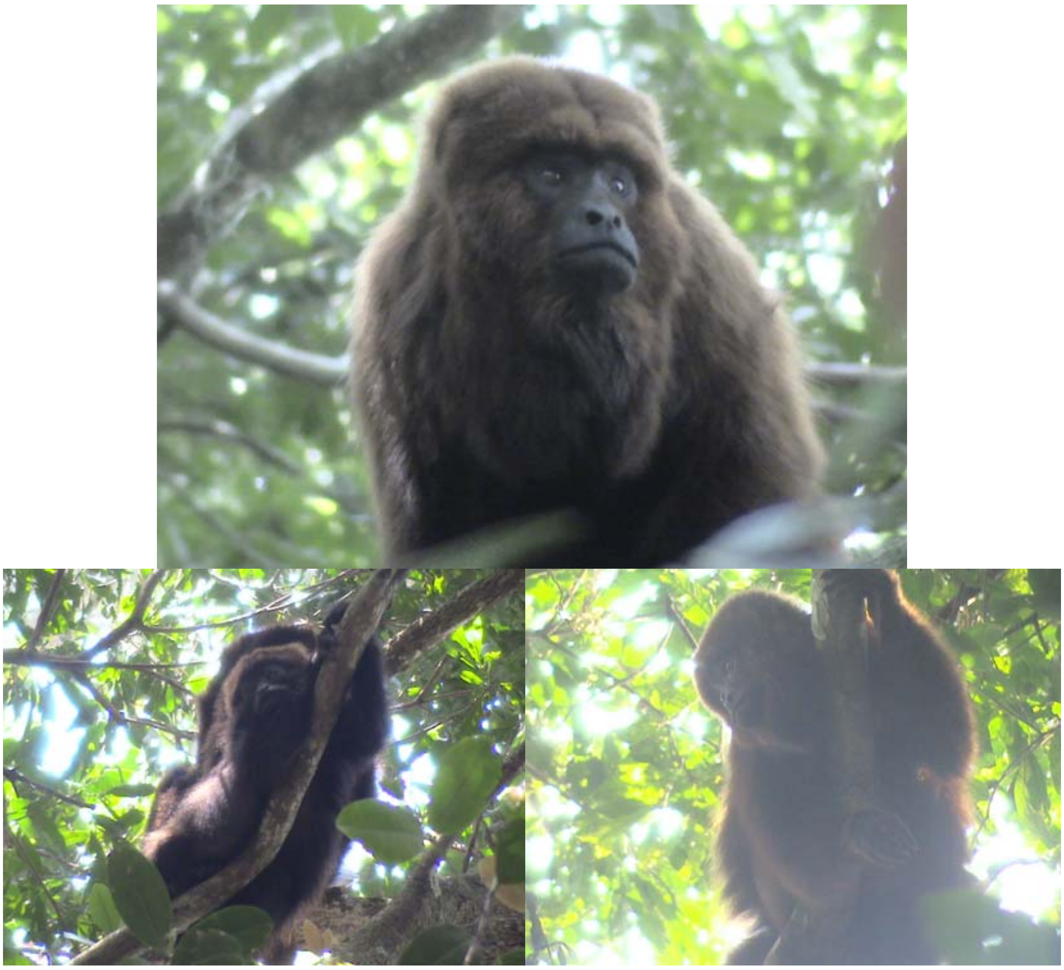
# SUMÁRIO



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# RESUMO

Este estudo teve como objetivo caracterizar os padrões de forrageamento de um grupo de bugios ruivos (Alouatta guariba clamitans), a fim de avaliar o uso de informações espaciais na localização de recursos alimentares em um fragmento de floresta de 5 ha em Barra do Ribeiro, RS, Brasil. O grupo de 6-7 indivíduos foi acompanhado durante 20 dias, os quais foram divididos em três períodos entre março e outubro de 2007. O comportamento focal do grupo foi estimado por tempo e todas as árvores utilizadas (n = 654) foram identificadas, medidas e mapeadas. A visibilidade das árvores mais utilizadas pelos bugios (n = 26) foi estimada e comparada com a de outras árvores menos visitadas (n = 77). O levantamentto fitossociologico identificou 54 espécies (n = 267) das quais 12, descritas como importantes recursos alimentares para os bugios, tiveram todos seus exemplares mapeados e medidos (n = 417). No padrão de atividades, os comportamentos descanso (57.6 ± 8.3%) e alimentação (17.1 ± 5.2%) predominaram e a dieta foi baseada em folhas (53.3 ± 15.2%; 35 spp.), frutos (34.3 ± 17.4%, 10 spp.) e flores (12.2 ± 12.3%; 15 spp.) (n =38 spp., 239 árvores). Em média 919 ± 256 m foram percorridos por dia em 81.6 ± 20.6 árvores de 26.9 ± 5.3 spp. A maioria das árvores foi utilizada em apenas 1 ou 2 dias, mas 67% das árvores utilizadas por dia já haviam sido visitadas previamente. O grupo concentrou suas atividades naquelas árvores maiores e de maior visibilidade. Conforme mais árvores de uma espécie eram visitadas, maior era o consumo desta, porém maior era a seletividade das árvores usadas para alimentação. Em 45% dos registros de alimentação foi utilizada a árvore mais próxima daquela espécie, apesar de em 78% haver uma árvore de alimentação de outra espécie mais próxima. Os segmentos de árvores utilizados foram concentrados em uma direção, principalmente devido ao uso das espécies de figueiras. Os bugios apresentaram estratégias de forrageio distintas nos períodos amostrados que confirmam nossas predições baseadas em estratégias de primatas frugívoros, apesar da alta folivoria do grupo. O grupo utilizou rotas de locomoção com árvores de grande visibilidade com nódulos de decisão. Tais rotas possibilitaram o monitoramento da disponibilidade de importantes fontes de frutos, principalmente de figueiras. A distancia percorrida foi minimiza com o uso de fontes próximas e o ganho energético foi maximizado pelo uso de árvores mais produtivas. Apesar de tais dados não permitirem inferir a presença de mapas mentais em bugios, eles demonstram que o grupo observado fez uso de informações espaciais do meio para otimizar o seu forrageio, inclusive em períodos de baixa disponibilidade de frutos.

# ABSTRACT

This study aimed to characterize the foraging patterns of a brown howler monkey group (Alouatta guariba clamitans), evaluating the use of spatial information during resource feeding use in a 5 ha forest fragment located in Barra do Ribeiro, RS, Brazil. The group was composed by 6-7 individuals and was observed over 20 days distributed in three periods between March and October/2007. The behavioral method was used to estimate the time spent in each behavior. All trees visited by the group (n = 654) were identified, measured and mapped. The visibility of the most used trees (n = 26) was estimated and compared with other less frequently used trees (n = 77). The phytosociological survey identified 54 plant species (n = 267) of which 12, described as important feeding sources for howlers, had all their trees mapped and measured (n = 417). Their activity budget was based on resting (57.6 ± 8.3%) and feeding (17.1 ± 5.2%) and their diet was composed by leaves (53.3 ± 15.2%; 35 spp.), fruits (34.3 ± 17.4%, 10 spp.) and flowers (12.2 ± 12.3%; 15 spp.) (n =38 spp., 239 trees). The mean day range was 919 ± 256 m in which they used a mean of 81.6 ± 20.6 trees and 26.9 ± 5.3 species each day. Most of the trees were used for only 1 or 2 days, however 67% of the trees used daily had already been used at a previous sampling day. The group concentrated their activities on large high visibility trees. The greater the visitation percentage within specific tree species, the higher the consumption rate and greater was the selectivity within these species' trees used for feeding. The closest feeding source of a given species was used in 45% of the feeding bouts, however in 78% of the feeding records there was non-used feeding tree closer than the one used. Besides, the overall route segments were aligned in a specific direction, due, especially, the use fig species. Throughout the study, the group presented foraging strategies that corroborate with our predictions that were made based on evidence gathered that indicate spatial knowledge in frugivorous primates, even with the high degree of folivory observed. They used traveling routes that include high visibility trees as decision nodes. These routes enhanced the monitoring of fruits availability, particularly within fig species. The distance travel was minimized by using closer feeding sources and energetic gain was maximized by using the most productive trees. Although we can't infer that howler monkeys have mental maps based on this data, they do show that our group used spatial information of the environment to optimize foraging, even during lean periods.

# INTRODUÇÃO GERAL

## Cognição Animal

Desde a década de 60, o estudo do comportamento animal sofreu profundas alterações relacionadas à sua abordagem e pressupostos. A visão de que o comportamento dos animais resulta de processos simples que agem relacionando estímulos pontuais a respostas comportamentais específicas, predominante desde Lorenz (1941 *apud* Kamil 1998), foi, gradualmente, substituída por uma abordagem em que o desenvolvimento cognitivo de cada espécie está intimamente relacionado às respostas comportamentais observadas (Kamil 1998). Tal "revolução cognitiva", como Balda et al.(1998, p. vii) tratam, resulta do desenvolvimento simultâneo em diferentes áreas de estudo do comportamento animal, desde a psicologia à ecologia comportamental, de estudos nos quais o comportamento é abordado como reflexo do desenvolvimento cognitivo de cada espécie.

Apesar de historicamente terem se desenvolvido independentemente, os campos da etologia e da psicologia animal tem cada vez mais se aproximado no sentido de reconhecer as implicações e influências da evolução e ecologia no comportamento (Shettleworth 1998). Diversas linhas de estudo foram propostas neste sentido, podendo-se citar a etologia cognitiva (Griffin 1978), a ecologia cognitiva (Dukas 1998, Real 1994), a psicologia evolucionista (Daly & Wilson 1999) e a cognição comparada (Wasserman 1993). Independente das diferenças destes campos de estudo (ver Dukas 1998, Kamil 1998, Shettleworth 1998), o processamento de informações e a tomada de decisões em animais passaram a ser tratados como produto da evolução das espécies, sendo, assim, passíveis de processos de seleção.

Se considerado que a origem de novas estruturas morfológicas no curso da evolução das espécies tem relação causal em alterações comportamentais (Futuyama

1986) e que muitos dos comportamentos, então fixados, necessitam de subsídio de processos cognitivos para ocorrerem, logo, as características morfológicas e comportamentais observadas hoje estão intrinsecamente correlacionadas ao desenvolvimento cognitivo característico em cada espécies. Por cognição entendem-se todos os mecanismos pelos quais os animas adquirem, processam, armazenam e aplicam as informações do meio (Shettleworth 1998), como a percepção, aprendizagem, memória e tomada de decisões.

Grande parte dos estudos que investigaram as interpretações e representações que os animais fazem do meio abordaram as características do uso de tempo e espaço (ver para revisão Healy & Braithwaite 2000) e, como conseqüência das profundas e evidentes relações que o último tem com a aptidão das espécies, este tem sido mais extensiva e intensivamente estudado.

Desde a dispersão, migração, territorialidade e relações com predadores até a procura de parceiros sexuais, seleção de locais para nidificação, armazenamento de alimentos e forrageio, diferentes atividades requerem a movimentação precisa no espaço e influem diretamente na adequação de uma espécie a um nicho (Sherry 1998).

Em 1978, O'Keefe & Nadel propuseram que uma estrutura ancestral no encéfalo de vertebrados, o hipocampo, tem marcante função no processamento de informações relacionadas à orientação espacial, propondo ainda a existência de mapas cognitivos que seriam representações do meio conforme a percepção de cada espécie. Apesar da existência de mapas cognitivos ser considerada controversa por alguns (ver Bennett 1996), diversas evidências, de fato, apontam para um importante papel do hipocampo na orientação espacial de alguns vertebrados. Estudos feitos com aves (Krebs et al.1989, Sherry et al.1989) e roedores (Jacob et al. 1990) indicam uma correlação positiva entre o tamanho do hipocampo e os comportamentos que necessitam de memória espacial. Entretanto, até então não foram encontradas diferenças e variações no tamanho relativo do hipocampo nas diferentes espécies primatas (Barton 2000). Porém, se os comportamentos espaciais necessitam de substrato cognitivo para ocorrerem, que evidências existiriam em primatas que apontariam para um maior desenvolvimento cognitivo selecionado por pressões ambientais?

Após Jerison (1973 *apud* Barton 2000) propor a idéia da "encefalização", em que a massa cerebral é relacionada à massa corpórea, diversos estudos apontaram para o maior tamanho relativo do cérebro dos primatas comparado a outros vertebrados (Harvey & Krebs 1990). Estudos posteriores indicaram que, em análise mais refinada, o grande tamanho relativo do cérebro de primatas se dá devido a um tamanho diferencial do neocórtex (Dunbar 1992, Barton 1994), que representa até 60% do volume cerebral em primatas não humanos (Barton 2000). Esta estrutura está relacionada às funções sensoriais, locomotoras e inclui o sistema límbico responsável, entre outros, pela aprendizagem e memória espacial, tendo em vista o hipocampo que o compõe (Krebs et al. 1989).

Com o objetivo de identificar possíveis causas de tal volume cerebral relativo, diferentes autores realizaram estudos comparativos das estruturas cerebrais de primatas com diferentes características de vida observadas (ver Barton 2000). Entre estes, Clutton-Brock & Harvey (1980) e Harvey & Krebs (1990), ao relacionar a massa cerebral à dieta de primatas, encontraram uma correlação positiva entre encefalização e frugivoria. A partir disso, maiores índices de encefalização de frugívoros, quando comparados a folívoros, foram apontados como evidência de um maior desenvolvimento cognitivo de primatas de hábito frugívoro. Tal hipótese se baseia em uma suposta maior dependência do uso de memória espacial para o forrageio de frugívoros, uma vez que frutos estão dispersamente localizados no tempo e espaço enquanto folhas são mais uniformemente distribuídas (Milton 1981a, 1988).

A partir do momento que a folivoria teria co-evoluído com menores requerimentos cognitivos para localização espacial (Clutton-Brock & Harvey 1980, Harvey & Krebs 1990), tendo em vista o alto gasto energético associado aos processos neurais (Armstrong 1983, Martin 1981), a baixa oferta energética das folhas quando comparadas aos frutos e flores (Milton 1980, 1981a) e as teorias de adequação energética ao nicho ocupado (Rosenberger 1992, Rosenberger & Strier 1989), Milton (1981a, 1988, 2000) propôs que primatas folívoros utilizariam estratégias de forrageio baseadas no monitoramento de algumas poucas fontes alimentares principais para construir sua dieta, e não, necessariamente, fariam uso para seu deslocamento ou, sequer, possuiriam representais mentais do espaço. Entretanto se, de fato, tal hipótese for válida, porque não seriam evidenciadas especializações nas estruturas cognitivas relacionadas à orientação espacial, como o hipocampo, nas espécies de primatas que ocupam nichos ecológicos distintos, como apontado por Kappeler (2000)? Será que, de fato, primatas com hábitos alimentares diferentes têm desenvolvimento cognitivo correlato a este devido ao uso diferencial do espaço ou as diferenças nas características neocorticais observada em haplorrhinos – társios, macacos, grandes símios e homem – se devem, acima de tudo, à especialização de estruturas visuais, como apóia Barton (2000)? Segundo este autor, o reconhecimento e a comunicação visual intraespecífica (Brothers 1990), seriam as principais forças seletivas atuantes no aumento do tamanho relativo do neocórtex, e conseqüentemente, do cérebro dos primatas.

Se assim for e o menor tamanho relativo do cérebro de folívoros não tiver relação com sua orientação espacial, será que primatas folívoros usam o espaço de forma a aumentar sua aptidão conforme a variação temporal, espacial e a disponibilidade de recursos, como proposto para frugívoros (Milton 1981a, 1988)? Apesar de folhas serem uniformemente dispersar no espaço, pode-se dizer que a composição nutricional varia nas diferentes partes vegetais e espécies (Garber 1987), que, por sua vez, têm disponibilidade e localização variáveis. Será que uma composição nutritiva da dieta diversa tem reflexo no uso do espaço por primatas folívoros?

Schoener (1971) propõe que a eficiência do forrageio é maximizada por seleção natural. A partir disso, um forrageio que maximize o aporte de energia com o menor gasto em deslocamento combinado a uma diversificação nutricional é esperado, se considerado que os comportamentos de deslocamento caracterizados nos táxons terminais tendem a se aproximar de um forrageio ótimo.

## Orientação espacial

De forma a se locomover eficientemente no espaço, os animais, incluindo o homem, utilizam características externas provenientes do meio e representações internas que compreendem a forma como estas informações são integradas cognitivamente (Garber 2000). Com estudos sobre a orientação espacial em distintos animais, diferentes variáveis do meio que influenciam no deslocamento espacial foram identificadas e suas relações com a aprendizagem, estabelecidas.

Apesar de a aprendizagem ser, usualmente, considerada benéfica por possibilitar ajustes comportamentais conforme a situação, essa pode se mostrar desvantajosa em condições em que as características do meio variam muito lentamente em relação à duração das gerações de determinada espécie (Dyer 1998). Se uma condição ambiental, por exemplo, se modifica pouco ao longo do tempo, as respostas comportamentais a tal situação tenderiam a ser similares para as diferentes gerações de uma espécie. Nesse cenário, a aprendizagem individual destas respostas não representaria uma característica benéfica à aptidão da espécie, uma vez que diferentes soluções comportamentais associadas à aprendizagem representariam um aumento na probabilidade dos animais não se adequarem às condições do meio ou o fazerem de forma sub-ótima. A partir disso, pode-se dizer que respostas independentes de experiência prévia, ou comportamentos inatos, tenderiam a ser selecionadas em condições ambientais relativamente estáticas (Dukas 1998).

Do ponto de vista da movimentação espacial, características como o campo magnético da Terra, utilizado como referência espacial por aves migratórias (Wiltschko & Wiltschko 1996), pingüins (Walcott & Green 1974 *apud* Balda et al. 1998) e abelhas (Collet & Baron 1994), e a posição dos corpos celestes, de uso descrito para aves de migração noturna (Able & Able 1996, Wiltschko & Wiltschko 1991 *apud* Dyer 1998), podem ser citados como exemplos de condições do meio relativamente estáticas no tempo e que são utilizadas para orientação espacial em comportamentos inatos.

Já em condições ambientais de curta previsibilidade, a aprendizagem de estratégias comportamentais que possibilitem rápida adaptação a tais condições seria benéfica. Nesse sentido, a identificação e associação de características fixas em um ambiente em constante mutação à recompensas alimentares, por exemplo, deveria ser uma estratégia selecionada. E, de fato, o uso de marcos referenciais (*landmarks*), que são objetos ou superfícies fixas utilizados como referência na identificação de um local no espaço (Sherry 1998), é amplamente descrito tanto em vertebrados quanto em invertebrados (ver Dyer 1998, Potí et al. 2005). Tais marcos referenciais são, em geral, detectados visualmente pelo animal, mas também podem ser detectados por outros sentidos, tais como o olfato, conforme as características da espécie (ver Bicca-Marques 2000, Garber 2000).

Entretanto, nem sempre existem características do ambiente que podem ser reconhecidas para orientação. Em tais situações, estudos controlados em laboratório demonstraram que, ainda assim, os animais têm capacidade de se orientarem espacialmente a partir de representações internas do meio (ver Cheng & Newcombe 2005). Tal orientação pode ocorrer a partir de um ponto de vista egocêntrico, no qual um sistema de coordenadas é estabelecido com referência ao corpo do animal, e a partir de um referencial geocêntrico, em que a referência é um ponto fixo no espaço (Gallistel & Cramer 1996).

A partir disso, diferentes representações cognitivas do meio foram propostas. Em uma delas, a representação interna do espaço se dá, a partir de coordenadas egocêntricas e geocêntricas, de forma geométrica, onde a disposição geométrica de características do espaço é utilizada para localização de um ponto (Cheng 1986 *apud* Cheng & Newcombe 2005). Nessa representação, os marcos referenciais são utilizados para o referenciamento espacial, sendo que a relação entre eles possibilita a orientação no espaço. Descrita em distintas espécies, principalmente em estudos controlados em laboratório (ver Cheng & Newcombe 2005), esta representação é limitada a situações em que o animal tem prévio conhecimento dos pontos referenciais no ambiente.

Já em outra representação proposta, tal conhecimento prévio do meio não é pré-requisito para orientação. A *path integration* ou *dead reckoning* considera que o espaço é representado por sucessivas atualizações da localização do animal com relação à direção e distância da movimentação a partir de um ponto de partida, ou seja, de uma coordenada geocentrada (Etienne & Jeffery 2004, Gallistel 1990, Poucet 1993). Este processo é amplamente descrito para vertebrados e invertebrados (ver Dyer 1998, Ettiene et al.1996, Etienne & Jeffery 2004, Poucet 1993,) e pode ser usado tanto durante a navegação por ambientes desconhecidos, como na movimentação por locais familiares

(Etienne & Jeffery 2004). Além disso, sua atualização é tida como automática e constante durante a movimentação (Gallistel & Cramer 1996).

A partir do conceito de *path integration*, Gallistel (1989) propôs que a combinação da orientação obtida por pontos geocentrados e o uso de marcos referenciais do meio resulta em mapas cognitivos de representação do espaço. Anteriormente, o conceito de mapas cognitivos havia sido proposto por Toolman, em 1948, e estendido por O'Kneefe & Nadel, em 1978, como a capacidade de representar o espaço de forma a navegar por pontos conhecidos utilizando caminhos desconhecidos e inferidos pelo mapa (novos atalhos). Entretanto, como já citado, este conceito é muito controverso por explicar comportamentos que podem ter explicações mais simples baseadas em outros conceitos, a ponto de Bennet (1996) desaconselhar seu uso. Muitos autores, apesar disso, consideram que diferentes espécies possuem mapas cognitivos (ver Poucet 1993).

## Movimentação espacial em primatas

Estudos de orientação espacial em primatas foram, experimentalmente, desenvolvidos tanto em laboratório (Andrews 1988, Cramer & Gallistel 1997, Gallistel & Cramer 1996, Hemmi & Menzel 1995, Menzel 1991, Menzel Jr. 1973, 1996, Menzel & Juno 1982, 1985), quanto em campo (Bicca-Marques 2005, 2006, Bicca-Marques & Garber 2003, 2004, Di Bitetti & Janson 2001, Garber & Dolins 1996, Garber & Paciulli 1997, Janson 1996, 1998, Janson & Di Bitetti 1997). Enquanto a primeira abordagem tem como vantagem o controle sistemático das variáveis que podem influenciar no comportamento, a outra possibilita a averiguação do uso das informações disponíveis ao animal em seu ambiente natural, além de permitir a determinação da organização hierárquica destas informações durante o forrageio (Garber 2000). Condições artificiais de estudos em laboratório, ademais, não refletem, necessariamente, comportamentos selecionados naturalmente e desconsideram influências sociais durante a movimentação espacial (King & Fobes 1982).

Apesar da grande contribuição de abordagens experimentais, entretanto, estudos naturalísticos descritivos da utilização do espaço por primatas foram historicamente mais utilizados, respondendo por grande parte do conhecimento acumulado sobre a movimentação espacial destes animais (p.e. Milton 1980, 1981, Sigg & Stolba 1981, Terborgh 1983, Boesch & Boesch 1984, Estrada & Coates-Estrada 1984, Chapman 1988, Chapman et al. 1989, Garber 1988, 1989, Norconk & Kinsey 1994, Ostro et al. 1999, Pochron 2001, Ramos-Fernández et al. 2004, Janmaat et al. 2006, Cunningham and Janson 2007, Di Fiore and Suarez 2007, Valero and Byrne 2007).

Em geral, os primatas tendem a deslocar-se em linha reta durante o forrageio utilizando fontes alimentares previamente já visitadas. Garber (2000) considera que este padrão comportamental é remanescente do *traplinig*, observado em insetos, pássaros e outros mamíferos. Este conceito descreve um padrão de forrageamento em que o animal tem conhecimento da localização das fontes alimentares e visita estas minimizando a distancia percorrida, sem, entretanto, re-visitar fontes já inspecionadas à uma curto intervalo de tempo (Thomson et al.1997). Janson (1998), da mesma forma, observou tal padrão no deslocamento em *Cebus apella nigritus* e o comparou ao padrão de “inércia” definido por Cody (1971 *apud* Janson 1998) para pássaros, considerando-o, entretanto, como uma fraca evidência do uso de memória espacial.

Outros estudos evidenciam que, durante o forrageio, os primatas fazem uso de uma série de regras e estratégias que tendem a maximizar o retorno energético líquido da alimentação. Tal forrageio baseado em regras (*rule-guided*) (Menzel 1996) consiste na habilidade de utilizar informações de eventos de alimentação passados na resolução de problemas presentes de aquisição de alimento, de forma a gerar soluções efetivas sem a necessidade de re-aprender relações de causa e efeito a cada nova situação (Garber 2000). Como a disponibilidade de recursos no meio varia temporal e espacialmente, saber quando e onde utilizar uma determinada fonte de alimento ou seguir para outra área previamente visitada tende a aumentar a eficiência do forrageio ao minimizar o tempo e a energia gastos em deslocamento aleatório (Gallistel 1989).

A efetividade da regra utilizada varia conforme a fenologia e a taxa de renovação da fonte de alimento, assim como com o número de indivíduos e grupos explorando o recurso simultaneamente (Bicca-Marques 2000). Fobes & King (1982) descreveram nove possíveis regras ou estratégias de forrageio que poderiam ser utilizadas na resolução de problemas relacionados à tomada de decisões em experimentos de laboratório com *Macaca mulatta*. Destas, pode-se dizer que *win-stay/lose-shift*, *win-shift/lose-stay* e *lose-return* são aquelas de uso mais recorrente por primatas (ver Menzel & Juno 1982, 1985, Andrews 1988, Garber & Dolins 1996, Bicca-Marques 2005). É importante ressaltar que as características das árvores utilizadas por primatas para alimentação influenciam diretamente nas regras de forrageio adotadas (Garber 1989).

Entretanto, primatas tendem a avaliar não apenas informações ecológicas para a decisão das regras de forrageio a serem utilizadas, mas também sociais (Bicca-Marques 2005). Assim como outros animais sociais (ver Galef & Giraldeau 2001 para uma revisão), o forrageio de primatas que vivem em grupos é baseado tanto em informações públicas, que são aquelas obtidas pelo monitoramento dos padrões de forrageio, alimentação, vocalização e outras formas de comunicação intraespecíficas, quanto em informações privadas, as quais respondem ao conhecimento individual gerado e acumulado (Garber 2000).

Em grupos que forrageiam de forma coesa a informação pública e privada tende a ser muito similar (Boinski 2000). Já em primatas que utilizam recursos espacialmente dispersos e que se deslocam por grandes distâncias, muitas vezes distribuídos em subgrupos, o acesso às informações do meio é distinto entre os indivíduos e o sucesso do forrageio pode ser diferencial (ver Chapman et al.1989, Symington 1988, Janson & Di Bitetti 2001).

## Gênero *Alouatta* Lacépède, 1799

*Alouatta* é o gênero mais amplamente distribuído de primatas Neotropicais e, talvez como conseqüência, seja o gênero mais estudado destes (Crockett e Eisenberg 1987, Neville et al. 1988). Da península Yucatán no México, a 20°N, à cidade de Canta Galo no Estado do Rio Grande do Sul, Brasil, a 31°S, o gênero é encontrado em toda extensão latitudinal (Printes et al. 2001). São encontrados em uma grande variedade de ambientes, desde o nível do mar até 3200 metros de altitude (Crockett 1998). É característica marcante do gênero a habilidade de sobreviver em ecossistemas intactos ou antropogenicamente alterado, como fragmentos florestais de poucos hectares associados à agricultura e pecuária (ver Bicca-Marques 2003 para revisão).

Popularmente conhecidos como bugios, barbados, guaribas, roncadores ou “howler monkeys” em inglês e “monos aulladores” em espanhol, os animais do gênero recebem diversa denominação em sua extensa distribuição.

Das características morfológicas marcantes do grupo, destaca-se a presença de um osso hióide hipertrofiado, formando uma câmara de ressonância; mandíbula desenvolvida; dimorfismo sexual acentuada dos caninos; achatamento da caixa craniana, principalmente nos machos e; grande alongamento do terceiro molar inferior comparado aos demais gêneros de Atelidae (Gregorin 2006), o que, segundo Degusta et al. (2003) em estudo com *A. palliata*, representaria uma característica selecionada para folivoria. Todas as espécies do gênero, como também observado nas demais espécies de Atelidae, apresentam cauda preênsil com terço inferior distal nu, agindo como um quinto membro (Neville et al. 1988). Em indivíduos adultos, é característico o dimorfismo sexual no peso e tamanho, sendo que, em *A. caraya* e *A. guariba clamitans*, também ocorre o dicromatismo sexual (Neville et al., 1988). Hirano (2004) atribuiu o dicromatismo em *A.guariba clamitans* à existência de uma glândula sudorípara modificada que produz pigmento vermelho.

É característica a organização social no gênero em grupos que tem composição entre 2 e 23 indivíduos, com média de 10,7 animais por grupo, sendo que a variação deste número ocorre tanto dentro da mesma espécie como entre as diferentes espécies, tendo relações com as características do habitat ocupado (Chapman & Balcomb 1998, Crockett 1998). A proporção entre machos e fêmeas por grupo varia de 1:0,71 a 1:4,11 e entre fêmeas e imaturos de 1:0 a 1:1,18 (Chapman & Balcomb 1998). Formam grupos sociais compostos por um a poucos machos reprodutores não aparentados, duas a quatro fêmeas organizadas hierarquicamente e seus infantes (Clarke et al. 1998). Indivíduos de ambos os sexo migram (Zucker & Clarke 1998), sendo característico a organização social em torno de um macho dominante em populações de baixa densidade e multimachos com hierarquização etária em altas densidades (Ostro et al. 2001).

Em primatas neotropicais de grande porte, como é o caso do gênero *Alouatt*a, os comportamentos evoluíram de forma a suprir grandes necessidades energéticas (Rosenberger 1992). *Alouatta* é descrito como um gênero de primatas folívoro-frugívoro (Crockett & Eisenberg 1987), sendo a maior parte da sua dieta composta por folhas, itens pobres em carboidratos e ricos em proteínas de difícil digestão (Milton 1980, 1981). Além da baixa constituição energética das folhas, compostos secundários e a parede celular constituintes dificultam a digestão dos outros componentes foliares, acarretando em uma digestão lenta, retardada ainda mais por bactérias intestinais simbiontes (Milton 1998, 2000). Tendo em vista a dieta do mais folívoro primata neotropical (Eisenberg et al. 1972, Neville et al. 1988), diferentes autores propuseram hipóteses que possibilitassem a maximização do ganho enérgico, uma vez seu grande tamanho corporal.

Milton (1980) propôs que o baixo valor energético da dieta implica em comportamentos de baixo custo energético, exemplificados pelos grandes períodos de inatividade descritos para o gênero. Já Zunino (1986), complementa a idéia de Milton (1980) ao sugerir que esses animais empregam duas estratégias para maximização do aporte de energia. Em situações as quais a disponibilidade de energia é baixa, com poucos frutos e flores, ocorreria uma redução nos gastos energéticos, com longos períodos de inatividade e redução do tempo gasto em locomoção, sendo adotada uma estratégia de baixa recompensa - baixo custo. Em situações de grande disponibilidade de alimentos energeticamente ricos, entretanto, maiores deslocamentos seriam vantajosos ao possibilitar maior qualidade na dieta que supri os gastos energéticos envolvidos na locomoção, sendo adotado, assim, uma estratégia de alta recompensa - alto custo.

Tal hipótese é consistente com a correlação positiva observada entre a disponibilidade de frutos e a porcentagem de frugivoria na dieta, que está ainda relacionada a um aumento da área de uso em tais períodos (Milton 1980, Marsh 1999). Bicca-Marques (2003) aponta que o tamanho da área de uso é correlacionado positivamente com o tamanho do fragmento utilizado, porém não está relacionado ao tamanho do grupo e à distância diária percorrida, que é similar nas diferentes espécies e varia de 11 a 1564 metros (média de 497 metros). Por sua vez, a distância diária média percorrida está correlacionada positivamente ao número de espécies utilizados na dieta por dia, mas não tem relação com o tamanho do fragmento habitado (Bicca-Marques 2003). A partir disso e da grande sobreposição de área de diferentes grupos (Milton 1980), pode-se dizer que a disponibilidade de itens energeticamente ricos no meio e a relacionada qualidade da dieta dos bugios são os principais fatores limitantes na utilização do meio por estes animais, explicando sua grande adaptabilidade a áreas fragmentadas.

Foi observado que os bugios tendem a concentrar seu forrageio em agregados de algumas espécies preferenciais, com grande destaque para o gênero *Fícus* (Milton 1980), o que poderia estar relacionado a uma assincronia na produção de frutos entre os indivíduos e espécies do gênero (Milton 1991). A assincronia na disponibilidade de frutos de *Fícus* sp. (Milton 1991) e o cálculo de que a localização de árvores do gênero por bugios seria acima do esperado em um forrageio aleatório (Milton 2000), levaram a autora a concluir que estes animais adotam como estratégia de forrageio o monitoramento do estado fenológico de algumas poucas árvores em sua área de uso, sendo evidência disso, o uso de cerca de 50% da área de uso anual a cada cinco dias, em média (Milton 2000). Como já citado (ver item 1.1), tais dados são subsidio da hipótese que relaciona um menor tamanho relativo do cérebro de primatas folívoros a um menor requerimento para orientação espacial (Milton 1981a, 1988).

Porém, se tal estratégia de forrageio em bugios “descarta uma dependência de memória espacial de longo prazo” (Milton 2000, p. 391), como explicar o forrageio de populações que não baseiam sua alimentação em espécies frutíferas assincrônicas? Bicca-Marques (2003) evidencia que em 59% dos estudos revisados com o gênero, *Fícus* representou uma das duas principais fontes de alimentos. Porém, além de Julliot (1994) afirmar que tal preferência tem o viés da família Moraceae ser muito abundante em florestas secundárias, onde a maioria dos estudos com bugios foram realizados, a dieta no gênero é altamente adaptável à composição florestal disponível (Crockett & Eisenberg 1987, Crockett 1998, Bicca-Marques 2003, Silver & Marsh 2003), sendo, inclusive, descrito grande dependência em espécies exóticas (Bicca-Marques & Calegaro-Marques 1994). Será, então, que a grande adaptabilidade do gênero não poderia também estar relacionada a uma plasticidade no forrageio que garantisse a maximização do ganho energético em ambientes de grande heterogeneidade e em constante variação?

Para responder tais perguntas, baseado em evidencias de uso de informações espaciais em outros primatas, prevemos que um primata folivoro-frugivoro:

1) Realize movimentos retilíneos a mais próxima arvore disponível de algumas espécies importantes de alimentação, minimizando a distancia percorrida;

2) Monitore a disponibilidade de grandes fontes de frutos, principalmente figueiras, maximizando o ganho energético com a utilização de fontes mais produtivas;

3) Faça uso repetido de rotas de locomoção composta por árvores de grande porte, fonte de maiores quantidades de alimentos e que possibilitam grande visibilidade da sua área de uso, reduzindo a quantidade de informação armazenada para o forrageio;

4) Use árvores de grande visibilidade como nódulos ou pontos de decisão, onde diferentes rotas se cruzam, padrão característico de espécies que apresentam mapas mentais topológicos ou baseados em rotas (Byrne 1979, Poucet 1993).

Este estudo tem como objetivos principais caracterizar o padrão de atividade, o comportamento alimentar e o uso de espaço por um grupo de *Alouatta guariba clamitans* em um fragmento de mata no município de Barra do Ribeiro, RS, Brasil.

# Cognitive ecology and foraging of
# *Alouatta guariba clamitans* Cabrera, 1940:
# Do brown howler monkeys have mental maps?

# INTRODUCTION

Since the so called “cognitive revolution” (Balda et al. 1998, p.vii) that has gradually become more influential since the 1960´s and has developed into several research programs, such as cognitive ethology (Griffin 1978), cognitive ecology (Real 1994, Dukas 1998a), evolutionary psychology (Daly and Wilson 1999) and comparative cognition (Wasserman 1993), animal behavior has been studied as more than simple processes that related simple stimuli to specific behaviors (Lorenz 1981). Although an evolutionary origin of differentiation in mental function has been noted since Darwin (Richards 1987), it was not until Real’s view that “all organisms are information processors that may have undergone various degrees of evolutionary specialization for processing information in specific ways” (Real 1994, p.127) that studies focusing on cognitive traits of behavior started to be more intensively developed (reviewed in Healy and Braithwaite 2000). Most studies conducted since then, focusing on a better understanding of animals’ subjective representation of environmental patterns, investigated their use of space and the processes involved in decision-making (Healy and Jones 2002).

Behaviors that require accurate movements across space (such as dispersion, migration, territoriality, mate searching, nest site selection, predator avoidance, food storing and foraging) have direct influence on niche segregation and individual fitness (Sherry 1998). Therefore, they have been studied as ideal models for understanding how spatial knowledge is mentally integrated by animals.

Space can be internally represented through egocentric or geocentric, also known as allocentric, mechanisms. The use of egocentric mechanisms implies that the animal locates the environmental framework with respect to itself. *Path integration* or “*dead reckoning”*, in which the animal continually updates information on distance and direction of its current position to the goal, is an example of an egocentric mechanism (reviewed by Gallistel 1990; Wehner and Wehner 1990; Dyer 1994). On the other hand, geocentric mechanisms locate the animal with respect to some external frame of reference in the environment. Landmarks, as fixed features of the environment, are extensively studied as reference marks that can guide animals to a goal (Collett and Graham 2004), but other frames like the sun (Wehner et al. 1996), the earth’s magnetic field (Wiltschko and Wiltschko 1996) and other celestial cues (Muheim et al. 2006) are also known to be used as reference points in space.

Apart from the neural machinery background involved, similar spatial representations are found in distinct taxa. *Path integration*, for example, has been described for arthropods, such as ants, bees and spiders (Wehner 1992; Dyer 1994) and mammals (Ettienne et al. 1996; Ettienne and Jeffery 2004), including humans (Cornell and Heth 2004). Similarly, the use of landmarks has been documented in both vertebrates and invertebrates (see Blaisdell and Cook 2005), whereas the earth’s magnetic field and the sun compass are usually described for migratory species (Wiltschko and Wiltschko 1998). In fact, the use of different mechanisms simultaneously is usually described for the orientation of animals when reaching a goal (see Collet et al. 1992, Dyer 1994).

Although different mechanisms are known to guide foraging, it is commonly believed that animals have mental maps, also called cognitive maps, where the environment is represented in distance and direction vectors that can be mentally operated. This concept was first proposed by Toolman (1948) and its basic property was the ability to make novel shortcuts to a goal. O’Keefe and Nadel (1978) extended the concept to an allocentric, connected and unitary spatial representational framework in which experience locates objects and events, also highlighting the importance of novel shortcuts and proposing a differentiation between maps and routes, being the first not based on goals and allowing more flexible behaviors. On the other hand, Gallistel (1990) proposed a cognitive map to be a combination of geocentric representations of points and angles with egocentric representations of the environment, accepting almost every computation of direction and distance as evidence of a cognitive map.

Although a map, as a ‘view from above’, is a powerful metaphor for spatial knowledge, the different concepts and their interpretations, in addition to the simpler mechanisms that would explain the same patterns of spatial orientation attributed to cognitive maps, were considered by Bennet (1996) when suggesting the avoidance of the term. Besides, proving the existence of such a detailed representation would be extremely difficult since it would have to be demonstrated that the animal is choosing both efficient and novel travel routes (Janson 2000).

Even though different authors don’t support the concept of cognitive maps (Poucet 1993, Benhamou 1996, Bennet 1996), another proposition made by O’Keefe and Nadel (1978), that a cognitive module located in the hippocampus of vertebrates is related to spatial memory, has been, at least for some species, well established. The hippocampus of food-storing birds is as much as twice the size of this module in birds with comparable brain and body size that do not store food (Sherry et al. 1989, Krebs et al. 1989). In fact, hippocampal size correlates with the amount of food typically stored in food-storing corvid and parid species (Healy and Krebs 1992, Hampton et al. 1995, Basil et al. 1996), with age and migratory experience in passerine migrants (Healy et al. 1996) and is also larger in homing pigeons strains than in non-homing strains (Rehkämper et al. 1988). Although birds and mammals have evolved independently for at least 310 million years, Jacobs and Spencer (1994) demonstrated that a scatter hoarder kangaroo rat species has a larger hippocampus than a non-scatter hoarder and the hippocampal size is sex-related in polygamous vole species, since males, that have larger home ranges during the breeding season, have larger hippocampus than females, but not in monogamous vole species (Jacobs et al. 1990).

Even though there are clear evidences of hippocampal specialization, the hippocampus is a small brain structure and differences in hippocampus size are not related with differences in the overall brain size (Sherry et al. 1989). Primates, for example, that are usually considered to posses larger brains relative to other mammals (assumption based only on monkeys and apes, since strepsirhines are much smaller brained than haplorhines), show no correlation of ecological features and hippocampal size (Barton 2000). In fact, although primate's large brains show evidence of selection on specific regions, any mental structure or other proximate mechanisms has yet been identified to act specifically on primate's spatial orientation and have differentially evolved for it (Barton 2000).

Different selective pressures have already been proposed to explain primates' larger brain size relative to body size.  Particularly, the apparently 'great knowledge' of their area in frugivorous primate species with large home ranges was proposed to be an evidence of a selective trait that favored the enhancement of mental processing capacity, that would explain the large brain observed in those species (Mackinnon 1978, Milton 1981a, 1988, 2000, Taylor and van Schaik 2007). When comparing a large number of primate species, Clutton-Brock and Harvey (1980) found a positive correlation between brain size and both range area and degree of frugivory. Thus, detecting patchy and sparsely distributed resources, which availability varies in time and space with the complex seasonality of tropical forest would be a fair reason, according to these authors, for an increased memory dependence and, therefore, development.

Although different authors disagree that the spatial cognition explains why frugivores have larger brains than folivorous species (Byrne 1994, 1996, Barton 2000, Byrne and Bates 2007), most of the studies done specifically on primates' spatial ability in nature focused on mainly frugivores species (Japanese monkeys – Menzel 1991; mangabeys – Janmaat et al. 2006; saki monkeys – Cunningham and Janson 2007; saki and spider monkeys – Norconk and Kinsey 1994; spider monkeys – Milton 1981b, 1988, Chapman et al. 1989, Ramos-Fernández et al. 2004, Valero and Byrne 2007; titi monkeys – Bicca-Marques and Garber 2004, Bicca-Marques 2005; woolly and spider monkeys – Di Fiore and Suarez 2007), insectivores/gummivores (tamarins – Garber 1988, 1989, Garber and Dolins 1996, Menzel and Beck 2000, Bicca-Marques and Garber 2003, 2005, Bicca-Marques 2005, 2006, Bicca-Marques and Nunes 2007; tamarins and night monkeys – Bicca-Marques and Garber 2004) and omnivores (baboons – Sigg and Stolba 1981; Pochron 2001, Noser and Byrne 2006, 2007; capuchin monkeys – Janson 1996, Garber and Paciulli 1997, Janson and Di Bitetti 1997, Janson 1998, Garber and Brown 2006, Gomes 2006; chimpanzees: Boesch and Boesch 1984). Whether it is a consequence of the spatial cognition hypothesis or its conditioning characteristics (that is, primates with large home ranges and/or with dietary habits that are based on sparsely and patchily distributed ephemeral resources), the fact is that little knowledge has been gathered on folivorous primates' spatial abilities (Milton 1980, 1981b, Chapman 1988, Ostro et al. 1999, Garber and Jelinek 2006).

It is known that primates tend to forage on nearly direct or "straight-line" travel paths through previously visited food patches, what is considered to be reminiscent of *traplining*, a behavioral pattern also described for insects, birds and other mammals (Garber 2000). Janson (1998) describes it as an evidence of *inertia*, like in finch flocks

(Cody 1971 *apud* Janson 1998), rejecting the possibility of taking this as an evidence of spatial knowledge (Janson 1998, 2000, Janson and Byrne 2007). Since most primates live in social groups, the social environment, habits and the private/public information available for the group also play important roles on their foraging and group cohesion (Symington 1988, Chapman et al. 1989, Boinski 2000, Garber 2000, Bicca-Marques and Garber 2005). Besides, foraging rules, such as win-stay/lose-shift or win-shift/lose-stay, are extensively described to maximize primates' foraging success (Fobes and King 1982, Menzel and Juno 1982, 1985, Andrews 1988, Garber and Dolins 1996, Menzel 1996, Garber 2000, Bicca-Marques 2005, Bicca-Marques and Nunes 2007).

It is commonly considered that a primate aware of resource knowledge locations would increase its fitness by: 1) minimizing the distance traveled, moving to the closest available resource (Menzel 1973, Garber 1988, Janson 1998); 2) maximizing energy net gain by using the best available resources, avoiding low-productive resources nearby in favor of more distant but much more productive ones (Garber 1989, Janson 1998, Noser and Byrne 2006, Cunningham and Janson 2007, Valero and Byrne 2007); 3) increasing speed of movement when approaching target resources, considering this target to be more distant than the maximum distance where resource perception can occur (Janson 1998, Pochron 2001, Janmaat et al. 2006); 4) reducing memory load by the use of repeated travel pathways, in a way of remembering only a set of route segments that lead to many potential food sources, simplifying its monitoring, instead of remembering the location of hundreds of individual trees (Sigg and Stolba 1981, Terborgh 1983, Noser and Byrne 2006, 2007, Di Fiore and Suarez 2007); and 5) monitoring the state of ripeness of important fruit trees (Milton 1980, Terborgh 1983, Di Fiore 2003, Janmaat et al. 2006). Janson and Byrne (2007) critically reviewed those evidences of spatial knowledge on primates, highlighting the importance, among others, of accurately predicting in simple habits or in lean seasons “the movements of an individual or a group, if one possessed the same information that they do about food source location, the costs of potential travel paths, resource value and preference” (p.365).

Howler monkeys (*Alouatta* sp), a large folivorous-frugivorous neotropical primate, tend to travel in a single line progression as a cohesive unit (Carpenter 1964, Milton 1980, Bicca-Marques and Calegaro-Marques 1997, Garber & Jelinek 2006), and, as a consequence, all group members have access to the same ecological information (Milton 2000). Studies with different species of the genus, the most widely distributed of neotropical primates (Crockett and Eisenberg 1987), indicate a great adaptability to varying habitat types and floristic composition through a highly flexible diet and a conservative activity budget (Crockett and Eisenberg 1987, Neville et al. et al. 1988, Crockett 1998, Bicca-Marques 2003). Howlers may both present a strong dependence on leaf resources during periods when higher nutritional quality items are scarce (Prates and Bicca-Marques 2008) and an effective use of fruits when available (Milton 1980). The species of the genus *Ficus*, particularly, are known as important components of howlers’ diet (Milton 1980, Estrada 1984, Marsh 1999, Bicca-Marques 2003, Serio-Silva et al. 2002, Asensio et al. 2007). Thus, Milton (1980, 2000) suggests that the use of repetitive route paths along a few pivotal trees, specially *Ficus* species, would be an efficient strategy that would “permit a troop to keep a fairly close eye on phenological activity within its total home range without the need for strong dependence on long-term memory” (Milton 2000, p.391).

According to the optimal foraging theory (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976), an optimal folivorous species would tend to be much more selective on their feeding behavior than frugivorous species to deal with possible overloads of toxins present on leafs, although sampling of unfamiliar plants and mixing small amounts of different species should be favored (Charnov 1976). Dealing with the avoidance of a high level secondary compounds diet requires sophisticated gustatory, digestive and sensory feedback systems (Garber 1987). Beecham (2001), modeling the way an herbivore cognitive ability would evolve in a competing environment, suggests that they would tend to occupy a cognitive niche that is complementary to other competing species, processing information in a way of maximizing energy gain and avoiding competition with other species.

If foraging efficiency is to be maximized by natural selection (Schoener 1971), we hypothesize that a “behavioral folivore” species, as referred to by Milton (1980) for howler monkeys, should adopt foraging strategies that maximize energy and nutrient net gain, even in low fruit availability periods, by an efficient use of the spatial information in their range area. Considering the evidences proposed to be indicative of primates’ spatial knowledge, it is further hypothesized that an *Alouatta* species:

1) Use straight-line movements to the nearest available tree of a few target species, thereby minimizing travel distance;
2) Monitor the availability of larger or preferred fruit sources, particularly fig species, thereby maximizing energy net gain using the most productive trees available;
3) Repeat travel pathways that include large and high visibility trees, allowing both the use of large leaf resources and an enhanced visibility of the forest fragment from some trees, thereby reducing the memory load of information;
4) Use high visibility trees as nodes or decision points, where different routes intersect, indicative of topological, network or, also called, route-based maps (Byrne 1979, Poucet 1993).

In this research, these predictions are tested using behavioral data from a group of a group of brown howler monkeys (*Alouatta guariba clamitans* Cabrera, 1940) and the floristic composition of its habitat, a small forest fragment in Barra do Ribeiro, State of Rio Grande do Sul, Brazil.

# MATERIAL AND METHODS

## Study site and subjects

This study was carried out on a 5-hectare subtropical forest fragment (30°22’29”- 30°22’37”S, 51°27’25”- 51°27’37”W) located on a private farm at Barra do Ribeiro, State of Rio Grande do Sul, Brazil. Ten additional forest fragments (five of which inhabited by howler monkeys) varying in size from 1 to 75 hectares (mean ± s.d. = 14 ± 24 ha) and average distance of 98 ± 33 m from each other are also found at this farm. Within 16 months (July/2006-October/2007) of field study, no movement of howler groups across fragments was witnessed, although local people reported that it occasionally occurs. The main activities developed in the region are extensive cattle ranching and extensive tobacco, rice and *Eucaliptus* monocultures. Thus, historically the native forest area has been reduced to isolated and small forest fragments with decreasing animal diversity.

The climate of the region is strongly influenced by cold air masses migrating from Polar Regions, especially in Fall and Winter. The seasons are well defined and the rainfall is well distributed throughout the year (all months have at least 60 mm rainfall), with winter being the rainiest season. According to Köppen’s international climate classification, the region presents a humid subtropical climate (Cfa). Monthly rainfall averaged 115 ± 20 mm during the behavioral data collection period, March to October/2007 (minimum: 86 mm in April; maximum: 140 mm in August and September). Air temperature averaged 18 ± 3°C during the same period (minimum: 14°C in June and July; maximum: 23°C in March) (data available on http://br.weather.com/weather/climatology).

The 5-ha fragment was chosen because its small size that would allow for efficient monitoring of all food sources available to the howlers. In addition, the presence of a single brown howler monkey group inhabiting the fragment eliminated the possibility intergroup encounters that would affect traveling patterns, thereby hampering an evaluation of their relationship to food availability and foraging. The study group was composed of 6-7 individuals (one adult male, 2 adult females, 1-2 juvenile males and 1-3 infant males), a group size and composition characteristic of the species (data available in Bicca-Marques 2003 and Fortes 2008). Finally, the high importance of fig species (*Coussapoa microcarpa*, *Ficus insipida* and *Ficus organensis* – see Appendix 1) to the structure of the forest was also taken into account when choosing this forest fragment. As previously mentioned, fig trees are important sources of food for howlers (Milton 1980, Marsh 1999, Bicca-Marques 2003) and are characterized by fruiting asynchrony (Shanahan et al. 2001) that may affect howler foraging (Milton 2000).

The floristic composition of the study site was determined through a phytosociological survey (September to November/2006) using the point-centered method, in which the 4 nearest trees to each point with a diameter at breast height (DBH) ≥ 10 cm were identified and measured (DBH and height) (Krebs 1998). A total of 267 trees belonging to 54 species and 27 families were identified in 77 points distributed at 25-m intervals. The most representative families in terms of the importance value index - IVI (that is, the sum of each family's relative density, frequency and dominance), were Euphorbiaceae, Myrtaceae and Moraceae, whereas the most diverse families sampled were Myrtaceae, Meliaceae and Flacourtiaceae (Appendix 1).

Before the start of the behavioral data collection the area was totally mapped (July to September/2006) by dividing it into 25x25-m quadrants limited by individually numbered wood stakes. The stakes were attached to each other by strings to facilitate the tree mapping described below. The grid of quadrants was arranged along N-S and E-W axes, so the position of the group or the location of a single tree could be accurately mapped using X and Y coordinates (Figure 1). Following this mapping and the phytosociological survey, 12 plant species (belonging to 10 families) known to be important food sources for brown howler monkeys based on a literature review (Prates 1989, Jardim 1992, Cunha 1994, Limeira 1996, Marques 1996, 2001, Gaspar 1997, Martins 1997, Fortes 1999, Fialho 2000, Lunardelli 2000, Liesenfeld 2003) were chosen for monitoring their tree use. All 417 trees with DBH ≥ 10 cm belonging to these species were mapped, tagged and measured (DBH and height) (November/2006 to February/2007) (Table 1). This was the best method for predicting the potential most important food sources available to the study group, because this was the first study on howler monkey ecology and behavior at this region.

## Data collection procedure

After habituation (February/2007), the study group was followed from dusk to dawn for 26 days (243 hours of observation) distributed in three periods between March and October 2007 (8 days in March/2007 - Summer; 8 days in May and June/2007 – Fall; 10 days in September and October/2007 - Winter and beginning of Spring). Since determining tree use and foraging patterns of the study group was the main goal of this study, sampling days (1) that started with at least one animal moving or away from the sleeping tree; (2) with gaps of more than four continuous trees of the group’s pathway while moving; (3) in which sight of view from at least a half plus 1 individuals of the group was lost for a minimum of 20 minutes; (4) without an accurate determination of the night sleeping tree; and (5) with severe weather conditions (rainy or windy days) were excluded from the analysis, decreasing the sample to 20 days (205 hours of observation). These limitations impeded having more than three continuous sampling days in each period.

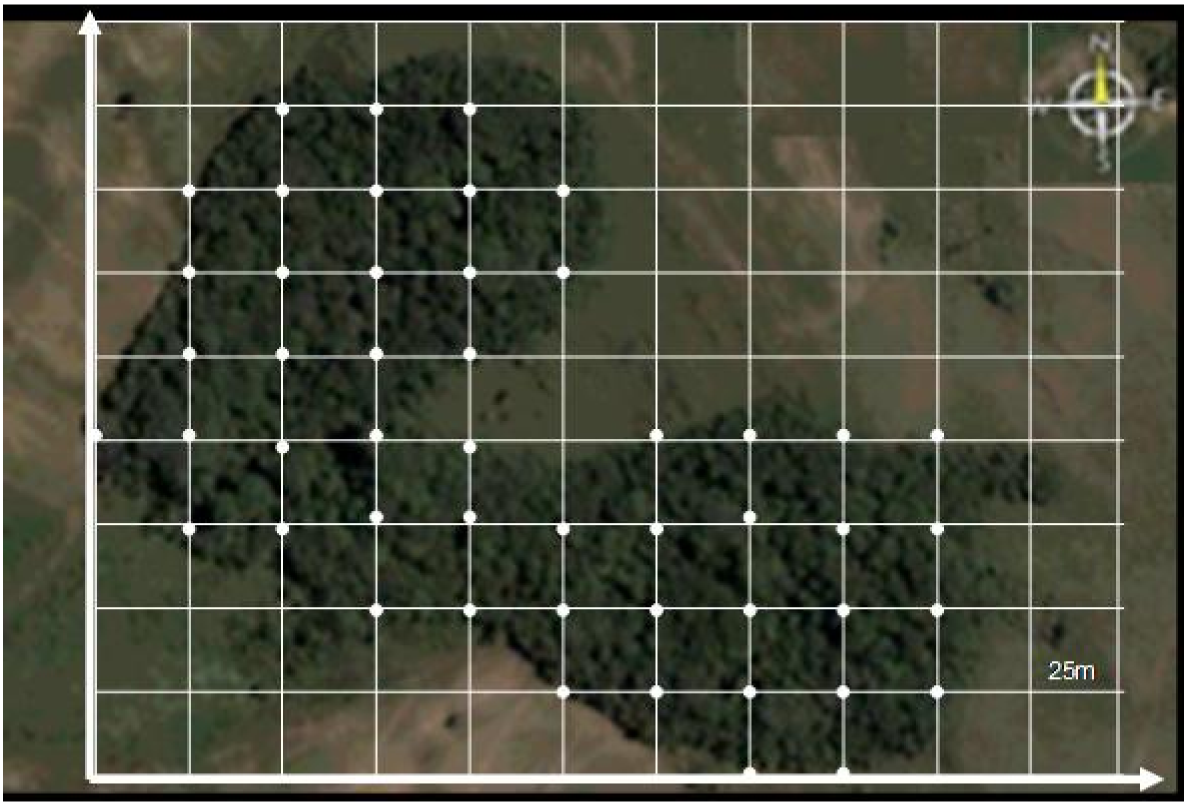

**Figure 1** – Study area and grid of quadrants positioned on N-S and E-W axes.

**Table 1** – Representation of selected plant species at the study site (n – number of trees; DBH – average ± s.d. diameter at breast height in centimeters; height – average ± s.d. height in meters) (See text for details on the selection criterion).

| Family | Species | n | DBH (cm) | HEIGHT (m) |
|---|---|---|---|---|
| Moraceae | *Ficus organensis* | 15 | 105.4 ± 27.3 | 19.8 ± 4.7 |
| Cecropiaceae | *Coussapoa microcarpa* | 68 | 48.7 ± 25.3 | 16.8 ± 4.5 |
| Moraceae | *Ficus insipida* | 12 | 38.9 ± 25.0 | 16.1 ± 3.9 |
| Tiliaceae | *Luehea divaricata* | 28 | 35.1 ± 13.1 | 15.4 ± 6.0 |
| Myrtaceae | *Campomanesia xanthocarpa* | 7 | 29.7 ± 15.4 | 13.2 ± 3.5 |
| Nyctaginaceae | *Guapira opposita* | 101 | 26.8 ± 11.2 | 13.8 ± 3.3 |
| Sapotacea | *Chrysophyllum gonocarpum* | 3 | 24.0 ± 14.3 | 17.1 ± 0.8 |
| Ebenaceae | *Diospyros inconstans* | 50 | 23.1 ± 27.0 | 13.3 ± 3.7 |
| Arecaceae | *Syagrus romanzoffiana* | 11 | 18.3 ± 4.5 | 12.8 ± 2.7 |
| Sapindaceae | *Allophyllus edulis* | 4 | 18.1 ± 3.3 | 11.4 ± 1.4 |
| Rutaceae | *Zanthoxylum hyemalis* | 70 | 12.2 ± 6.1 | 10.0 ± 3.4 |
| Rutaceae | *Zanthoxylum rhoifolium* | 48 | 11.1 ± 4.6 | 10.1 ± 2.4 |
| TOTAL | | 417 | 36.6 ± 14.7 | 14.2 ± 3.4 |

Data collection periods were conducted 2 to 3 months apart in a way of representing seasons varying in food availability. Each period comprised at least 8 days and was conducted through at most a month, while the phenological pattern of the forest fragment could be considered relatively the same and, theoretically, the foraging patterns of the group would be similar between the days sampled.

A total of 175 days (~1800 hours) were spent in the field throughout this 16-month study: 20 days for mapping the area, 30 days for the phytosociological survey, 55 days for identifying, mapping and measuring trees belonging to the selected species, 10 days for identifying, mapping and measuring trees used by the study group belonging to other species, and 60 days for studying the behavior.

## Behavioral data collection

The behavioral data collection consisted in the focal group behavioral method (Altmann 1974) by which the group was followed continuously and each behavior (feeding, resting, moving/traveling and social interaction) was recorded and timed. Feeding was defined as handling and ingesting plant material. Resting was defined as a period of inactivity. Moving/traveling was defined as any locomotion between trees of a half plus one individual of the group. Social interactions included vocalizations directed at other group members, physical contact, displacement, threats, huddling, and grooming.

Because the group was usually found as a cohesive unit at one or two adjacent trees, it was possible to record the group's behavior continuously. Besides, the presence of a second observer on most sampling days guaranteed the behavioral sampling when some individuals were located distant from the rest of the group. Behavioral recording began each day by the moment howlers woke up in the morning (which varied from 5:30 to 9:30 am) until their activities stopped for night sleep. In a way of standardizing the night resting timing, as the group was invariably sampled sleeping on the night sleeping tree at 6:00 pm, the behavioral timing analysis lasted until 6:00 pm.

All trees visited by the group in a given day were tagged, identified, mapped and measured (DBH), and the behavior of each individual howler visiting them recorded. At the end of each behavioral data collection period, the visibility index (VI – modified of the field-of-view index in Garber and Jelinek 2006) of all trees used for at least 2% of the total time recorded (11, 14 and 10 trees at each period, respectively) and at least 2% of the total feeding time (14, 16 and 6 trees at each period, respectively), was estimated. This measure took into account the height of all adjacent trees and the percentage of the target tree's crown that was covered at each stratum (1 – bottom of the crown; 2 – middle of the crown; 3 – top of the crown) and at each direction. For example, if the crowns of four of five trees that surround the target tree to the north overlapped the bottom of its crown, a 20% VI was scored for that height and coordinate. At the same time, if only one out of five tree crowns at this same coordinate obstructs the field of view of a howler located at the top of the target tree crown, an 80% VI was assigned. As already discussed by Garber and Jelinek (2006, pp 293), this only functions as “a crude and relative measure of the degree to which howlers could sight directly to a subsequent feeding/resting site”. The visibility index of random trees was also estimated to test whether visibility influences tree selection during foraging.

Several howler species have been described to move in single-line progressions (Carpenter 1964, Bicca-Marques and Calegaro-Marques 1997, Milton 2000, Garber and Jelinek 2006) through repeated pathways. To test if the study group follows the same pattern, all trees used for resting and moving by most group members were marked. In addition, every tree used for feeding, even by a single individual, was marked. A route was defined as a sequence of consecutive trees used by most group members, irrespective of its direction (i.e. A-B-C = C-B-A).

The item ingested (mature leaf – ML; young leaf – YL; leaf bud – LB; unidentified leaf – UL; ripe fruit – RFR; unripe fruit – UFR; open flower – OFL; flower bud – FLB) and the amount of time each howler spent feeding on the item at each tree was recorded during all feeding bouts. As preferences for different and specific plant parts have already been described for distinct primate species (Garber 1987) as well as indicative of monitoring of fruit ripeness (Janmaat et al. 2006), I observed the ripening state of the plant parts eaten to verify its influence on foraging. The contribution of each item, species or individual tree to the diet of the group at each period was estimated based on the average time spent feeding on them. Data on infant feeding was not included in these analyses.

The spatial distribution of trees used by howlers and of those trees belonging to prospective important food sources was determined by plotting their X and Y coordinates using a computer program developed by R. S. González and A. S. Martinez. These representations allowed an accurate determination of the group's day range based on the sum of the distances between used trees, since all tree coordinates were accurately measured *in-situ* with a high-precision laser distance meter (Leica DISTO$^{TM}$ A2).

Two different analyses were used to quantify the deviation from straight-line travel. First, the ratio between the most efficient route between two points (D), that was considered to be the straight line between them, and the observed route distance (L) was calculated, especially between feeding trees (D/L - Seguinot et al. 1998, Pochron 2001). A ratio of 1 indicates that the most efficient route was taken. In addition, the null hypothesis that segments between feeding trees were independent and uniformly distributed around a circumference rather than concentrated around a specific direction was tested for verifying the organization of successive segments. Clustering around 0/360° would indicate a dependent relationship between segments alignment, possibly over an efficient route traveling. For this analysis, the magnitude of the clockwise rotation needed to align with the bearing of a route segment $i$ when arriving at a feeding tree to the bearing of the route segment $i + 1$ when leaving this tree was computed. The daily computed bearing vectors between feeding trees were analyzed with circular statistics (Kovach 1999).

To test the hypothesis that brown howler monkeys minimize distance traveled, the straight-line distance between consecutive feeding trees was compared with the distance between the first tree of a given species visited and the nearest tree of the same species and the nearest tree used for feeding during the same sampling period independently of which species it belonged to.

Howler monkeys usually present 1 to 3 long-lasting periods of resting each day, that have been suggested to be important behavioral adaptations to maximize the digestion of fibrous and high-structured nutrients ingested (Smith 1977, Milton 1980, Glander 1982). Di Fiore and Suarez (2007) identified several nodes intersecting travel routes of spider and woolly monkeys that would act as decision points where the group could decide which route to take next. Using resting trees as nodes, or decision-points where different routes segments intersect, could be used as a strategy on howlers foraging since their repetitive use connecting distinct travel routes would favor a variation on the diet's composition throughout the day, as already described for howlers (Ganzhorn and Wright 1994). Certain routes may lead to important ephemeral fruit sources worth monitoring at the beginning of the day when the group still has time to forage in other locations if those items are not available, while other routes may end up at staple food sources that will guarantee a feeding bout before the night sleep. To identify whether resting trees used by howlers act as nodes, as described for spider and wooly monkeys (Di Fiore and Suarez 2007), it was considered the number of times each resting tree has been used, the distinct direction the had been reached and the angular deviation observed between the bearing the of the arrival route leading to it before resting and the direction of the route taken when leaving it was considered.

Changes in speed of travel have been used to infer spatial knowledge of the location of a goal (Pochron 2001, Janmaat et al. 2006). In the current research, it was impossible to determine whether change in travel speed was influenced by resource detection because average distance between consecutive feeding sources was inferior to

40 m. Histograms of the distances between feeding sites were plotted to analyze whether and how this variable acted on howlers' foraging.

### Data Analysis

All analyses were performed separately for each data collection period. Activity budgets were calculated based on the average time spent by the group in each behavior. Similarly, the contribution of each food item or species to the diet was based on the average time spent eating it in the feeding bouts. Only bouts lasting at least 5 minutes and in which more than two howler monkeys were feeding on the same tree were considered feeding target trees in the analyses of the minimum distance traveled between feeding trees, the straight-line distance and the angular deviation between them. The DBH was used as a surrogate of food abundance of individual trees. DBH is considered the most accurate method for comparing resource productivity by different plant species (Chapman et al. 1992).

Data were analyzed to observe statistical differences using One-Way Analysis of Variance (ANOVA), Student-t test and Z test for parametric data according to the number of observations at each sample and its variance, and, for non-parametric data, the Kruskal-Wallis test and two-sample Mann-Whitney test were used for independent samples of equal variance. Whenever two or more variables were tested simultaneously, the Bonferroni post-hoc test was used. To measure the strength of the relationship between independent variables, regression analyses were performed, whereas Spearman rank correlation coefficient ($r_s$) and Pearson correlation coefficient ($r_p$) were used to verify the correlation between non-parametric and parametric dependent variables, respectively. The Rayleigh test was used for the circular analyses on angular deviation between trees. All tests were two-tailed and performed using the software Biostat 5.0

(Ayres et al. 2007), except the circular statistic where it was used the software Oriana 1.06 (Kovach 1999).

# RESULTS

In 20 days of behavioral data collection the study group fed, rested and traveled in 654 trees (311, 301 and 418 trees in each period, respectively). The mean daily range was 919 ± 256 m, a distance that did not vary significantly between the sampling periods (F = 1.2761, *p* = 0.3046, *df* = 17). The howler group concentrated their activity budget on resting (57.6 ± 8.3%) and feeding (17.1 ± 5.2%), with a diet based on leaves (53.3 ± 15.2%), fruits (34.3 ± 17.4%) and flowers (12.2 ± 12.3%) (Table 2).

The group spent significantly more time resting during the Fall sampling period than it did in the Winter-Spring sampling period (t = 2.7055, *p* = 0.0191, *df* = 12). This difference was not observed between Summer and Fall (t = -1.0112, *p* = 0.3318, *df* = 12) and Summer and Winter-Spring (t = 0.5925, *p* = 0.5666, *df* = 10) (Figure 2). At the same time, the Winter-Spring sampling period was the only in which the percentage time resting was not significantly correlated with day range ($r_p$ = -0.4968, *p* = 0.3161, *df* = 4). Day range was negatively related to resting during Summer ($r_p$ = -0.08482, *p* = 0.0328, *df* = 4), Fall ($r_p$ = -0.07367, *p* = 0.037, *df* = 6) and the entire study ($r_p$ = -0.7403, *p* = 0.0002, *df* = 18).

Both percentage time feeding and total time (in minutes) spent feeding were significantly higher in Winter-Spring than in Summer (t = -3.3495, *p* = 0.0073, *df* = 10; t = -3.5486, *p* = 0.0053, *df* = 10), but no difference was observed between Summer and Fall (t = -1.5637, *p* = 0.1438, *df* = 12; t = -1.5593, *p* = 0.1488, *df* = 10), and Fall and Winter-Spring (t = -1.3391, *p* = 0.2053, *df*=12; t = -1.4500, *p* = 0.1726, *df* = 10). The contribution of leaves to the diet was similar throughout the study (F = 0.5094, *p* = 0.6147, *df* = 17).

**Table 2** – Mean daily activity budget, tree use and diet composition during the study.

| | Summer | Fall | Winter-Spring | Mean |
|---|---|---|---|---|
| resting (%) | 56.7 ± 12 | 61.4 ± 5.3 | 53.5 ± 5.6 | 57.6 ± 8.3 |
| feeding (%) | 13.4 ± 2.6 | 17.1 ± 5.3 | 20.8 ± 4.7 | 17.1 ± 5.2 |
| day range (m) | 1043.1 ± 361.1 | 825.5 ± 185.7 | 920.8 ± 193.5 | 919.4 ± 255.8 |
| used trees (n) | 77.2 ± 23.2 | 73.8 ± 20.4 | 96.5 ± 10.3 | 81.6 ± 20.6 |
| feeding trees (n) | 17.7 ± 4.3 | 19 ± 3.9 | 29 ± 6.6 | 21.6 ± 6.9 |
| resting trees (n) | 6.3 ± 2.9 | 5.6 ± 2 | 5 ± 2.6 | 5.7 ± 2.4 |
| traveling trees (n) | 55.8 ± 19.1 | 50.8 ± 18.1 | 72.3 ± 7.2 | 58.8 ±17.8 |
| feeding trees (%) | 24.3 ± 7.8 | 26.6 ± 4.6 | 29.8 ± 4.2 | 26.9 ± 5.7 |
| resting trees (%) | 8.2 ± 2.4 | 8.6 ± 4.7 | 5.2 ± 2.8 | 7.4 ± 3.7 |
| traveling trees (%) | 70.4 ±7.8 | 70.4 ± 6.5 | 66.4 ± 10 | 69.9 ± 7.8 |
| Leaves (%) | 55.7 ± 14.4 | 49.3 ± 15.2 | 57 ± 17.4 | 53.3 ± 15.2 |
| mature (%) | 37.2 ± 13.5 | 19.8 ± 16.6 | 14.8 ± 12.5 | 23.5 ± 16.7 |
| young (%) | 6.3 ± 4.7 | 21.3 ± 9.4 | 27.1 ± 15.4 | 18.5 ± 13.2 |
| bud (%) | 8.7 ± 7.5 | 4.1 ± 5.1 | 14.8 ± 9.5 | 8.7 ± 8.3 |
| unknown (%) | 3.6 ± 2.7 | 4 ± 5.1 | 0.4 ± 0.5 | 2.8 ± 3.8 |
| Fruits (%) | 42.5 ± 10.7 | 38.8 ± 13.7 | 20 ± 20.4 | 34.3 ± 17.4 |
| unripe (%) | 29.3 ± 5.9 | 37.8 ± 12.6 | 18.7 ± 19.7 | 29.5 ± 15.4 |
| ripe (%) | 13.2 ± 14.6 | 0.9 ± 2 | 1.4 ± 2.8 | 4.7 ± 9.6 |
| Flowers (%) | 1.7 ± 4.1 | 12 ± 5.3 | 22.9 ± 15.8 | 12.2 ± 12.3 |
| open (%) | 1.7 ± 4.1 | 3.3 ± 3.9 | 10.9 ± 6.7 | 5.1 ± 6.1 |
| bud (%) | 0.1 ± 0.1 | 8.7 ± 3.2 | 12.1 ± 16 | 7.1 ± 9.8 |

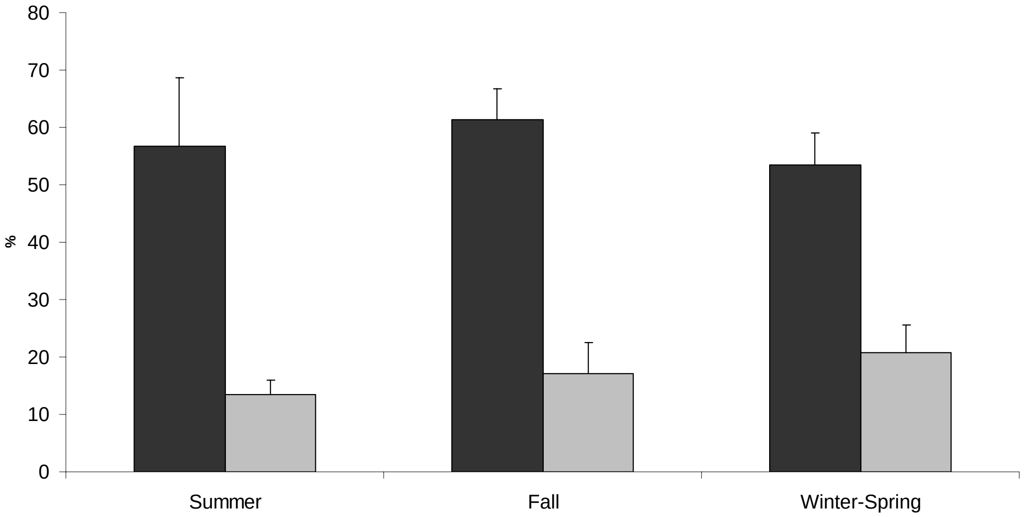

**Figure 2** – Mean percentage of time spent resting (black box) and feeding (gray box) by brown howler monkeys at each sampling period.

Similar results were found for fruits during Summer and Fall (t = 0.5466, *p* = 0.5946, *df* = 12) and Fall and Winter-Spring (t = 2.0653, *p* = 0.0611, *df* = 12) and for flowers during Fall and Winter-Spring (F=3.4613, *p* = 0.0847, *df* = 12). However, fruits contributed significantly more during the Summer than the Winter-Spring (t = 2.3845, *p* = 0.0383, *df* = 10). In the latter sampling period the study group ate significantly more flowers than in the Summer (Z = 2.5820, *p* = 0.0098, U = 4) and Fall (Z = 2.7222, *p* = 0.0065, U = 1). Figure 3 shows the mean percentage contribution of each food item per sampling period.

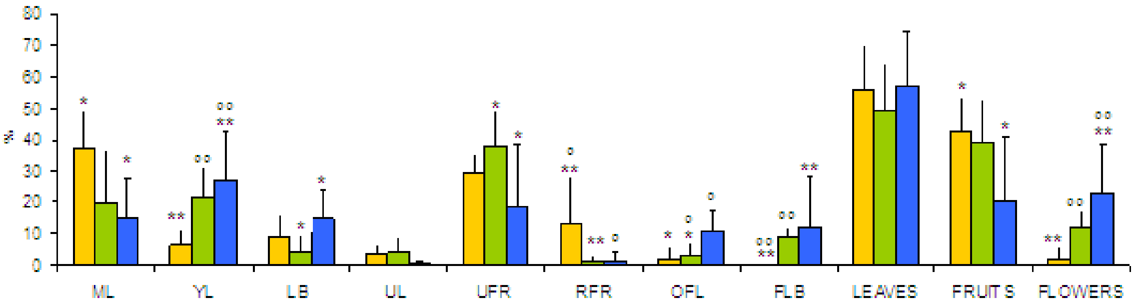

**Figure 3** – Mean percentage of time spent eating each food item during each sampling period (summer – orange; fall – green; winter-spring – blue). ML = mature leaf, YL = young leaf, LB = leaf bud, UL = unidentified leaf, UFR = unripe fruit, RFR = ripe fruit, OFL = open flower, FLB = flower bud, LEAVES = ML + YL + LB + UL, FRUITS = UFR + RFR, FLOWERS = OFL + FLB. Pairs that present statistical differences are indicated (* and ° $p < 0.05$; ** and °° $p < 0.01$).

Each sampling period showed distinct patterns of foraging and tree use. The Summer was marked by similar contributions of mature leaves (40.6%) and total fruits (43.0%; 9.2%=ripe fruits), long mean day range (1043 ± 361 m; range: 538 – 1505 m), and a low mean percentage feeding (13.4 ± 2.6%) (Table 2). During the Summer, day range was positively correlated with the percentage feeding on unripe fruits ($r_p$ =

0.8818, $p = 0.0201$, $n = 6$) that was related to the period feeding percentage ($r_p = 0.8552$, $p = 0.0299$, $n = 6$), while the minutes spent eating were positively related to the feeding time spent eating mature leaves ($r_p = 0.9167$, $p = 0.0101$, $n = 6$). The distance traveled also varied according to the number of trees used per day, as expected, ($r_p = 0.8365$, $p = 0.0375$, $n = 6$) and those used for resting ($r_s = 0.971$, $p = 0.0012$, $n = 6$), while the latter was positively related to the feeding percentage of unripe fruits ($r_s = 0.9122$, $p = 0.0112$, $n = 6$). The greater the amount of time the howlers spent eating unripe fruits, the less time they spent resting ($r_p = -0.8466$, $p = 0.033$, $n = 6$).

During this same sampling period, the feeding on ripe fruits showed a distinct pattern from the one described above for unripe fruits, since it was negatively related to the distance traveled ($r_p = -0.848$, $p = 0.0329$, $n = 6$). Moreover, the percentage of ripe fruits eaten also presented a negative relationship with the total number of trees used per day ($r_p = -0.8139$, $p = 0.0489$, $n = 6$).

On the other hand, during the Fall sampling period a short mean distance traveled was characterized (825.5 ± 185.7 m ; 467 – 990 m) and long periods of resting (61.4 ± 5.3%). The consumption of unripe fruits during the Fall sampling days was the highest among the sampling periods (32%) and the total consumption of flowers increased (17.6%) compared to the previous period, accompanied by a decrease in the total consumption of leaves (49.7%). As before, the distance traveled was positively related to the daily number of trees used ($r_p = 0.9623$, $p = 0.0001$, $n = 8$) and those used for feeding ($r_p = 0.7593$, $p = 0.0288$, $n = 8$), but, during this period, the latter varied with the amount of flower buds eaten ($r_p = 0.7481$, $p = 0.0327$, $n = 8$) and with the total consumption of leaves ($r_p = 0.8852$, $p = 0.0035$, $n = 8$). Likewise, the distance traveled was positively related to the total number of minutes spent eating leaves ($r_p = 0.7611$, $p = 0.0284$, $n = 8$). The more trees used, the more of them were used for feeding ($r_p =$

0.8913, $p = 0.0029$, n = 8), and the greater the percentage of trees used for feeding, the greater was the percentage of resting trees ($r_s = 0.7381$, $p = 0.0365$, n = 8). The percentage of daily feeding time was related to the percentage ingested of open flowers ($r_p = 0.7751$, $p = 0.0238$, n = 8), unripe fruits ($r_p = 0.8902$, $p = 0.0003$, n = 8) and total consumption of fruits ($r_p = 0.8629$, $p = 0.0058$, n = 8).

The last period sampled was marked by a high mean feeding percentage (20.8 ± 4.7%), which at the same time characterized a high mean number of trees used daily (96.5 ± 10.3%) as feeding trees (29 ± 6.6%) and trees used exclusively for locomotion (72.3 ± 7.2%). As a consequence, although the daily mean number of trees used for resting (5 ± 2.6) was similar to the patterns observed for Summer and Fall (6.3 ± 2.9 and 5.6 ± 2, respectively), the percentage of trees used daily for resting decreased during the Winter-Spring sampling period (5.2 ± 2.8%). During this period, the total consumption of leaves (64%) and flowers (22.7%) was as high as the consumption of young leafs (29.8%) and leaf buds (14.4%), while the percentage of time spent eating fruits (13.6%) was the lowest among the sampled periods. The daily feeding percentage increased along with the number of trees used daily ($r_p = 0.8977$, $p = 0.0152$, n = 6), those used daily for feeding ($r_p = 0.9568$, $p = 0.0028$, n = 6) and was negatively related to the feeding percentage of young leaves ($r_p = -0.885$, $p = 0.019$, n = 6). The higher the number of trees used, the higher was the number of those trees used for feeding ($r_p = 0.9159$, $p = 0.0103$, n = 6). On the other hand, to the contrary of the pattern observed during the other sampling periods, the daily mean distance traveled was not significantly correlated with the mean number of trees used daily ($r_p = 0.7481$, $p = 0.0871$, n = 6), although small sample size might have influenced these results.

## Tree use

Describing the study group tree use patterns was our first approach to better understand how the environmental features might influence howler behavior. The 654 trees used belonged to 57 plant species (Shannon-Wiener species richness index: H' = 3.357) (311 trees of 50 species in Summer, 299 trees of 46 species in Fall and 412 trees of 51 species during the Winter-Spring period). The overall mean number of trees used per day was 81.6 ± 20.6. The number of trees used daily was greater in Winter-Spring (96.5 ± 10.3) than in the Fall (74.6 ± 20.8: $t = -2.4833$, $p = 0.0287$, $df = 12$) (see Appendix 2). The group traveled through an average of 26.9 ± 5.3 species each day and used significantly more species in the Winter-Spring than in the two other sampling periods ($F = 6.4477$, $p = 0.0083$, $df = 17$). Likewise, the mean daily number of feeding species used during the Winter-Spring period (13.5 ± 3.3 plant species) was significantly greater ($F = 6.6832$, $p = 0.0073$, $df = 17$) than the means observed during the Summer (9.0 ± 1.4) and Fall (9.8 ± 2.0) periods. Ten of the 12 species previously selected as putative important food sources were responsible for 68.7% of the total time spent feeding by the study group.

The number of individual trees of a given species used was strongly related to the species importance value (IVI) in the forest fragment (Linear regression: $R^2 = 45.66$, $p < 0.0001$, $n = 46$). However, an analysis of residuals considering the species' IVIs as the predictor variable of tree use indicated that the howlers passed more through trees of three species (*Guapira opposita, Myrsine guianensis* and *Coussapoa microcarpa*) and through trees of *Sebastiania commersoniana*, the most frequently sampled species in the phytosociology, less that the predicted value (Figure 4A). Although the previous analyses did not indicate any statistically significant difference in the pattern of use, considering the number of visits per species predicted by species' IVIs ($R^2 = 46.11$, $p <$

0.0001, n = 46), *Coussapoa microcarpa* was visited significantly more than expected (ESD = 3.3181, $p < 0.05$, n = 50), while *Sebastiania commersoniana* was visited significantly less than expected (ESD = 3.3607, $p < 0.05$, n = 50) (Figure 4B).

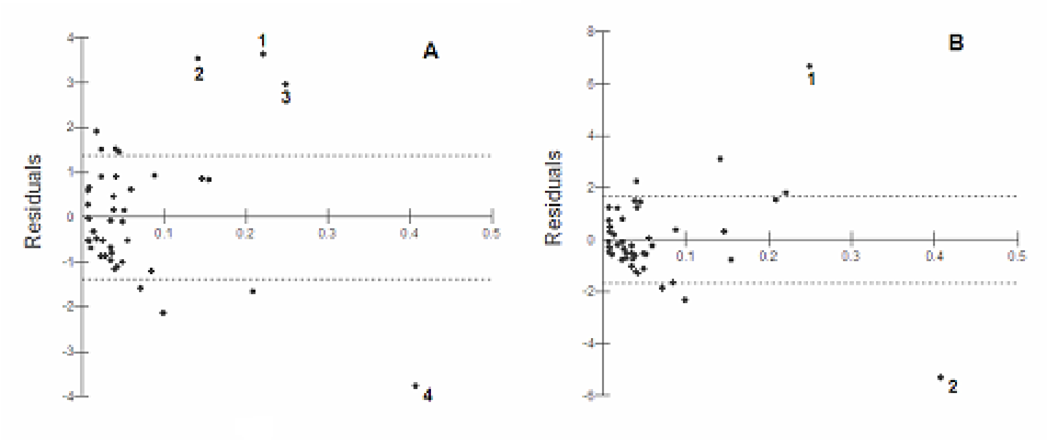

**Figure 4** – A) Residual number of trees used per species (1 - *Guapira opposita;* 2 - *Myrsine guianensis*; 3 - *Coussapoa microcarpa* and 4 - *Sebastiania commersoniana*) and B) Residual number of visits per species predicted by each species IVI value (1 - *Coussapoa microcarpa* and 2 - *Sebastiania commersoniana.* Dashed lines indicate mean residuals value ± SD.

Although the number of feeding trees varied from one period to another, being significantly higher during the Winter-Spring period than in the other two seasons sampled (t = -3.5068, $p = 0.0056$, $df = 10$; t = -3.5417, $p = 0.0040$, $df = 12$, respectively), the howlers used a similar percentage of feeding trees during the sampling periods (H = 2.2323, $p = 0.3275$, $df = 2$). Similarly, the percentage of resting trees and traveling trees also did not vary between the different seasons (F = 1.6384, $p = 0.2225$, $df = 17$; F = 3.2079, $p = 0.0646$, $df = 17$, respectively) (Figure 5).

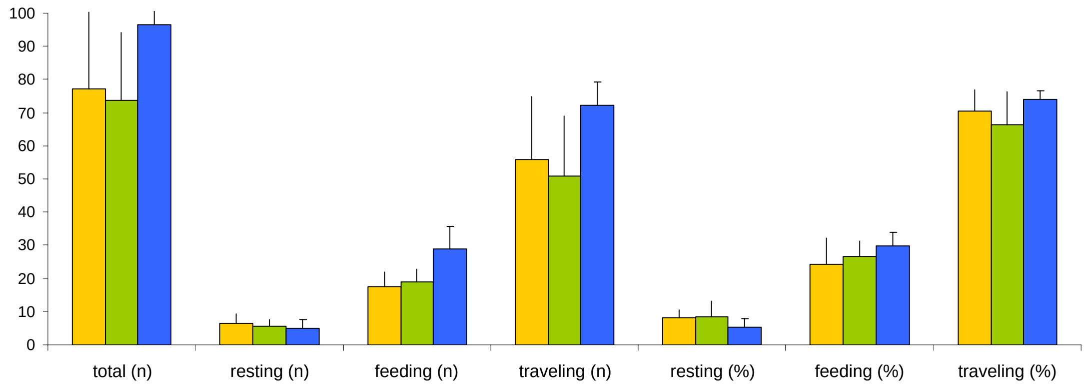

**Figure 5** – Mean tree use patterns (n and % of trees used) at each sampling period (Summer – orange; Fall – green; Winter-Spring – blue).

The same species that was used more than expected, as shown in the residual analysis plotted above (Figure 4a and b), also accounted for the highest numbers of feeding trees used (Appendix 3). *Coussapoa microcarpa* was the second most important feeding species during the days sampled (13.3% of the groups' feeding time), contributing with both leaves and fruits in all the periods sampled (Table 3).

The most important food source, *Ficus organensis*, contributed 18.5% of the total feeding time and accounted for 57.4% of the fruit feeding records (92.3% of those were unripe fruits). All 15 trees of *Ficus organensis* in the forest fragment were used, considering that 11 were used for feeding and 11 accounted for the greatest percentage of time spent resting in a single species in the study, 37.8% (Table 4). The 11 trees used for resting and those 11 trees used for feeding overlap in 10 individuals and 8 of them were among the 20 most used trees during the study. The time spent using this species comprised 26.0% of the group's tree use during the study, while the use of *Coussapoa microcarpa* represented 23.4%, also being the second most used species for resting.

**Table 3** – Plant species used for feeding and the relative contribution of its items to the group's diet during the study (mature leaf – ML; young leaf – YL; leaf buds – LB; unidentified leaf – UL; ripe fruit – RFR; unripe fruit – UFR; opened flower – OFL; flower bud – FLB).

| Species | % Feeding | ML | YL | LB | UL | RFR | UFR | OFL | FLB |
|---|---|---|---|---|---|---|---|---|---|
| *Ficus organensis* | 18.5 | 1.26 | 0.83 | 1.03 | 0.45 | 1.15 | 13.82 | 0 | 0 |
| *Coussapoa microcarpa* | 13.3 | 1.14 | 0.83 | 1.12 | 0.52 | 1.19 | 7.55 | 0.60 | 0.39 |
| *Ficus insipida* | 9.2 | 2.47 | 4.59 | 1.30 | 0.32 | 0 | 0.51 | 0 | 0 |
| *Guapira opposita* | 8.8 | 0.71 | 0.73 | 0.24 | 0.22 | 0 | 0 | 3.05 | 3.80 |
| *Zanthoxylum hyemalis* | 6.3 | 3.12 | 0.79 | 1.24 | 0.92 | 0 | 0 | 0.26 | 0 |
| *Diospyros inconstans* | 6.0 | 3.10 | 2.08 | 0 | 0 | 0 | 0 | 0.40 | 0.40 |
| *Dasyphilum spineeis* | 4.6 | 1.26 | 2.51 | 0.50 | 0 | 0 | 0 | 0 | 0.38 |
| *Zanthoxylum rhoifolium* | 4.0 | 3.38 | 0.28 | 0.31 | 0 | 0 | 0 | 0 | 0 |
| vine sp. | 3.7 | 0 | 1.00 | 0.19 | 0 | 0 | 0 | 1.23 | 1.33 |
| *Sorocea bonplandii* | 3.4 | 0.47 | 2.88 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Myrsine guianensis* | 2.5 | 0.23 | 0.08 | 0.04 | 0.12 | 0.07 | 0.61 | 0.26 | 1.11 |
| *Banara parviflora* | 1.9 | 1.13 | 0.30 | 0.20 | 0.22 | 0.05 | 0 | 0 | 0 |
| *Trichilia clausenii* | 1.5 | 0.81 | 0 | 0 | 0.24 | 0 | 0.49 | 0 | 0 |
| *Esenbeckia grandiflora* | 1.4 | 0.85 | 0.36 | 0.19 | 0.05 | 0 | 0 | 0 | 0 |
| *Chrysophyllum gonocarpum* | 1.2 | 0.68 | 0 | 0.52 | 0.02 | 0 | 0 | 0 | 0 |
| *Nectandra megapotamica* | 1.2 | 0.12 | 0 | 0.67 | 0 | 0 | 0 | 0.05 | 0.39 |
| *Lithraea brasiliensis* | 1.1 | 0.38 | 0.46 | 0.04 | 0.24 | 0 | 0 | 0 | 0 |
| *Luehea divaricata* | 0.9 | 0 | 0.46 | 0.16 | 0 | 0.07 | 0 | 0.25 | 0 |
| *Vitex megapotamica* | 0.8 | 0.46 | 0.30 | 0 | 0 | 0 | 0 | 0 | 0.07 |
| *Sebastiania commersoniana* | 0.7 | 0.13 | 0 | 0.33 | 0 | 0.11 | 0 | 0.06 | 0.06 |
| *Casearia decandra* | 0.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0.30 | 0.32 |
| *Ocotea pulchella* | 0.6 | 0 | 0.60 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Myrcianthes gigantea* | 0.6 | 0.24 | 0.11 | 0 | 0.02 | 0.12 | 0.07 | 0 | 0 |
| *Sloanea monosperma* | 0.5 | 0.49 | 0 | 0 | 0.05 | 0 | 0 | 0 | 0 |
| *Campomanesia xanthocarpa* | 0.5 | 0.23 | 0.05 | 0 | 0.12 | 0 | 0 | 0.04 | 0.04 |
| *Allophyllus edulis* | 0.4 | 0 | 0.12 | 0.29 | 0 | 0 | 0 | 0 | 0 |
| *Solanum peseudo-quina* | 0.4 | 0.21 | 0.16 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Inga uruguensis* | 0.3 | 0.33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Myrsine coreaceae* | 0.3 | 0.28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Psidium cattleianum* | 0.2 | 0.24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Xylosma pseudosalzmanii* | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0.19 | 0.05 |
| *Ilex brevisuspis* | 0.2 | 0 | 0.09 | 0.12 | 0 | 0 | 0 | 0 | 0 |
| *Matayba elaeagnoides* | 0.2 | 0 | 0.17 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cytharexyllum myrianthum* | 0.2 | 0 | 0 | 0 | 0 | 0.17 | 0 | 0 | 0 |
| *Miconia rigidiuscula* | 0.1 | 0.14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cabralea canjerana* | 0.1 | 0 | 0.09 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ilex dumosa* | 0.1 | 0.09 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Erythroxylum argentinum* | 0.1 | 0 | 0 | 0 | 0.07 | 0 | 0 | 0 | 0 |
| *Myrcia glabra* | 0.1 | 0 | 0 | 0 | 0.07 | 0 | 0 | 0 | 0 |
| undeterm. spp | 3.1 | 0.95 | 0.25 | 0.83 | 0.39 | 0.12 | 0 | 0.23 | 0.32 |
| TOTAL | 100 | 24.9 | 20.1 | 9.3 | 4.0 | 3.0 | 23.1 | 6.9 | 8.7 |

**Table 4** – Tree species used for resting during the study and its respective contribution, average use/per individual tree and DBH.

| **Species** | | | **use/tree** | | | |
|---|---|---|---|---|---|---|
| | **n tree** | **% resting** | **mean use/tree** | **min** | **max** | **DBH** |
| *Ficus organensis* | 11 | 37.80 | 3.44 ± 3.27 | 0.15 | 10.25 | 97.8 ± 35.2 |
| *Coussapoa microcarpa* | 19 | 36.21 | 1.91± 2.20 | 0.04 | 7.35 | 74.6 ± 23.8 |
| *Myrsine guianensis* | 5 | 6.03 | 1.21 ± 1.86 | 0.01 | 4.32 | 30.4 ± 5.2 |
| *Ficus insipida* | 4 | 2.85 | 0.71 ± 1.18 | 0.09 | 2.49 | 55.5 ± 11.9 |
| *Banara parviflora* | 3 | 2.32 | 0.77 ± 0.19 | 0.62 | 0.99 | 29.3 ± 9.4 |
| *Nectandra megapotamica* | 1 | 1.70 | | | | 56 |
| *Diospyros inconstans* | 3 | 1.35 | 0.45 ± 0.55 | 0.13 | 1.09 | 27.5 ± 5.3 |
| *Myrcianthes gigantea* | 3 | 1.10 | 0.37 ± 0.45 | 0.02 | 0.88 | 46.20 |
| *Guapira opposita* | 2 | 0.90 | 0.45 ± 0.56 | 0.05 | 0.85 | 36.1 ± 2.9 |
| *Trichilia clausenii* | 2 | 0.52 | 0.26 ± 0.14 | 0.16 | 0.36 | 35.6 ± 2.3 |
| *Myrcia glabra* | 1 | 0.49 | | | | 24.8 |
| *Sebastiania commersoniana* | 1 | 0.42 | | | | 21 |
| *Inga uruguensis* | 1 | 0.29 | | | | |
| *Chionanthus trichotomus* | 1 | 0.27 | | | | 41.1 |
| *Luehea divaricata* | 2 | 0.19 | 0.09 ± 0.05 | 0.05 | 0.13 | 53.2 ± 12.6 |
| *Cabralea canjerana* | 2 | 0.13 | 0.07 ± 0.06 | 0.02 | 0.11 | 52.2 ± 7.2 |
| *Gymnanthes concolor* | 1 | 0.12 | | | | |
| *Maytenos casineformis* | 1 | 0.12 | | | | |
| *Prunus selloi* | 1 | 0.04 | | | | |
| *Zanthoxylum rhoifolium* | 1 | 0.04 | | | | 12.7 |
| *Sloanea monosperma* | 1 | 0.04 | | | | 54.1 |
| undeterm. spp | 8 | 7.05 | 0.88 ± 1.14 | 0.04 | 3.39 | 38.4 ± 27.1 |
| TOTAL | 66 | 93 | | | | 59.6 ± 32.5 |

To classify the target trees used in each sampling period was considered the percentage of days sampled that each tree was used and the percentage of feeding and resting time observed for each individual tree (see Methods). Although the study group used a large number of trees, 39.0% were used for only a day and another 23.1% were visited in two days (Figure 6A). When only the feeding trees were considered, this percentage was even higher, since 66.3% and 16.9% of the trees were used for just a day or two, respectively (Figure 6B), while 37.8% of the resting trees were used for a single day and 12.2% for two days (Figure 6C). On the other hand, 18% of the overall trees, 7% of the feeding trees and 27% of the resting trees were used in at least five

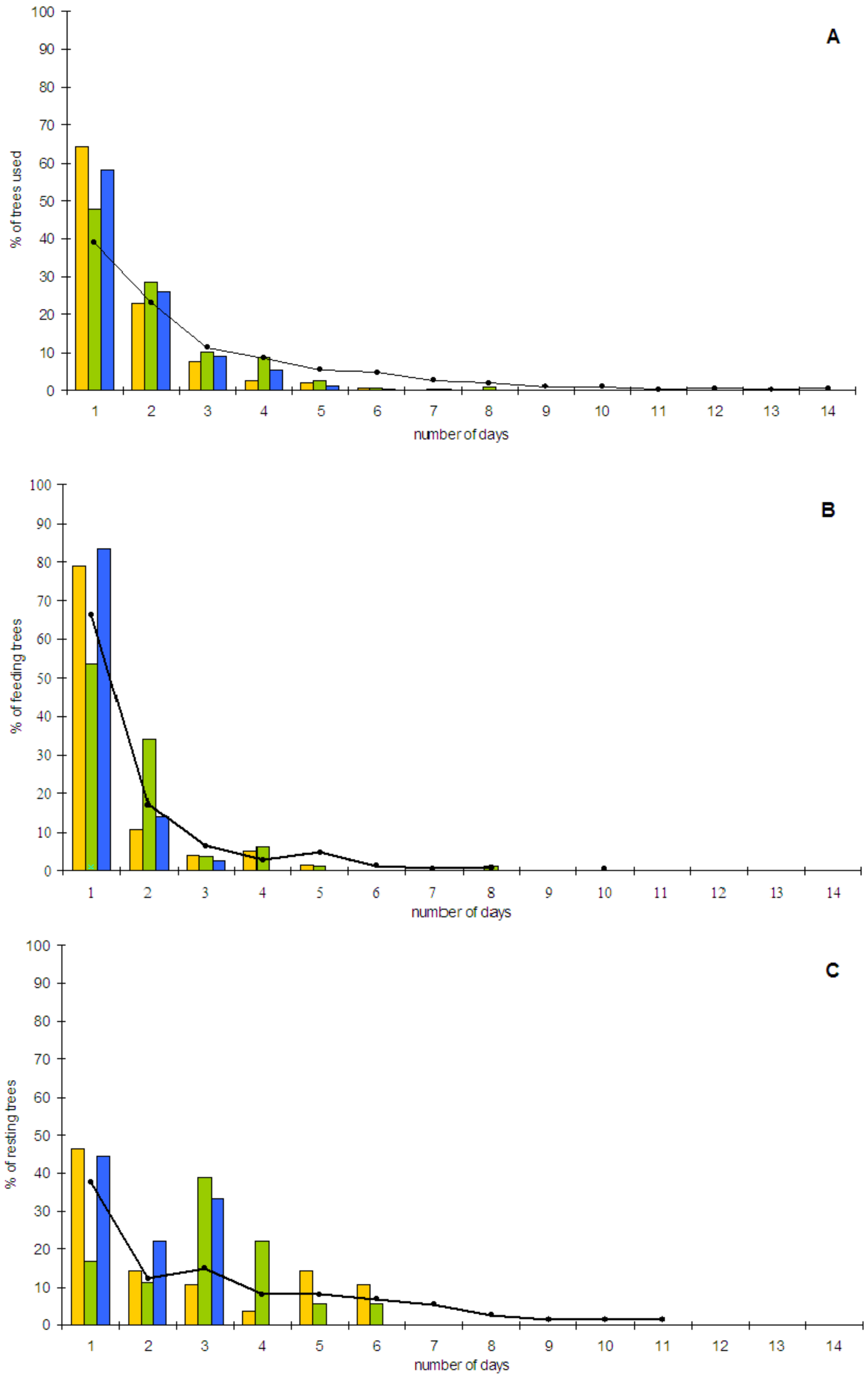

**Figure 6** – Intensity of tree use in accumulative days per sampling period observed, indicating total tree use (A), feeding tree use (B) and resting tree use (C) (Summer – orange; Fall – green; Winter-Spring – blue; total - dark line).

days. Among those, 11 trees were used for 32.8% of the total time recorded, being classified as target trees (five trees in Summer, five in Fall and three in Winter-Spring) (Table 5, but see data on angular deviation below).

## Visibility

The visibility index (VI) was determined for the trees used for the greatest percentage of feeding and total time (see Methods). This accounted for 14 trees during the Summer (12 feeding trees), 19 trees during the Fall (9 feeding trees), 13 trees during the Winter-Spring (3 feeding trees) and 16 trees for the entire study period (6 feeding trees), comprising a total of 26 trees (>2% of the total time recorded). Measures of VI values of other 77 trees widespread throughout the forest fragment were taken for comparison with the VI of the most used trees.

The forest fragment shows an irregular slope along its length, with the north coordinate facing up the hill. As a consequence, none of the trees used by the howlers showed significantly greater visibility in the north coordinate than the control trees. Another consequence of the forest fragment terrain, besides its shape, are the differences found between the visibility at each coordinate, where the south and east coordinate present a higher VI than the north and west coordinates (H = 11.8535, $p$ = 0.0079, $df$ = 3).

All the coordinates total visibility values, except the north coordinates, were significantly higher than those of the control trees (Table 6).The mean visibility at the bottom portion of the tree crowns was 22.3 ± 18.5%, in the middle portion of the crown was 47.8 ± 24.7% , and at its top was 63.8 ± 29.1. The visibility of the most used trees during each period and throughout the entire study did not differ from one another (F = 0.2659, $p$ = 0.8508, $df$ = 3).

**Table 5** – Trees classified as target trees due the intensity of their use and contribution on the group's feeding, resting and total time used.

| Tree ID | Species | % days used | | | | % feeding | | | | % resting | | | | % total use | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | summer | fall | winter-spring | TOTAL | summer | fall | winter-spring | TOTAL | summer | fall | winter-spring | TOTAL | summer | fall | winter-spring | TOTAL |
| 1.05 | *Ficus organensis* | 100.0 | 13.0 | 50.0 | 50.0 | 3.0 | - | 0.0 | 0.6 | 25.1 | 2.6 | 3.9 | 8.7 | 15.3 | 1.7 | 2.2 | 5.4 |
| 9.12 | *Coussapoa microcarpa* | - | 50.0 | 86.0 | 45.0 | - | 4.8 | 3.1 | 3.0 | - | 13.1 | 5.1 | 6.7 | - | 9.3 | 4.0 | 4.9 |
| 7.03 | *Ficus organensis* | - | 38.0 | 50.0 | 30.0 | - | - | 3.9 | 1.9 | - | 6.9 | 13.3 | 7.4 | - | 4.1 | 8.9 | 4.6 |
| 1.01 | *Coussapoa microcarpa* | 100.0 | 38.0 | 33.0 | 55.0 | 3.1 | 3.2 | 0.4 | 2.0 | 15.1 | 6.7 | | 6.3 | 9.1 | 4.8 | 0.2 | 4.1 |
| 1.12 | *Ficus organensis* | 100.0 | 38.0 | 33.0 | 55.0 | 12.5 | - | - | 2.6 | 4.1 | 3.8 | 5.4 | 4.5 | 5.6 | 2.8 | 3.1 | 3.6 |
| 2.66 | *Ficus insipida* | 83.0 | 50.0 | 33.0 | 55.0 | 9.7 | 3.6 | 2.9 | 4.6 | 8.4 | - | - | 2.1 | 6.8 | 1.0 | 1.0 | 2.5 |
| 10.16 | *Myrsine guianensis* | - | 63.0 | 17.0 | 30.0 | - | 1.5 | 3.4 | 0.5 | - | 6.9 | - | 3.8 | - | 4.8 | 1.9 | 2.4 |
| 1.40 | *Ficus organensis* | 33.0 | 100.0 | 17.0 | 55.0 | - | 11.3 | - | 4.0 | - | 2.6 | - | 1.0 | 0.1 | 4.9 | 0.0 | 1.8 |
| 2.39 | *Ficus organensis* | 67.0 | 13.0 | 50.0 | 40.0 | 2.2 | - | - | 0.5 | 3.0 | - | 3.5 | 2.1 | 2.6 | 0.2 | 2.0 | 1.5 |
| 16.08 | *Coussapoa microcarpa* | - | - | 50.0 | 15.0 | - | - | 0.8 | 0.5 | - | - | 6.9 | 2.1 | - | - | 3.3 | 1.3 |
| 9.02 | *Dasyphilum spineeis* | - | 63.0 | 33.0 | 35.0 | - | 6.7 | 0.1 | 2.4 | - | - | - | - | - | 1.9 | 0.0 | 0.7 |
| | **TOTAL** | 100 | 100 | 100 | 100 | 30.5 | 31.1 | 14.6 | 22.6 | 55.7 | 42.6 | 38.1 | 44.7 | 39.5 | 35.5 | 26.5 | 32.8 |

**Table 6** – Mean ± s.d. tree visibility index (VI, in %) for the most used trees during each period. Significant differences with the visibility of control trees are indicated (* indicates $p < 0.01$ and ** $p < 0.05$).

| | North | | | | South | | | | West | | | | East | | | | TOTAL | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | bottom | middle | top | TOTAL | bottom | middle | top | TOTAL | bottom | middle | top | TOTAL | bottom | middle | top | TOTAL | bottom | middle | top | TOTAL |
| **summer** | 14 ± 15 | 31 ± 34 | 46 ± 39 | 30 ± 26 | 37 ± 40 | 56 ± 39** | 70 ± 38 | 54 ± 37** | 7 ± 10 | 36 ± 40 | 57 ± 40** | 33 ± 28 | 27 ± 25** | 55 ± 38 | 72 ± 39 | 51 ± 31 | 21 ± 16** | 45 ± 26** | 61 ± 32 | 42 ± 23** |
| **fall** | 11 ± 16 | 28 ± 31 | 51 ± 37 | 30 ± 25 | 43 ± 40* | 65 ± 39* | 77 ± 37* | 62 ± 36* | 11 ± 18 | 49 ± 40* | 68 ± 36* | 43 ± 28* | 27 ± 33** | 51 ± 39 | 73 ± 36** | 50 ± 32** | 23 ± 19* | 49 ± 26* | 67 ± 28* | 46 ± 23* |
| **winter-spring** | 12 ± 16 | 34 ± 34 | 46 ± 35 | 31 ± 27 | 38 ± 37* | 66 ± 37* | 77 ± 36** | 60 ± 34* | 10 ± 18 | 35 ± 33* | 61 ± 36* | 35 ± 26* | 20 ± 22 | 57 ± 41 | 74 ± 37** | 50 ± 30 | 20 ± 18 | 48 ± 24* | 64 ± 25** | 44 ± 22** |
| **TOTAL** | 13 ± 17 | 30 ± 33 | 50 ± 36 | 31 ± 26 | 48 ± 42* | 69 ± 37* | 83 ± 33* | 67 ± 35* | 11 ± 17 | 51 ± 39* | 76 ± 34* | 46 ± 26* | 29 ± 31** | 56 ± 40 | 77 ± 34** | 54 ± 32** | 25 ± 18* | 52 ± 24* | 71 ± 25* | 49 ± 21* |

## Monitoring

Three species during the Summer, four species during the Fall and five species in the Winter-Spring sampling period accounted for 50% of the feeding records, while nine, eight and 11 species accounted for 80% of them in each period, respectively. Overall, five and 11 species accounted for 50 and 80% of the group's diet, respectively, during the study.

The number of trees used of a given species was significantly correlated with its contribution to the group's diet during all the periods sampled (Summer: $r_s = 0.5606$, $p = 0.0044$, n = 24; Fall: $r_s = 0.4815$, $p = 0.0171$, n = 24; Winter-Spring: $r_s = 0.5763$, $p = 0.002$, n = 26). However, when only those species that have contributed more than 2% of the feeding time in each period are considered, a significant relationship was only observed during the Winter-Spring period ($r_p = 0.7019$, $p = 0.0075$, n = 13).

The greater contribution of a large number of trees to the group's diet during the Winter-Spring period was also seen when the ratio of feeding trees to total number of trees used of each species was considered. While during the Summer period, of those species that contributed 50% to the group's diet, an average of 49% of the trees visited were consumed, during the Fall period this value increased to 62% of the trees used and reached its maximum use during the Winter-Spring period with a contribution of 71% of feeding use (Figure 7). Besides, in all the sampling periods, the more a species was visited, the less the number of trees used for feeding of that species (Summer: $r_s = -0.6368$, $p = 0.\ 0008$, n = 24; Fall: $r_s = -0.5633$, $p = 0.0041$, n = 24; Winter-Spring: $r_s = -0.4542$, $p = 0.0197$, n = 26). In other words, the greater the tree use of a plant species, the greater was the selectivity of its consumption.

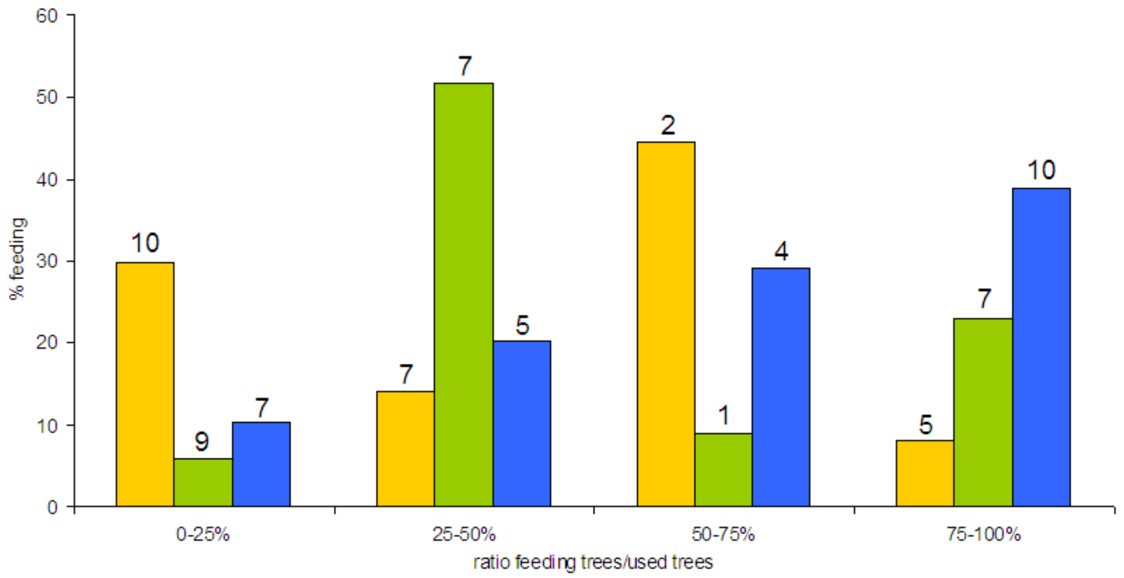

**Figure 7** – Percentage of feeding trees of the total number of trees used per species (Summer – orange; Fall – green; Winter-Spring – blue). Data are presented in feeding contribution per interval of percentage of trees used for feeding (from the total number of each species used trees). Numbers of species representative of each value are presented (feeding of vine species not included).

## Memory load

Although the study group used 654 trees and the consumption of the 249 feeding trees was highly variable, route-based foraging patterns can be identified. The first evidence that indicates the use of travel routes in our study was the repetition of tree use patterns observed (Figure 8). A daily average of 67% of repetitive tree use was observed during the study period. In the Winter-Spring, the last sampling period, an average of 74% of the trees used daily had already been visited before. When only feeding trees were considered, a daily average of 67% of the trees has already been used in previous days (47% in the Summer, 81% in the Fall and 66% in the Winter-Spring), as summarized in Figure 9. It should be noted that, although the number of trees that can be used by the group in the forest fragment is limited, there are, at least, 3000 trees with DBH > 10 cm in the area, based on species density data.

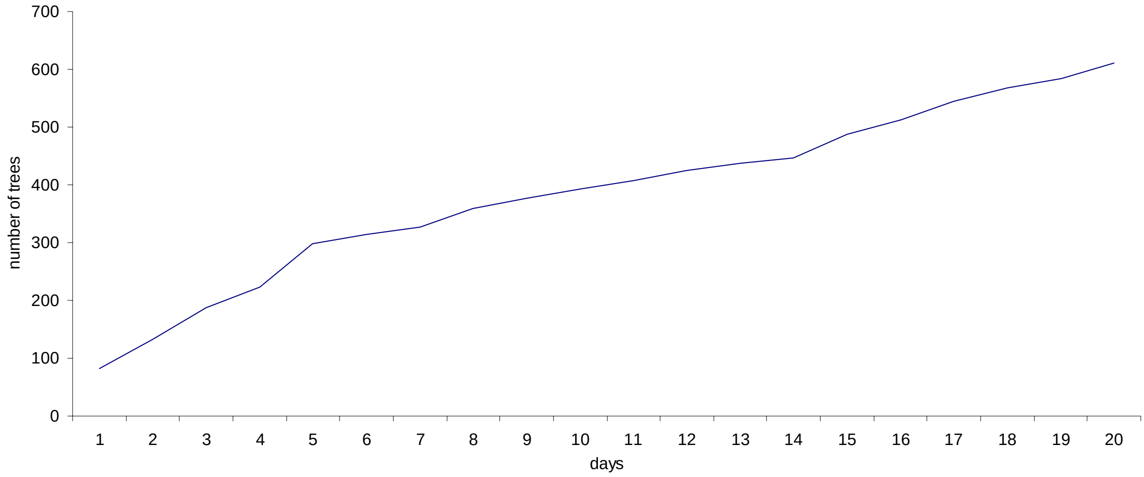

**Figure 8** – Accumulative number of trees used by the study group during the study.

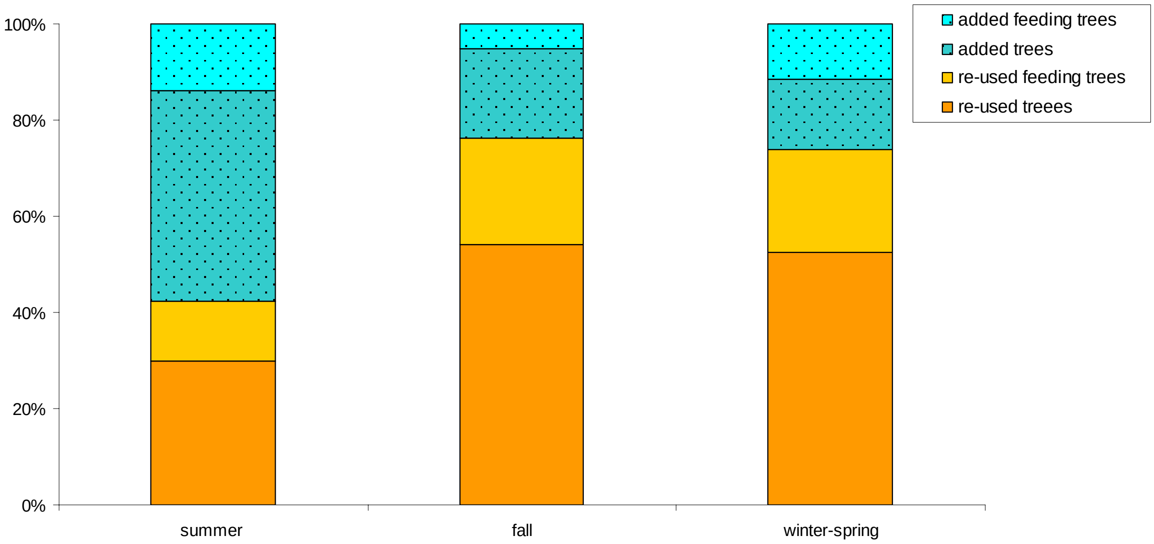

**Figure 9** – Mean daily percentage of trees and feeding trees added and re-used during each sampling period.

During the Winter-Spring period, when the group used the highest daily mean number of trees and feeding species during the study, 40% of the feeding time was spent on trees used only during this period (N = 77 trees), while the other 44% (n = 53 trees) and 16% (n = 19 trees) were consumed on trees first used during the Summer and Fall periods, respectively. During the Fall period, on the other hand, of the 75 feeding trees used in Summer, 55 were re-used and represented 71% of the group's diet, while 30 newly used trees in the Fall period comprised the other 29% of their feeding time.

Similar patterns observed on large-scale analyses were also seen when a small-scale tree to tree use pattern was considered. In order to address this question, the number of neighboring trees of 389 randomly selected trees used by the group was counted. Then, the number of surrounding trees that were used from the target tree and a ratio between the trees used and the possibilities of use from the target tree was determined. From 41% of the target trees (n = 389 trees), up to 40% of the neighboring trees were used (Figure 10). If only the target trees used for traveling are considered, this percentage increases to 50% of the trees used. On the other hand, of 69% of the trees used for resting, more than 60% of the surrounding trees were used, highlighting their use as important pivotal trees (see further evidence below).

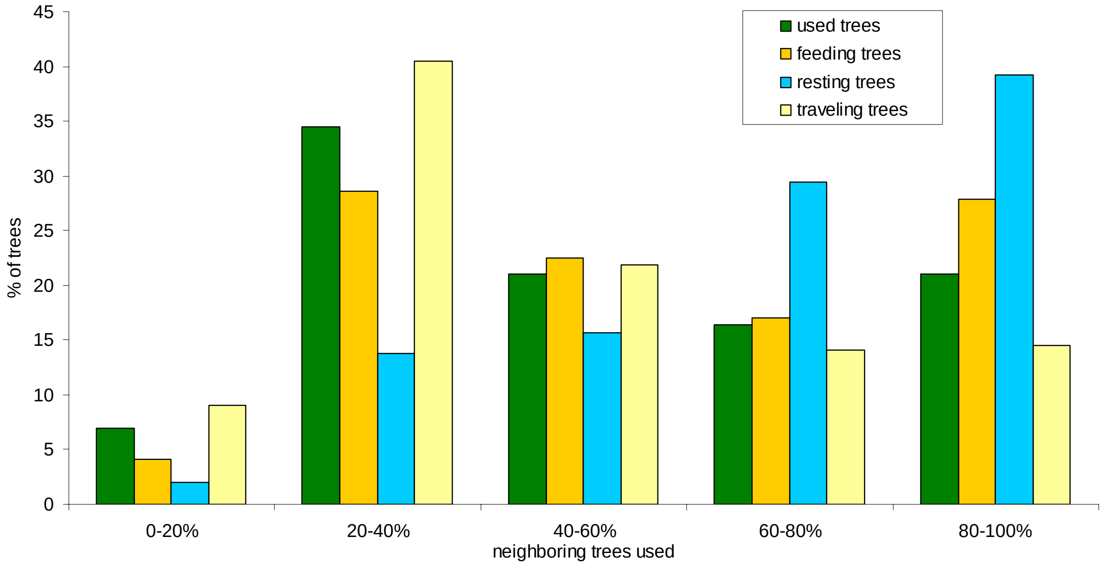

**Figure 10** – Intensity of use of neighboring trees considering the activity observed at each target tree (feeding, resting and traveling).

## Distance traveled

To analyze the extent to which the howlers minimize the distance traveled between feeding sites, the efficiency of the routes taken compared to the shortest distance between the used feeding trees (D/L – see Methods) was first tested. While the mean distance traveled between feeding trees was 81.6 m in Summer, 71.9 m in Fall and 52.8 m in Winter-Spring, the mean shorter distance between those trees was 39.6 m, 40.6 m and 28.0 m at each period sampled, respectively. These values were significantly lower than the patterns observed in all sampling periods ($U = 24660.5$, $p < 0.0001$, $n = 265$). During Summer and Fall, respectively, 33 and 42% of the steps between feeding trees were shorter than 40 m, while in the Winter-Spring sampling period this value increased significantly to 53% of the distance traveled ($H = 9.6667$, $p = 0.0019$, $df = 1$; $H = 5.1932$, $p = 0.0227$, $df = 1$, respectively), as shown in Figure 11A. Likewise, when considered the straight-line distance between consecutive feeding trees, up to 75% of consecutive feeding trees where less than 40 m apart of one another in the Winter-Spring period (Figure 11B), significantly higher than the pattern observed during the Summer (62%) and Fall (63%) ($H = 5.9945$, $p = 0.0144$, $df = 1$; $H = 9.5443$, $p = 0.002$, $df = 1$, respectively).

The average straight-line distance between used feeding trees was 35.5 m and the mean efficiency value of traveling (D/L) was 0.67 (Figure 12), being significantly lower during the Summer sampling period (0.59) only when compared with the higher efficiency rate observed during the Fall sampling period (0.70) ($H = 5.5932$, $p = 0.018$, $df = 2$), which was similar to the pattern observed during the Winter-Spring period (0.68) ($H = 0.292$, $p = 0.589$, $df = 2$) (Table 7).

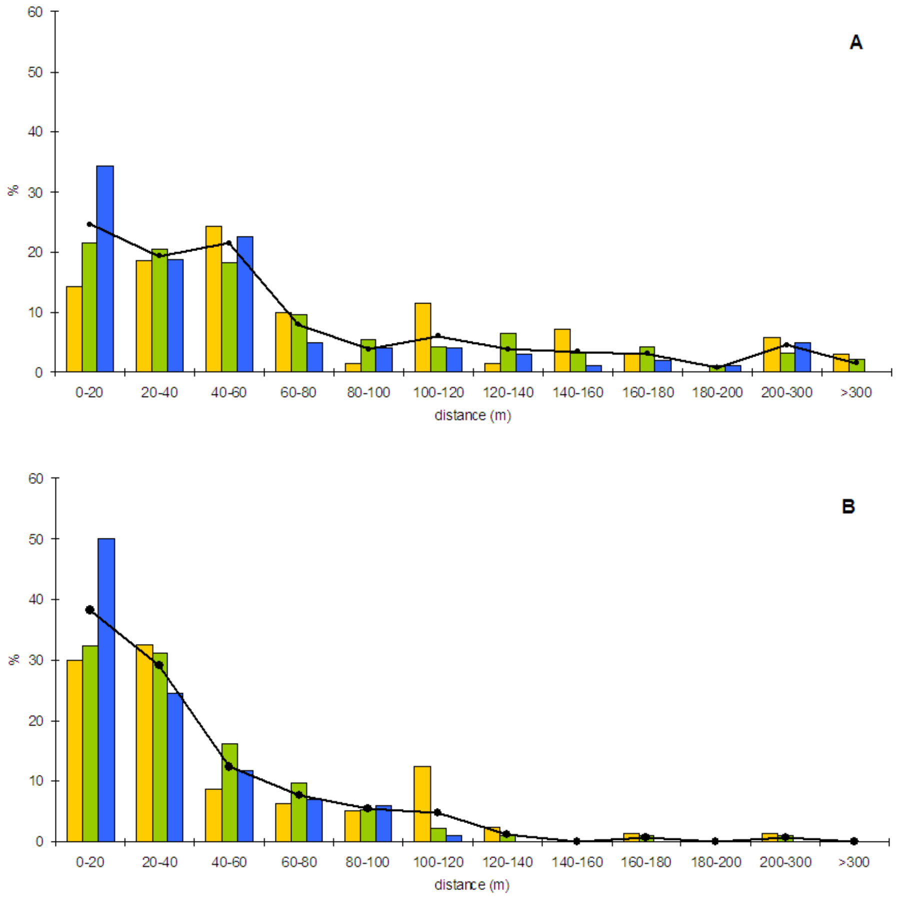

**Figure 11** – (**A**) Distance traveled (l) and (**B**) straight-line distance (d) between feeding trees used consecutively during each sampling period (Summer – orange; Fall – green; Winter-Spring – blue; total - dark line).

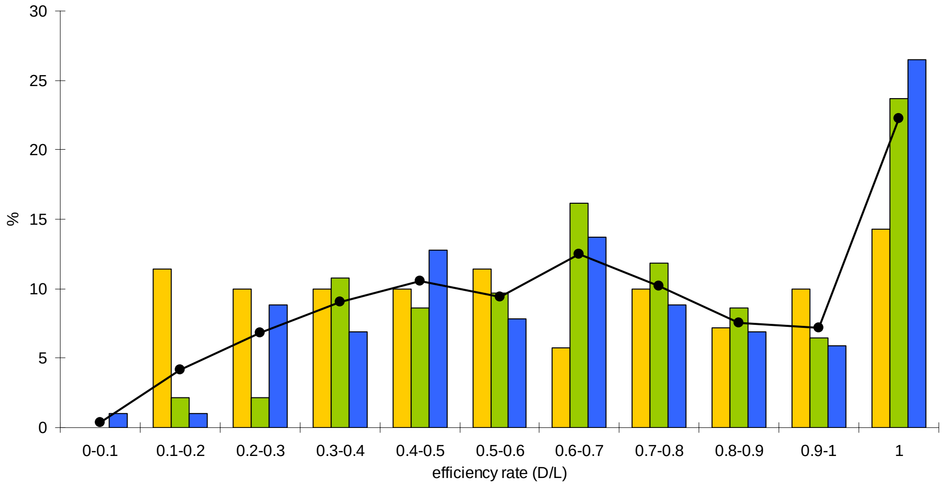

**Figure 12** – Average efficiency rate (straight line distance between feeding trees/observed distance) of tree use during the periods sampled (Summer – orange; Fall – green; Winter-Spring – blue; total - dark line).

**Table 7** – Average efficiency rate (straight line distance between feeding trees/observed distance) observed per species in each period sampled (number of feeding trees indicated in parenthesis).

| Species | Summer | Fall | Winter-spring | TOTAL |
|---|---|---|---|---|
| *Miconia rigidiuscula* | - | 1.00 (1) | - | 1.00 (1) |
| *Nectandra megapotamica* | - | - | 0.96 (2) | 0.96 (2) |
| *Sloanea monosperma* | 0.91 (1) | - | - | 0.91 (1) |
| *Diospyros inconstans* | - | 0.83 (3) | 0.92 (8) | 0.89 (11) |
| *Matayba elaeagnoides* | 1.00 (1) | - | 0.64 (1) | 0.82 (2) |
| *Banara parviflora* | 0.83 (3) | 0.62 (1) | 0.79 (5) | 0.78 (9) |
| *Trichilia clausenii* | 0.73 (3) | - | - | 0.73 (3) |
| *Guapira opposita* | 0.63 (6) | - | 0.74 (19) | 0.71 (25) |
| *Casearia decandra* | - | - | 0.71 (1) | 0.71 (1) |
| *Sorocea bonplandii* | 0.74 (1) | - | 0.67 (7) | 0.68 (8) |
| *Zanthoxylum hyemalis* | 0.34 (1) | 0.74 (8) | 0.66 (8) | 0.68 (17) |
| *Ficus organensis* | 0.64 (24) | 0.73 (22) | 0.58 (5) | 0.68 (51) |
| *Ficus insipida* | 0.57 (11) | 0.75 (13) | 0.67 (10) | 0.67 (34) |
| *Coussapoa microcarpa* | 0.37 (7) | 0.66 (21) | 0.81 (10) | 0.65 (38) |
| *Solanum peseudo-quina* |  | - | 0.64 (2) | 0.64 (2) |
| *Myrsine guianensis* | 0.42 (1) | 0.68 (6) | 0.64 (3) | 0.61 (10) |
| *Zanthoxylum rhoifolium* | 0.77 (2) | 0.68 (5) | 0.50 (6) | 0.61 (13) |
| *Allophyllus edulis* | - | - | 0.59 (3) | 0.59 (3) |
| *Dasyphilum spineeis* | 0.26 (1) | 0.71 (6) | 0.49 (6) | 0.57 (13) |
| *Psidium cattleianum* | - | 0.56 (1) | - | 0.56 (1) |
| *Myrcianthes gigantea* | 0.56 (1) | - | - | 0.56 (1) |
| *Vitex megapotamica* | 0.29 (1) | 1.00 (1) | 0.39 (1) | 0.56 (3) |
| *Inga uruguensis* | - | 0.52 (1) | - | 0.52 (1) |
| *Campomanesia xanthocarpa* | - | 0.51 (1) | - | 0.51 (1) |
| *Luehea divaricata* | 0.84 (1) | - | 0.29 (2) | 0.47 (3) |
| *Chrysophyllum gonocarpum* | 0.46 (4) | - | 0.32 (1) | 0.43 (5) |
| *Lithraea brasiliensis* | 0.18 (1) | 0.59 (1) | - | 0.38 (2) |
| *Sebastiania commersoniana* | - | 0.31 (2) | 0.43 (1) | 0.35 (3) |
| *Ocotea pulchella* | - | - | 0.30 (1) | 0.30 (1) |
| TOTAL | 0.59 (70) | 0.70 (93) | 0.68 (102) | 0.67 (265) |

A second analysis verified the difference between the straight-line distance connecting two consecutive feeding trees (A-B) and the distance between A and the nearest tree to A belonging to the same species as B. In 45.5% of the feeding trees analyzed the howlers utilized the nearest tree of species B (41.4% in Summer, 42.6% in

Fall and 51% in Winter-Spring) and in 38% of the cases the distance to the nearest tree belonging to species B was only 30 m shorter than the distance to the tree used for feeding (41.4% in Summer, 36.2% in Fall and 37.3% in Winter-Spring) (Figure 13). Only during the Fall sampling period the group fed from trees located significantly more distant than those available of the same species as B (H = 5.4516, $p = 0.0196$, $df = 1$). When species with a higher contribution to the group's diet are considered, only the feeding trees of *Coussapoa microcarpa* and *Guapira opposita* were located more distant than those available from these species (H = 10.0739, $p = 0.0015$, $df = 1$; F = 9.5713, $p = 0.0036$, $df = 1$, respectively). This pattern was not observed in relation to feeding trees of *Ficus organensis* (H = 0.6832, $p = 0.4085$, $df = 1$), *Ficus insipida* (H = 0.2348, $p = 0.628$, $df = 1$), *Zanthoxylum hyemalis* (H = 1.7139, $p = 0.1905$, $df = 1$) and *Diospyros inconstans* (H = 2.9165, $p = 0.0877$, $df = 1$).

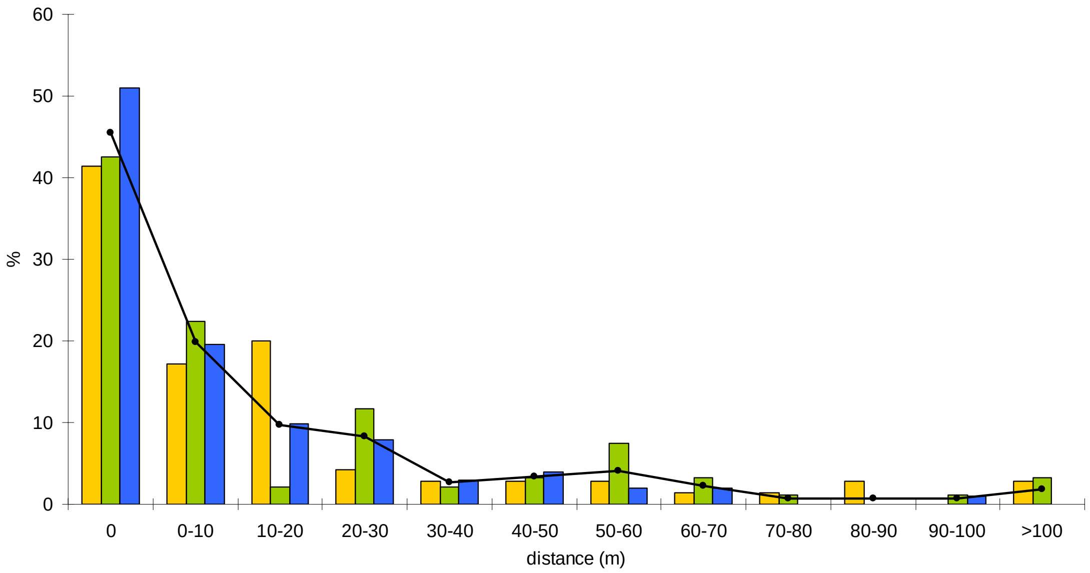

**Figure 13** – Difference between the distance to the nearest feeding tree of species B after departing from tree A to the distance between the feeding tree of species B used from tree A at each period sampled (Summer – orange; Fall – green; Winter-Spring – blue; total - dark line). Data are presented in percentage of trees per distance difference interval.

On the other hand, when the straight-line distance between consecutive feeding trees (A-B) and the distance between A and the nearest tree used for feeding in each sampled period, apart from its identification, were compared, another pattern was observed. Only 21.8% of the feeding trees used were the nearest feeding tree from tree A (17.1% in Summer, 16% in Fall and 30.4% in Winter-Spring), while 47.4% were at most 30 m more distant than another tree used for feeding during the same period (50% in Summer, 48.9% in Fall and 44.1% in Winter-Spring) (Figure 14).

Feeding trees were significantly more clumped during the Summer than in Fall (H = 5.4322, *p* = 0.0198, *df* = 1), but in every period sampled there was a feeding tree located significantly closer to feeding tree A than the following feeding tree used (Summer: H = 51.8458, *p* < 0.0001, *df* = 1; Fall: H = 45.2025, *p* < 0.0001, *df* = 1; Winter-Spring: H = 16.8006, *p* < 0.0001, *df* = 1) (Table 8).

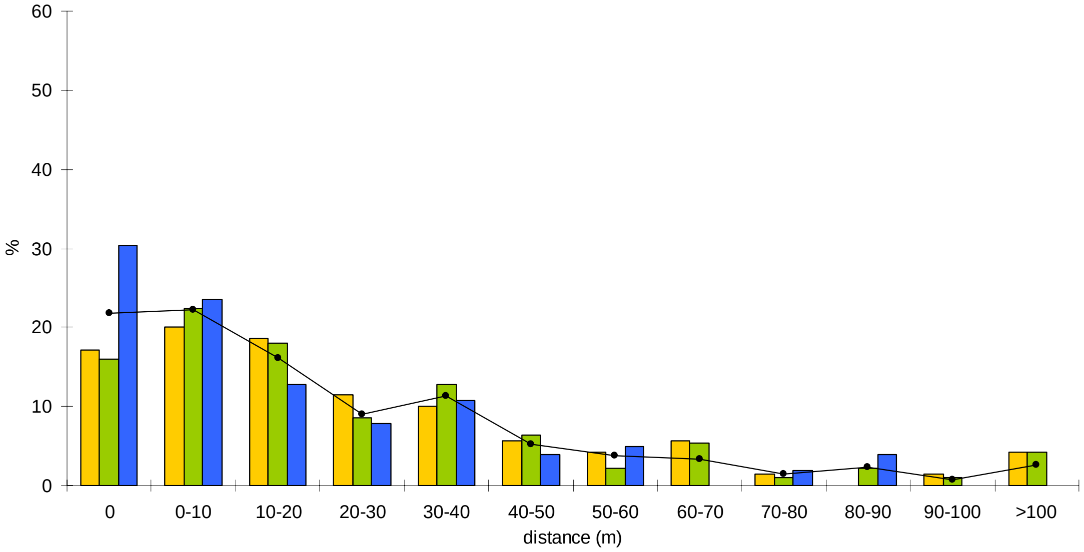

**Figure 14** – Difference between the distance of the closest feeding tree used at each period from tree A to the distance between the feeding tree used from tree A at each period sampled (Summer – orange; Fall – green; Winter-Spring – blue; total - dark line). Data are presented in percentage of trees per distance difference interval.

**Table 8** – Species distances between tree A and the used feeding tree B, the closest tree from species B and the closest feeding tree, apart from its identification. If the closest tree was the one being used, the next was considered. Number of feeding bouts considered per species is indicated.

| Species | straight-line distance between A-B | closest tree (spp B) | closest tree (feeding tree) | n |
|---|---|---|---|---|
| *Ficus organensis* | 49.0 ± 43.3 | 37.7 ± 22.7 | 12.4 ± 8.0 | 51 |
| *Coussapoa microcarpa* | 37.3 ± 40.5 | 18.3 ± 10.5 | 15.1 ± 9.9 | 38 |
| *Ficus insipida* | 45.3 ± 40.2 | 31.8 ± 16.4 | 13.1 ± 7.5 | 34 |
| *Guapira opposita* | 30.1 ± 24.8 | 13.8 ± 9.1 | 13.1 ± 7.6 | 25 |
| *Zanthoxylum hyemalis* | 27.9 ± 22.9 | 18.4 ± 14.7 | 9.6 ± 6.9 | 17 |
| *Dasyphilum spineeis* | 36.2 ± 25.2 | 56.3 ± 35.9 | 12.6 ± 7.2 | 14 |
| *Zanthoxylum rhoifolium* | 20.4 ± 18.1 | 15.8 ± 17.9 | 12.9 ± 9.4 | 13 |
| *Diospyros inconstans* | 10.2 ± 11.0 | 14.7 ± 9.1 | 15.6 ± 5.4 | 11 |
| *Myrsine guianensis* | 26.7 ± 19.1 | 20.4 ± 10.9 | 16.0 ± 11.7 | 10 |
| *Banara parviflora* | 35.5 ± 26.1 | 38.3 ± 28.0 | 11.6 ± 10.2 | 9 |
| *Sorocea bonplandii* | 25.0 ± 27.3 | 50.6 ± 40.5 | 13.0 ± 8.9 | 8 |
| *Chrysophyllum gonocarpum* | 14.4 ± 5.3 | 17.4 ± 8.3 | 8.8 ± 3.3 | 5 |
| *Vitex megapotamica* | 39.7 ± 49.2 | 39.1 ± 11.5 | 13.6 ± 3.2 | 3 |
| *Luehea divaricata* | 37.2 ± 33.5 | 34.1 ± 21.5 | 9.6 ± 4.7 | 3 |
| *Allophyllus edulis* | 32.2 ± 32.3 | 48.8 ± 37.9 | 22.7 ± 17.2 | 3 |
| *Trichilia clausenii* | 22.4 ± 5.1 | 20.6 ± 9.6 | 17.9 ± 9.6 | 3 |
| *Sebastiania commersoniana* | 16.7 ± 14.3 | 20.5 ± 4.3 | 8.2 ± 9.1 | 3 |
| *Solanum peseudo-quina* | 58.7 ± 16.9 | 154.5 ± 1.2 | 27.7 ± 5.2 | 2 |
| *Lithraea brasiliensis* | 26.2 ± 15.0 | 22.7 ± 1.0 | 21.7 ± 6.9 | 2 |
| *Nectandra megapotamica* | 20.2 ± 5.6 | 19.2 ± 11.1 | 9.5 ± 3.5 | 2 |
| *Matayba elaeagnoides* | 13.3 ± 6.5 | 32.6 ± 4.0 | 5.9 ± 4.8 | 2 |
| *Myrcianthes gigantea* | 94.9 | 13.4 | 20.8 | 1 |
| *Ocotea pulchella* | 67.4 | 96.3 | 8.7 | 1 |
| *Campomanesia xanthocarpa* | 40.8 | 16.6 | 10.5 | 1 |
| *Psidium cattleianum* | 39.9 | 40.4 | 6.1 | 1 |
| *Casearia decandra* | 23.0 | 32.1 | 23.1 | 1 |
| *Miconia rigidiuscula* | 22.3 | 13.6 | 9.3 | 1 |
| *Inga uruguensis* | 17.7 | 11.9 | 12.4 | 1 |
| *Sloanea monosperma* | 16.8 | 5.5 | 13.6 | 1 |
| TOTAL | 35.5 ± 34.0 | 29.1 ± 25.0 | 13.2 ± 8.4 | 266 |

## Energy gain

DBH of the major feeding trees was compared with the DBH of trees of the same species that were not used for feeding to analyze the extent to which howlers maximize energy gain by using the largest resources available. DBH of the 58 feeding trees belonging to eight species was significantly greater than the DBH of those trees not used for feeding (H = 16.3412, $p < 0.0001$, $df = 1$). However, a per species analysis indicates only feeding trees of *Coussapoa microcarpa* (t = 3.6775, $p = 0.0005$, $df = 66$) and *Guapira opposita* (F = 10.6051, $p = 0.0019$, $df = 99$) were significantly greater than their not used conspecifics. When associating the overall species consumption of the most important feeding species (> 1% of the overall feeding) with the average DBH of these species feeding trees, species consumption rate showed to be positively related to DBH (Linear regression: $R^2 = 60.99$, $p < 0.0006$, n = 14; Figure 15).

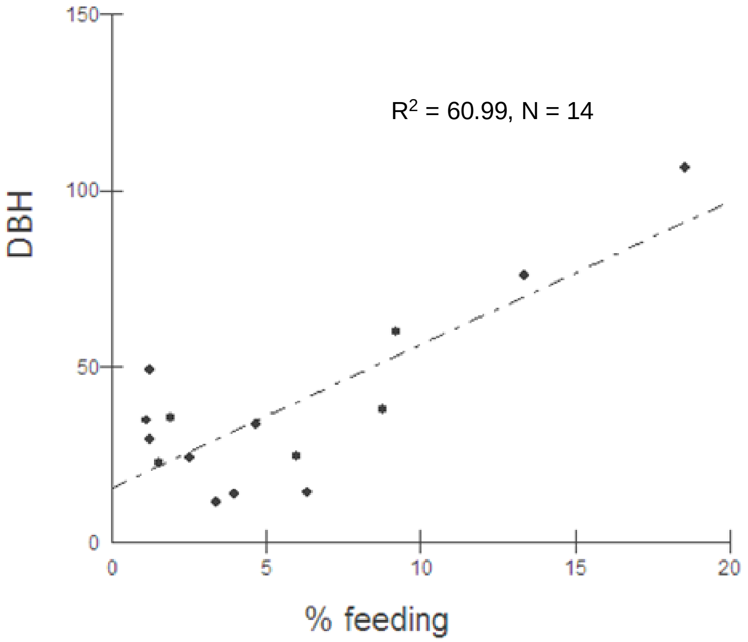

**Figure 15** – Relationship between species consumption and feeding trees' DBH.

These results have to be interpreted cautiously since, when removing the three larger and most important feeding species (*Ficus organensis*, *Coussapoa microcarpa* and *Ficus insipida*), this relationship disappears ($R^2 = -5.92$, $p < 0.5541$, n = 11). However, when considering all the trees eaten of this three species and their relative feeding contribution during the study, the same significant positive association is presented, ($R^2 = 11.28$, $p < 0.0322$, n = 39) (Figure 16).

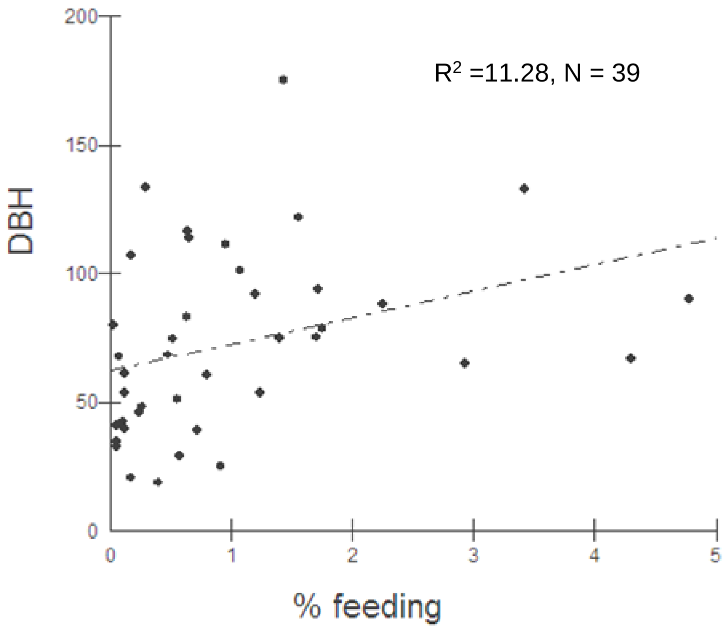

**Figure 16** – Relationship between tree consumption and feeding trees' DBH of *Ficus organensis*, *Coussapoa microcarpa* and *Ficus insipida*.

### Angular deviation

If the group moves through independent route segments, it could be expected the angular deviation between consecutive feeding trees to be uniformly distributed around a 360° circumference rather than concentrated in a particular direction. On the other hand, such a concentration would support the idea howler monkeys forage over aligned, possibly more efficient, traveling routes. The Rayleigh test ($Z$), in fact, indicated that during the Fall ($r = 0.0929$, $Z = 0.8715$, $u = 2.9881$, $p$ = ns, $n = 101$) and Winter-Spring ($r = 0.0802$, $Z = 0.733$, $u = 2.9894$, $p$ = ns, $n = 114$) the routes between feeding trees were not clumped in any specific direction. However, angles are significantly clumped during the Summer ($r = 0.2351$, $Z = 5.0294$, $u = 4.5723$, $p < 0.01$, $n = 91$) and when all routes between feeding trees used throughout the study are analyzed together ($r = 0.1024$, $Z = 3.2112$, $u = 2.992$, $p < 0.05$, $n = 306$) (Figure 17). The clumping observed during the Summer sampling period may be partially attributed to non-uniform distribution of the angular deviation in feeding trees of *Ficus organensis* (Figure 18), the most important feeding species in this period ($r = 0.3779$, $Z = 3.5699$, $u = 2.966$, $p < 0.05$, $n = 25$). This distribution was also presented for *Ficus insipida* during the Fall sampling period ($r = 0.5644$, $Z = 3.5039$, $u = 2.926$, $p < 0.05$, $n = 11$) and when all feeding bouts at this species were analyzed together ($r = 0.3232$, $Z = 3.2375$, $u = 2.9715$, $p < 0.05$, $n = 31$; Figure 19).

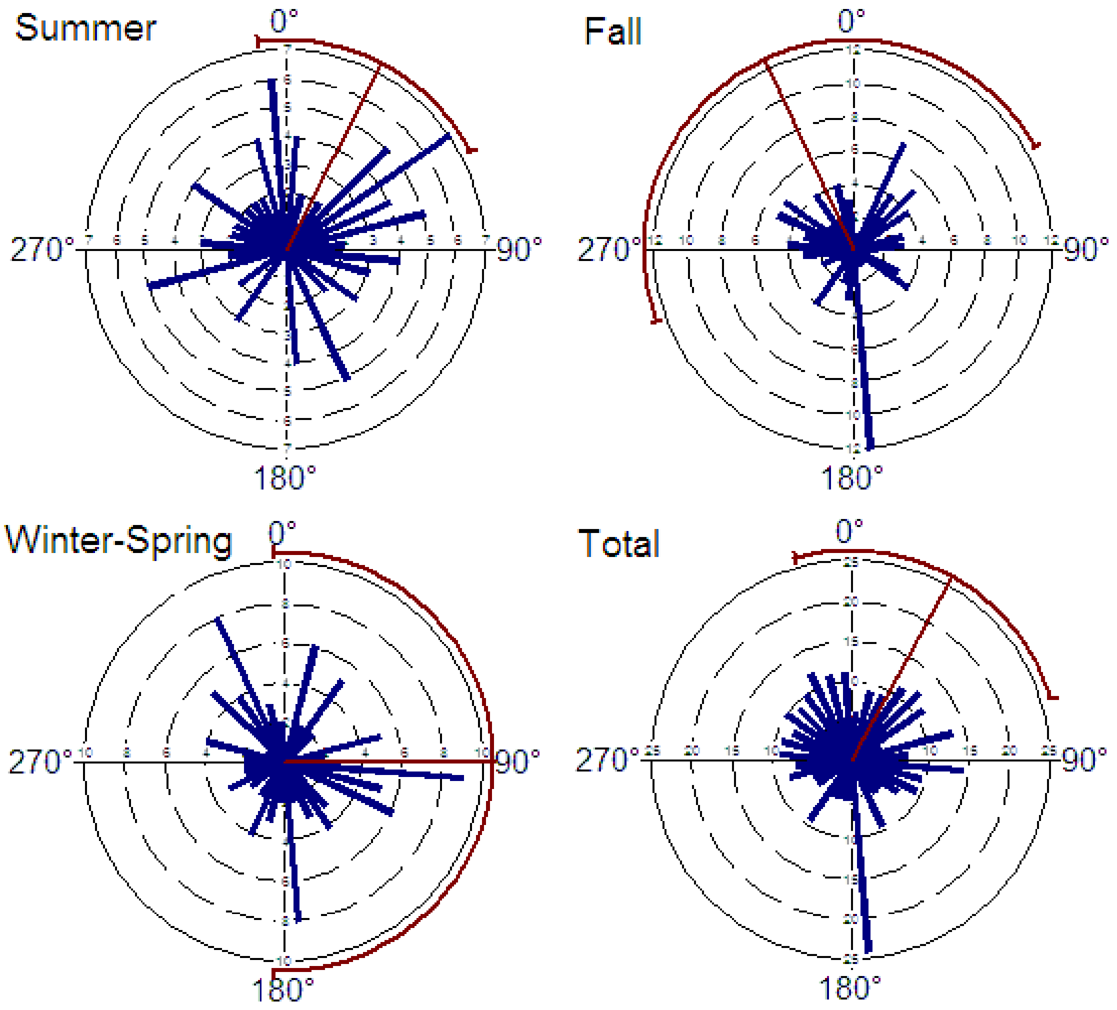

**Figure 17** – Circular distribution plot of the turning angle between consecutive feeding trees in the periods sampled and during the entire study.

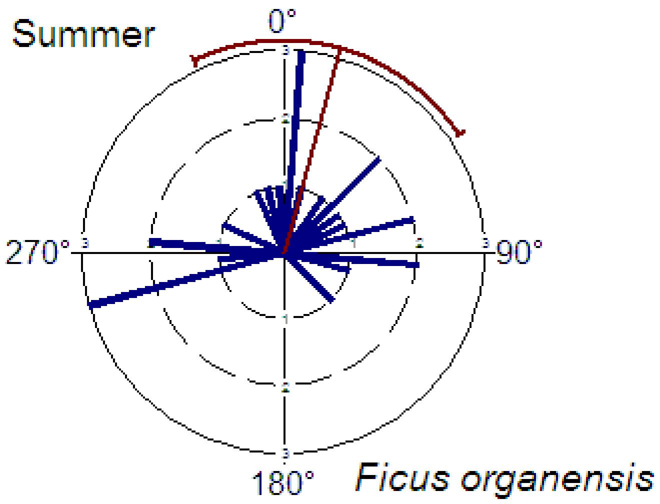

**Figure 18** – Circular distribution plot of the turning angle between feeding bouts on trees of *Ficus organensis* during the Summer.

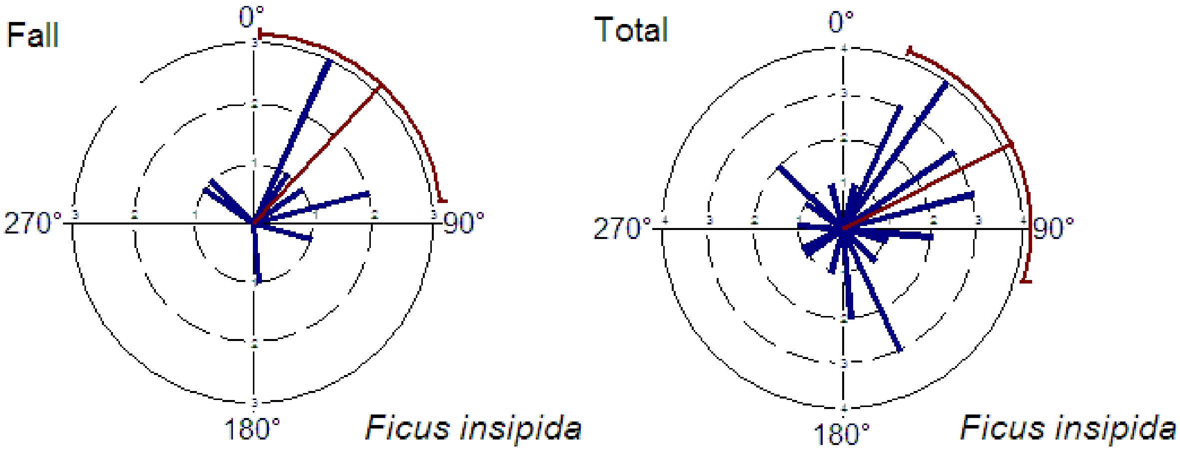

**Figure 19** – Circular distribution plot of the turning angle between feeding bouts on trees of *Ficus insipida* in the Fall and during the entire study.

As the number of feeding records per tree (see Material and Methods) was insufficient to perform statistical analyses at each sampling period, it was only analyzed the sum of the total angular deviation observed at each tree. None of the target trees (see memory load results) angular deviation was clumped around specific directions. Similar results were found when only resting trees were considered in the analyses.

# DISCUSSION

Evaluating the extent to which animals use spatial information during foraging can be as difficult as affirming they don’t (see Bennet 1996, Janson and Byrne 2007). Based on existing evidence of primate spatial knowledge, four predictions were tested on how environmental features influence the foraging behavior of a folivore-frugivore primate species. Overall, the differences found at each period sampled indicate that environmental features used by animals to obtain positional and directional information during foraging vary spatially and temporally (Dyer 1998).

The prediction that howlers minimize the distance traveled by consecutively visiting the nearest tree of a few preferred species was partially confirmed. In almost half of the feeding bouts analyzed, the group used the nearest available feeding tree of a given species. Besides, they used more distant feeding trees of only two of the six most consumed species, considering that they both occur at high densities at the forest fragment. On the other hand, in 78% of the feeding bouts there was a closer feeding tree of a different species available and, in addition, the feeding trees used in Fall were located significantly further away than the closest tree available of particular species, indicating that minimizing distance traveled was not always the foraging strategy used by the group.

Primates are usually described to move to the nearest resource available, considering that previous studies reported that 44 to 85% of the moves between feeding patches follow this pattern (Menzel 1973, Garber 1989, Janson 1998). Whenever primates do not move to the nearest resource available, it is suggested they bypass them in favor of more productive sources (Garber 1989, Janson 1998, Cunningham and Janson 2007) or irreplaceable ones, such as water holes (Sigg and Stolba 1981, Noser and Byrne 2007). If traveling to the nearest resource indicates the monkeys know the spatial location of their targets and ways to minimize energy spent traveling, the movements to more distant patches also may be interpreted as evidence of spatial knowledge. In this case, this strategy could maximize energy gain if the resources located farther away are more productive (Prediction 2). In fact, during the only period when howlers fed from trees significantly more distant than the nearest sources belonging to the same species, they used a lesser number of *Ficus organensis* trees for consumption that in Summer (9 trees in Summer and 5 in Fall, although similar number of trees of this species were visited during these periods – 14 and 12, respectively), but ate a similar amount of fruits from this species in both periods. Besides, during Fall they also visited this species in a lesser degree than in Summer (9% of the visited trees in Summer and 6% in Fall).

Although seasonal variations in trees' productivity were not analyzed, if considered that howlers tend to intensively use fruits when available (Milton 1980, Julliot 1996, Silver et al. 1998, Pavelka and Knoff 2004, Cristóbal-Azkarate and Arroyo-Rodríguez 2007), the greater fruits availability during Fall of a few *Ficus organensis* trees, can also be inferred once a few fruiting trees were used for more consecutive days and more intensively (greater consumption per visit) than during the previous period. These results during Fall, thus, corroborate with the second prediction that the troop used intensively a few highly productive feeding sources, responding for the high fruit consumption of the species during the period, in expense of closer, but less valuable, trees of this species.

The second prediction is also confirmed when considering DBH as a surrogate for estimating tree productivity (Chapman et al. 1992). Not only the average species DBH was positively related with species consumption, but feeding trees were significantly larger than those of the same species that were visited but not used as food sources. However, larger targets are also visible from longer distances than small ones (Janson and Di Bitetti 1997, Noser and Byrne 2006, 2007). The mean straight line distance between feeding trees was similar or smaller than the field of visual perception of forest-dwelling primates (Terborgh 1983 – 10 to 15 m, Garber and Hannon 1993 – 20 m, Janson and Di Bitetti 1997 – 25-50 m, Dominy et al. 2001 – 20 to 30 m). This field of visual detection may vary as a consequence of resource type (Noser and Byrne 2007), resource size (Janson and Di Bitteti 1997) and forest type (Terborgh 1983). But if the distance between consecutive feeding trees was within the field of perception, why did the study group traveled significantly farther to reach them?

Although direct travel to feeding trees would be a good strategy to minimize distance traveled and optimize energy gain, another strategy may be inferred from the pattern observed. The third tested prediction states that howlers would use a repetitive number of trees and paths in a way of both reducing the memory input of information and monitoring the availability of potential food sources. By the end of the study, the group visited only 20% of the available trees with DBH ≥10 cm, although tree use rates were strongly predicted by species IVI, and presented a daily mean repetitive tree use of 67%. Although the number of days analyzed was small, the trees that were added in the last two periods were located next to sources already visited. Carperter (1964) notes that howlers move “roughly over the same route”, while Milton (1977, 1980, 2000) notes that, at times, it can be predicted where the troop is going by the time they begin to travel and what they will eat when they get there. Translocated troops were described to progressively limit their range area and establish traveling paths over areas of greater relative cover of major feeding species, whereas established groups showed greater knowledge of travel paths and more intensive use of quality food resources (Ostro et al. 1999, 2000).

Traveling longer distances would be favored if monitoring a few preferred species enhances the net energy gain, especially if it is considered that the energetic costs of traveling are, usually, overrated (Steudel 2000). The howlers presented a tree use pattern of the most important feeding species inversely associated with the amount of those trees used for feeding. This outcome may suggest monitoring of a few staple food species, if considered that the detection of an important ephemeral item in one of these sources would lead to the visit of a great number of individual trees of that species and the selective consumption of those most productive individual trees.

At the same time, the howlers' feeding species consumption rate being positively related with species tree use indicates the opportunistic consumption of many different plant species described for howlers (Milton 2000). A folivorous species should favor the sampling and an opportunistic diet, favoring the reduction in the ingestion of toxic secondary components (Garber 1987).

Diverse foraging strategies characterized seasonal varying exploitation of different resources. During Summer, the overall great availability of *F. organensis* fruits, shown by the intensive use of most of this species trees for feeding, led to a distinctive foraging pattern according the consumption of ripe or unripe fruits of this species. Previous studies with wolly monkeys (Di Fiore 2003) and mangabeys (Janmaat et al. 2006) report that keeping track of species unripe fruits availability is a way of predicting future ripe fruits production. The more the troop fed on unripe fruits in Summer more they traveled and less they slept, making use of a greater number of resting trees for shorter periods of inactivity. Ripe fruits are a high-energy resource rich in nonstructural carbohydrates and simple sugars, easily digested, while unripe fruits may contain considerable amounts of fiber and secondary compounds (Milton 1998), making it worth to seek for ripe fruits. During Summer, accordingly, the greater was the consumption of ripe fruits of *F. organensis*, less they traveled and lower was the number of trees visited, corroborating with the monitoring of fruit species ripeness of prediction two.

Unlike the Summer and the Fall, a period also characterized by a high consumption of unripe fruits of *Coussapoa microcarpa* and vine flowers, the Winter-Spring presented a different foraging pattern possibly coupled with a decrease in fruit consumption. The high leaf, particularly young leaves, and flowers feeding was accompanied by a high linearity rate between feeding trees, mostly attributed to the clumped fashion they were distributed and the high use of a greater number of species and trees for feeding. The majority of the diet was obtained from species that the howlers used most of the visited trees for feeding, particularly on leaves. Leaves are usually considered as being uniformly distributed in space (Schoener 1971), however foods eaten by howlers, apparently, must provide them with high-quality protein and energy (Milton 1998). At this period, the high feeding percentage, the greater diversity of leaf species eaten and, especially, the great contribution of young leaves on diet, that usually have lower concentrations of secondary compounds and higher in protein (Garber 1987), infer a selectiveness over a higher nutritional and low toxic compounds diet.

And, although more than 50% of the feeding trees of this period haven’t been used at the previous periods (44% of the added trees were used for feeding), 60% of the diet was based on trees already used by the group. Also, if considered the 74% daily mean travel over previously marked trees and the 92% of resting at those trees (21 of 27 trees used for resting had been used at the previous periods), it was concluded that the troop intensively used known travel paths and fed, opportunistically, from small amounts of newly used trees located adjacent to the routine travel paths. This pattern has been suggested by Milton (2000) as a strategy that would avoid cognitive overload, while Janson and Byrne (2007), applying optimal patch-foraging rules (Stephens and Krebs 1987), point that the use of less valuable resources include short movements and fewer skipped resources, which is opposite of the patterns observed during Fall.

A route-based foraging pattern implies that the animal navigates effectively and relatively more efficient over a network of nodes in the environment (Di Fiore and Suarez 2007). From the 654 used trees, 33% of the time recorded was spent on 11 trees that were labeled as target trees of the study group. Those trees were reached from different directions during the study, connecting distinct route segments, and allowed greater visibility of the forest canopies as predicted. Although Garber and Jelinek (2006) reported distinct tree use (the mean number of trees used per day was nearly half the number used by the study group) and ranging pattern (travel paths were as low as one third the observed at the present study), possibly due to environmental, activity patterns, social influences, species-specific and methodological differences, they also reported *Alouatta palliata* to concentrate their foraging on a few larger trees of greater visibility that could be reached from different directions. Likewise, Milton (2000) highlights that the frequent use of routes between pivotal trees and along important feeding sources (acting as nodes or decision points) would increase howlers' foraging efficiency. Although major resting trees were not used as major feeding trees, their role as important decision-points still can be addressed, since the highest mean use of neighboring trees from these trees was observed, leading to diverse feeding patches, while the minority of neighboring trees was used from traveling tree, where more directional movement would occur. This would be an important characteristic in howlers' foraging once different dietary requirements throughout the day would be sufficed through distinct foraging paths, as already proposed.

Animals are generally known to use landmarks for location in familiar environments (Collett and Graham 2004) and lab studies on primates indicate that they have egocentric views of space (Poti 2000), consistent with the use of landmark in nature (Di Fiore and Suarez 2007, Noser and Byrne 2007). Following obvious fixed features of the environment may simplify the memorization and learning of specific routes between feeding patches (Di Fiore and Suarez 2007). The forest fragment presents a smooth declivity along its length, but as the density of trees canopies were quite regular, the probability of long distance orientation through visual detection field was reduced. However, the howlers did use more intensively trees of greater visibility and the shape of the forest fragment, similar to a "horseshoe" (see Figure 1), also led to distinct visibility from different directions (South and East coordinates presented higher visibility than North and West). Could this be interpreted as evidence that the howlers were using environmental features to visually locate feeding sources?

No, if considered that all fruits eaten by the group are cryptic in trees canopy (fruits of *Ficus organensis* and *Coussapoa microcarpa* length, at most, 2 cm) and the direction alignment of movements leading to *F. organensis* during Summer and *F. insipida* during Fall and the overall results were presented due the intensive use of two individual trees (tree IDs 1.05 and 2.66, considering the last was used 4 times more than the following most used *F. insipida* tree – see table 5) that were mostly reached through north oriented movements, where visibility was lower. Besides, the forest terrain presents declivity only in a small upper portion, and the majority of the routes and most used trees were located at a largest even portion. But yes, if considered that in large trees, food availability is relatively greater, particularly important if the species is regarded as staple source, as identified target trees (*Ficus organensis, F. insipida* and *Coussapoa microcarpa)*, and that the location of the majority of those most used trees were peripheral to the fragment. Then, rather than affirming the troop used visual perception for foraging, it can be said that the shape of the forest fragment influences the use of large pivotal trees located in its peripheries that can, thus, be label as landmarks.

The model of mental maps proposed by Gallistel (1990) and Gallistel and Cramer (1996) suggests that cognitive maps consist of landmarks placed on a geocentric frame of reference by vector addition. In other words, geocentric position is determined by path integration and positional fixes on known landmarks are used to deal with the error accumulation of path integration. Further models of mental map (Toolman 1948, O'Keefe and Nadel 1978) usually rely on the use of novel shortcuts, but Bennet's review (1996) of such pattern in distinct taxa points as premature such premise. Besides, identifying novel shortcuts would imply that the observer has complete knowledge of animals past experience, extremely rare in studies on nature.

Di Fiore and Suarez (2007), proposing the use of route-based maps in wolly and spider monkeys, consider that the use of routes would require only the store of distance information and linked views that would allow the recognition of routes during foraging, reinforced by repetitive use. This would, theoretically, reduce the need for "on-line processing" and continuously updating of distance and direction moved, attribute on path integration (Poucet 1993), leading the authors to conclude that the most probable representation of space used by their study groups was route-based maps.

Our data on brown howler monkeys is not sufficient to reach such conclusions. However, all four predictions proposed to explain howler foraging were, in some extent, supported by the group's foraging patterns. They not only used the nearest feeding tree of a few species, but also maximized energy gain by using more distant high productive sources. Networks of fixed routes of repetitive use between great visibility pivotal trees were observed, avoiding a cognitive overload in foraging and, indeed, were built along major feeding species that were monitored, especially during fruits availability periods, but also in lean high-energy food periods.

Our predictions were made based on evidence of non-folivore species, however they suit the behavior of howlers, apart from the greater overall contribution of leaves on their diet. Feeding on leaves would, actually, be a viable option for primates, since their abundance and availability, even of young parts, is much greater than flowers and green or ripe fruits (Milton 1998). Still, although advantageous, very few species base their diet on leaves as howlers (Eisenberg et al. 1972), since a great number of feeding adaptations, among digestive, anatomical and behavioral (see Crockett and Eisenberg 1987, Neville et al. et al. 1988, Crockett 1998, Milton 1998), have been reported to have evolved allowing such diet. Lucas et al. (2003) proposed that the evolution of trichromatic vision in catarrhine, routinely trichromatic (Kainz et al. 1998), and in *Alouatta*, what is unusual for platyrrhine species (Jacobs et al. 1996), is an adaptation that favors the consumption of higher quality leaves, namely young leaves. Dominy et al. (2003) went further, proposing that trichromatic vision was related with the biogeographic history of figs and palms, where evolved trichromacy would allow the exploitation of protein-rich young leaves as a replacement resource during periods of fruits shortage of these staple sources.

If different biological features, including sensory, evolved in the genus favoring its diet composition, why the spatial ability should be different? Our data supports that, although leaves are uniformly distributed on space, howlers present efficient use of spatial information that optimize a high-nutrient foraging intake, even in lean fruit periods. Considering that, brain size differences should not predict spatial skills and dietary patterns in primates, as already proposed (Mackinnon 1978, Clutton-Brock and Harvey 1980, Milton 1981a, 1988, 2000, Taylor and van Schaik 2007). Instead, the way neural network is organized, the amount of synapses presented and its plasticity are more likely to influence a species' cognitive capabilities.

Cognitive phenotypes are determined by genes and environment (Dukas 2004) and determining how cognitive demands posed by each species' environment should be further investigated, mainly on plastic phenotypes. Models, like mental maps, are useful for a better understand of congruent animals' evolution, but the diverse evidences of efficient use of spatial information, already observed at distinct taxa (see Dukas 1998, Sherry 1998, Shettleworth 1998), highlight the need for a better understand on how each species environment information are interpreted and represented, influencing on niche segregation (Beecham 2001).

This study presents evidences that brown howler monkeys use spatial information of the environment and its temporal varying productivity patterns during foraging. As primates that depend on ephemeral and sparsely located fruit sources, this frugivore-folivorous species also optimizes high-nutrient foraging intake using nearest resources available and high-productivity trees through travel routes composed of large and high-visibility trees that enhance the monitoring of important fruit sources. The travel routes used also contribute to the opportunistic consumption of several leaves' sources, reducing the ingestion of toxic compounds and maximizing nutrient intake during lean periods. These data don't allow the conclusion that brown howler monkeys have mental maps as the concepts defines it (Toolman 1948, O'Keefe and Nadel 1978, Gallistel 1990), or route-based maps (Poucet 1993), once it can't be stated they used neither novel shortcuts or *path integration* during foraging. However, the use of spatial information and varying strategies during foraging, as other behaviors described to enhance the species adaptability in different environments (see Crockett and Eisenberg 1987, Neville et al. et al. 1988, Crockett 1998, Bicca-Marques 2003), was observed allowing an optimization of nutrient intake in different availability periods.

Future studies indicating quantitative measures of nutrient intake and how they relate with plant species use and behavioral patterns observed might clarify the extent to which howlers optimize foraging intake. Besides, social influences during route traveling, how those routes are used through longer periods and their establishment over time, particularly in newly released troops, are important questions that should be answered to the better understand of how howlers use spatial information of the environment.

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Appendix 1 – Results of the phytosociology at the study area (n – number of individuals sampled per species; RDe – relative density; RF – relative frequency; RDm – relative dominance; IVI – importance value index; IVI family – sum of each species IVI per family).

| Family | Species | n | Rde | RF | RDm | IVI | IVI family |
|---|---|---|---|---|---|---|---|
| Euphorbiaceae | *Sebastiania commersoniana* | 51 | 0.175 | 0.123 | 0.11062 | 0.408 | |
| | *Gymnanthes concolor* | 13 | 0.045 | 0.040 | 0.01523 | 0.099 | 0.508 |
| Myrtaceae | *Myrtus selloi* | 3 | 0.010 | 0.012 | 0.00682 | 0.029 | |
| | *Blepharocalix salicifolius* | 3 | 0.010 | 0.012 | 0.02132 | 0.043 | |
| | *Campomanesia rhombea* | 1 | 0.003 | 0.004 | 0.01830 | 0.026 | |
| | *Campomanesia xanthocarpa* | 1 | 0.003 | 0.004 | 0.00632 | 0.014 | |
| | *Eugenia schueschiana* | 7 | 0.024 | 0.028 | 0.02064 | 0.072 | |
| | *Eugenia uniflora* | 1 | 0.003 | 0.004 | 0.00010 | 0.007 | |
| | *Myrcia glabra* | 6 | 0.021 | 0.024 | 0.00725 | 0.052 | |
| | *Myrcia palustris* | 1 | 0.003 | 0.004 | 0.00144 | 0.009 | |
| | *Myrcianthes gigantea* | 6 | 0.021 | 0.024 | 0.01520 | 0.060 | 0.312 |
| Moraceae | *Sorocea bonplandii* | 3 | 0.010 | 0.012 | 0.00214 | 0.024 | |
| | *Ficus insipida* | 3 | 0.010 | 0.012 | 0.01693 | 0.039 | |
| | *Ficus organensis* | 4 | 0.014 | 0.016 | 0.17978 | 0.209 | 0.273 |
| Cecropiaceae | *Coussapoa microcarpa* | 18 | 0.062 | 0.059 | 0.12767 | 0.249 | 0.249 |
| Nyctaginaceae | *Guapira opposita* | 22 | 0.076 | 0.067 | 0.07789 | 0.221 | 0.221 |
| Meliaceae | *Guarea macrophylla* | 1 | 0.003 | 0.004 | 0.00165 | 0.009 | |
| | *Trichilia clausenii* | 19 | 0.065 | 0.063 | 0.02636 | 0.155 | |
| | *Cabralea canjerana* | 1 | 0.003 | 0.004 | 0.00002 | 0.007 | |
| | *Cedrela fissilis* | 1 | 0.003 | 0.004 | 0.00813 | 0.016 | 0.187 |
| Flacourtiaceae | *Xylosma pseudosalzmanii* | 1 | 0.003 | 0.004 | 0.00193 | 0.009 | |
| | *Banara parviflora* | 4 | 0.014 | 0.016 | 0.01287 | 0.042 | |
| | *Casearia decandra* | 5 | 0.017 | 0.020 | 0.01178 | 0.049 | |
| | *Casearia sylvestris* | 10 | 0.034 | 0.036 | 0.01468 | 0.085 | 0.185 |
| Myrsinaceae | *Myrsine guianensis* | 15 | 0.052 | 0.055 | 0.03465 | 0.142 | |
| | *Myrsine laetevirens* | 1 | 0.003 | 0.004 | 0.00033 | 0.008 | 0.149 |
| Ebenaceae | *Diospyros inconstans* | 17 | 0.058 | 0.063 | 0.02518 | 0.147 | 0.147 |
| Lauraceae | *Ocotea pulchella* | 4 | 0.014 | 0.016 | 0.01053 | 0.040 | |
| | *Nectandra megapotamica* | 3 | 0.010 | 0.012 | 0.01247 | 0.035 | |
| | *Nectandra oppositifolia* | 1 | 0.003 | 0.004 | 0.02115 | 0.029 | 0.103 |
| Verbenaceae | *Vitex megapotamica* | 4 | 0.014 | 0.016 | 0.00992 | 0.039 | |
| | *Cytharexyllum myrianthum* | 3 | 0.010 | 0.012 | 0.02724 | 0.049 | 0.089 |
| Melastomataceae | *Miconia rigidiuscula* | 11 | 0.038 | 0.043 | 0.00775 | 0.089 | 0.089 |
| Sapidanceae | *Dodonaea viscosa* | 1 | 0.003 | 0.004 | 0.00143 | 0.009 | |
| | *Allophyllus edulis* | 1 | 0.003 | 0.004 | 0.00103 | 0.008 | |
| | *Matayba elaeagnoides* | 4 | 0.014 | 0.016 | 0.02653 | 0.056 | 0.073 |
| Rutaceae | *Zanthoxylum rhoifolium* | 2 | 0.007 | 0.008 | 0.00916 | 0.024 | |
| | *Esenbeckia grandiflora* | 3 | 0.010 | 0.012 | 0.00124 | 0.023 | |
| | *Zanthoxylum hyemalis* | 1 | 0.003 | 0.004 | 0.01018 | 0.018 | 0.065 |
| Tiliaceae | *Luehea divaricata* | 3 | 0.010 | 0.012 | 0.02369 | 0.046 | 0.046 |
| Rubiaceae | *Faramea montevidensis* | 5 | 0.020 | 0.020 | 0.00395 | 0.041 | 0.041 |
| Anacardiaceae | *Lithraea brasiliensis* | 4 | 0.014 | 0.016 | 0.01147 | 0.041 | 0.041 |
| Sapotacea | *Chrysophyllum marginatum* | 1 | 0.003 | 0.004 | 0.00184 | 0.009 | |
| | *Chrysophyllum gonocarpum* | 2 | 0.007 | 0.008 | 0.01425 | 0.029 | 0.038 |
| Mimosoideae | *Inga uruguensis* | 3 | 0.010 | 0.008 | 0.01752 | 0.036 | 0.036 |
| Clusiaceae | *Garcinia gardneriana* | 4 | 0.014 | 0.016 | 0.00585 | 0.035 | 0.035 |
| Erythroxylaceae | *Erythroxylum argentinum* | 4 | 0.014 | 0.016 | 0.00540 | 0.035 | 0.035 |
| Proteaceae | *Roupala brasiliensis* | 2 | 0.007 | 0.008 | 0.00358 | 0.018 | 0.018 |
| Aquifoliaceae | *Ilex dumosa* | 1 | 0.003 | 0.004 | 0.00033 | 0.008 | |
| | *Ilex brevicuspis* | 1 | 0.003 | 0.004 | 0.00111 | 0.008 | 0.016 |
| Celastraceae | *Maytenos casineformis* | 1 | 0.003 | 0.004 | 0.00450 | 0.012 | 0.012 |
| Asteraceae | *Dasyphilum spineeis* | 1 | 0.003 | 0.004 | 0.00122 | 0.009 | 0.009 |
| Icacianaceae | *Citronella* spp. | 1 | 0.003 | 0.004 | 0.00056 | 0.008 | 0.008 |
| Oleaceae | *Chionanthus trichotomus* | 1 | 0.003 | 0.004 | 0.00033 | 0.008 | 0.008 |
| | | | | | | 3.000 | |

Appendix 2 – Total use of trees during each sampled period. The number of trees used per species is indicated in parenthesis and the highest mean values at each sampling period are indicated in dark.

| | **% of total trees used (n trees)** | | | | **% of visits/period** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Summer** | **Fall** | **Winter-Spring** | **TOTAL** | **Summer** | **Fall** | **Winter-Spring** | **TOTAL** |
| *Guapira opposita* | **9.3 (29)** | **5.7 (17)** | **8.7 (36)** | **8.0 (52)** | **7.7** | 4.7 | **8.3** | **6.8** |
| *Coussapoa microcarpa* | **10.9 (34)** | **11.0 (33)** | **8.9 (37)** | **7.8 (51)** | **14.3** | **12.7** | **10.6** | **12.3** |
| *Myrsine guianensis* | 3.9 (12) | **8.4 (25)** | **6.5 (27)** | **6.6 (43)** | 5.5 | **8.0** | **6.0** | **6.5** |
| *Trichilia clausenii* | **5.8 (18)** | 1.7 (5) | 3.4 (14) | 4.1 (27) | 5.3 | 1.0 | 2.8 | 2.9 |
| *Diospyros inconstans* | 3.5 (1) | 3.7 (11) | 4.3 (18) | 4.0 (26) | 3.6 | 3.9 | 3.9 | 3.8 |
| *Sebastiania commersoniana* | 2.9 (9) | 4.7 (14) | 4.1 (17) | 3.7 (24) | 3.2 | 3.2 | 4.4 | 3.5 |
| *Miconia rigidiuscula* | 1.9 (6) | 3.0 (9) | 3.6 (15) | 3.1 (20) | 2.8 | 2.4 | 3.0 | 2.7 |
| *Lithraea brasiliensis* | 3.5 (11) | 3.7 (11) | 3.1 (13) | 2.9 (19) | 2.6 | 5.2 | 2.8 | 3.6 |
| *Luehea divaricata* | 3.2 (10) | 2.7 (8) | 3.6 (15) | 2.9 (19) | 3.4 | 2.4 | 3.0 | 2.9 |
| *Zanthoxylum hyemalis* | 2.3 (7) | 2.3 (7) | 2.9 (12) | 2.9 (19) | 1.7 | 2.4 | 2.3 | 2.1 |
| *Zanthoxylum rhoifolium* | 2.3 (7) | 1.7 (5) | 2.7 (11) | 2.6 (17) | 1.5 | 1.5 | 2.3 | 1.8 |
| *Ficus organensis* | 4.5 (14) | 4.0 (12) | 3.1 (13) | 2.5 (16) | **8.7** | **6.1** | 4.4 | 6.3 |
| *Banara parviflora* | 2.8 (8) | 2.7 (8) | 1.9 (8) | 2.3 (15) | 3.0 | 2.9 | 2.1 | 2.6 |
| *Myrcianthes gigantea* | 2.6 (8) | 2.0 (6) | 1.0 (1) | 2.3 (15) | 1.7 | 1.5 | 1.2 | 1.5 |
| *Sorocea bonplandii* | 0.6 (2) | - | 3.1 (13) | 2.0 (13) | 0.4 | - | 2.3 | 0.9 |
| *Ficus insipida* | 1.9 (6) | 2.3 (7) | 1.7 (7) | 1.8 (12) | 2.8 | 3.4 | 2.3 | 2.8 |
| *Myrcia glabra* | 1.3 (4) | 1.7 (5) | 1.4 (4) | 1.7 (11) | 0.9 | 1.0 | 1.2 | 1.0 |
| *Xylosma pseudosalzmanii* | 1.0 (3) | 1.0 (3) | 2.2 (9) | 1.5 (10) | 0.6 | 0.5 | 1.8 | 1.0 |
| *Vitex megapotamica* | 0.6 (2) | 0.3 (1) | 1.7 (7) | 1.5 (10) | 0.4 | 0.2 | 1.6 | 0.7 |
| *Cabralea canjerana* | 1.9 (3) | 1.3 (4) | 1.9 (8) | 1.4 (9) | 0.6 | 2.9 | 1.8 | 1.9 |
| *Casearia decandra* | 0.3 (1) | 1.3 (4) | 1.4 (6) | 1.4 (9) | 0.2 | 0.8 | 1.8 | 1.0 |
| *Nectandra megapotamica* | 1.3 (4) | 0.7 (2) | 1.7 (7) | 1.2 (8) | 1.1 | 0.5 | 1.6 | 1.0 |
| *Matayba elaeagnoides* | 1.3 (4) | 1.3 (4) | 1.0 (4) | 1.1 (7) | 1.5 | 2.0 | 1.1 | 1.7 |
| *Ilex brevicuspis* | 1.0 (3) | 1.0 (3) | 1.4 (6) | 1.1 (7) | 1.3 | 1.0 | 1.9 | 1.4 |
| *Casearia sylvestris* | 1.3 (4) | 0.3 (1) | 0.7 (3) | 0.9 (6) | 1.1 | 0.2 | 0.5 | 0.6 |
| *Dasyphilum spineeis* | 0.6 (2) | 1.0 (3) | 1.2 (5) | 0.8 (5) | 0.6 | 1.7 | 1.2 | 1.2 |
| *Psidium cattleianum* | 1.3 (4) | 0.3 (1) | - | 0.8 (5) | 0.9 | 0.3 | - | 0.3 |
| *Ilex dumosa* | - | 0.3 (1) | 1.0 (4) | 0.8 (5) | - | 0.3 | 0.9 | 0.4 |
| *Campomanesia xanthocarpa* | 1.0 (3) | 1.0 (3) | 0.7 (3) | 0.6 (4) | 0.9 | 1.5 | 0.7 | 1.0 |
| *Erythroxylum argentinum* | 0.3 (1) | 1.0 (3) | 1.0 (4) | 0.6 (4) | 0.2 | 1.2 | 0.7 | 0.7 |
| *Campomanesia rhombea* | 0.3 (1) | 1.3 (4) | 0.7 (3) | 0.6 (4) | 0.2 | 1.2 | 0.7 | 0.7 |
| *Sloanea monosperma* | 1.0 (3) | 1.3 (4) | 1.0 (4) | 0.6 (4) | 0.6 | 1.0 | 0.7 | 1.1 |
| *Roupala brasiliensis* | 0.6 (2) | 1.0 (3) | 0.7 (3) | 0.5 (3) | 0.4 | 0.7 | 1.1 | 0.7 |
| *Cytharexyllum myrianthum* | 0.3 (1) | 0.7 (2) | 0.2 (1) | 0.5 (3) | 0.2 | 0.3 | 0.5 | 0.4 |
| *Inga uruguensis* | 0.3 (1) | 0.7 (2) | 0.5 (2) | 0.5 (3) | 0.9 | 0.3 | 0.4 | 0.5 |
| *Allophylus edulis* | - | - | 0.2 (2) | 0.3 (2) | - | - | 0.7 | 0.2 |
| *Eugenia rostrifolia* | 0.3 (1) | - | 0.2 (1) | 0.3 (2) | 0.2 | - | 0.4 | 0.2 |
| *Eugenia schueschiana* | - | - | 0.5 (2) | 0.3 (2) | - | - | 0.4 | 0.1 |
| *Blepharocalix salicifolius* | 0.3 (1) | - | 0.2 (1) | 0.3 (2) | 0.2 | - | 0.2 | 0.1 |
| *Tabebuia cassinoides* | 0.3 (1) | 0.7 (2) | 0.2 (1) | 0.3 (2) | 0.6 | 1.0 | 0.4 | 0.7 |
| *Nectandra oppositifolia* | 0.3 (1) | 0.7 (2) | - | 0.3 (2) | 0.4 | 0.7 | - | 0.4 |
| *Myrsine latevirens* | 0.3 (1) | 0.7 (2) | 0.5 (2) | 0.3 (2) | 0.4 | 0.7 | 0.5 | 0.6 |
| *Garcinia gardneriana* | 0.3 (1) | 0.3 (1) | - | 0.3 (2) | 0.2 | 0.3 | - | 0.2 |
| *Chrysophyllum marginatum* | 0.6 (2) | 0.7 (2) | 0.5 (2) | 0.3 (2) | 0.4 | 0.3 | 0.5 | 0.4 |
| *Chionanthus trichotomus* | 0.3 (1) | 0.7 (2) | 0.5 (2) | 0.3 (2) | 0.2 | 0.3 | 0.5 | 0.4 |
| *Chrysophyllum gonocarpum* | 0.6 (2) | 0.3 (1) | 0.2 (1) | 0.3 (2) | 1.1 | 0.2 | 0.5 | 0.6 |
| *pau leiteiro* | 0.3 (1) | - | - | 0.2 (1) | 0.2 | - | - | 0.1 |
| *Solanum peseudo-quina* | - | - | 0.2 (1) | 0.2 (1) | - | - | 0.5 | 0.2 |
| *Gymnanthes concolor* | 0.3 (1) | - | 0.2 (1) | 0.2 (1) | 0.2 | - | 0.4 | 0.2 |
| *Ocotea pulchella* | - | - | 0.2 (1) | 0.2 (1) | - | - | 0.4 | 0.1 |
| *Cupania vernalis* | 0.3 (1) | - | 0.2 (1) | 0.2 (1) | 0.2 | - | 0.2 | 0.1 |
| *Alchornea triplinervia* | - | - | 0.2 (1) | 0.2 (1) | - | - | 0.2 | 0.1 |
| *Ocotea catarinensis* | - | - | 0.2 (1) | 0.2 (1) | - | - | 0.2 | 0.1 |
| *Prunus selloi* | 0.3 (1) | 0.3 (1) | 0.2 (1) | 0.2 (1) | 0.2 | 1.4 | 0.4 | 0.7 |
| *Esenbeckia grandiflora* | 0.3 (1) | 0.3 (1) | - | 0.2 (1) | 0.2 | 0.5 | - | 0.2 |
| *Maytenos casineformis* | 0.3 (1) | 0.3 (1) | - | 0.2 (1) | 0.2 | 0.3 | - | 0.2 |
| *Myrsine coreacea* | 0.3 (1) | 0.3 (1) | 0.2 (1) | 0.2 (1) | 0.2 | 0.2 | 0.4 | 0.2 |
| unidentif. spp | 17.7 (55) | 17.4 (52) | 11.8 (49) | 17.6 (115) | 13.9 | 15.1 | 11.5 | 13.6 |
| | 100 (311) | 100 (299) | 100 (411) | 100 (653) | 100 | 100 | 100 | 100 |

Appendix 3 – Relative species contribution on feeding during the study. The number of trees used per species is indicated in parenthesis and the highest mean values at each sampling period are indicated in dark.

| **Species** | **% Feeding (n trees)** | | | | **Leaves** | | | | **Fruits** | | | | **Flowers** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Summer** | **Fall** | **Winter-Spring** | **TOTAL** | **Summer** | **Fall** | **Winter-Spring** | **TOTAL** | **Summer** | **Fall** | **Winter-Spring** | **TOTAL** | **Summer** | **Fall** | **Winter-Spring** | **TOTAL** |
| *Guapira opposita* | 5.3 (8) | 1.4 (3) | **18.1 (23)** | 8.8 (28) | 5.3 | 0.7 | 0.5 | 1.9 | 0 | 0 | 0 | 0 | 0 | 0.7 | **17.6** | **6.9** |
| *Coussapoa microcarpa* | **9.9 (8)** | **14.9 (13)** | **11.5 (13)** | **13.3 (24)** | **6.0** | 1.0 | 4.8 | 3.6 | 3.9 | **13.4** | **6.8** | **8.7** | 0 | 0.5 | 0 | 1.0 |
| *Zanthoxylum hyemalis* | 3.6 (6) | 7.1 (6) | 7.1 (12) | 6.3 (18) | 3.6 | **7.1** | 6.4 | **6.1** | 0 | 0 | 0 | 0 | 0 | 0 | 0.7 | 0.3 |
| *Myrsine guianensis* | 1.2 (3) | 3.3 (8) | 2.1 (6) | 2.5 (17) | 1.0 | 0.1 | 0.2 | 0.5 | 0 | 0 | 1.6 | 0.7 | 0.2 | **3.2** | 0.3 | 1.4 |
| undenterm. spp | 3.0 (6) | 4.0 (5) | 2.1 (6) | 3.1 (16) | 2.5 | 2.8 | 1.9 | 2.4 | 0.5 | 0 | 0 | 0.1 | 0 | 1.2 | 0.2 | 0.5 |
| *Zanthoxylum rhoifolium* | 0.5 (1) | 4.2 (5) | 5.8 (10) | 4.0 (15) | 0.5 | 4.2 | 5.8 | 4.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Diospyros inconstans* | 2.9 (2) | 3.7 (3) | 7.9 (11) | 6.0 (12) | 2.9 | 3.7 | **7.9** | **5.2** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.8 |
| *Sorocea bonplandii* | 1.3 (1) | - | **8.1 (12)** | 3.4 (12) | 1.3 | - | **8.1** | 3.4 | 0 | - | 0 | 0 | 0 | - | 0 | 0 |
| *Ficus organensis* | **33.6 (9)** | **20.8 (5)** | 4.7 (2) | **18.5 (11)** | **9.8** | 1.6 | 0.1 | 3.6 | **23.8** | **19.2** | **4.7** | **15.0** | 0 | 0 | 0 | 0 |
| vine spp | 5.5 (3) | **14.4 (14)** | 1.7 (3) | 3.7 (20) | 5.5 | 3.5 | 1.7 | 1.2 | 0 | 0.2 | 0 | 0 | 0 | **10.7** | 0 | **2.6** |
| *Ficus insipida* | **12.1 (4)** | 9.9 (5) | 6.4(6) | **9.2 (9)** | **10.0** | **9.9** | 6.4 | **8.7** | 2.1 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 |
| *Banara parviflora* | 0.7 (3) | 0.9 (1) | 3.6 (4) | 1.9 (6) | 0.5 | 0.9 | 3.6 | 1.9 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Trichilia clausenii* | 5.7 (6) | - | - | 1.5 (6) | 3.7 | - | - | 1.0 | 2.0 | - | - | 0.5 | 0 | - | - | 0 |
| *Nectandra megapotamica* | - | - | 3.3 (6) | 1.2 (6) | - | - | 2.1 | 0.8 | - | - | 0 | 0 | - | - | 1.4 | 0.4 |
| *Vitex megapotamica* | 0.5 (1) | 0.7 (1) | 1.2 (4) | 0.8 (6) | 0.5 | 0.7 | 1.0 | 0.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2 | 0.1 |
| *Luehea divaricata* | 1.0 (1) | - | 1.8 (4) | 0.9 (5) | 0.0 | - | 1.7 | 0.6 | 0 | - | 0.2 | 0.1 | 1.1 | - | 0 | 0.3 |
| *Sebastiania commersoniana* | - | 0.8 (2) | 1.0 (3) | 0.7 (5) | - | 0.5 | 0.7 | 0.5 | - | 0 | 0.3 | 0.1 | - | 0.3 | 0 | 0.1 |
| *Dasyphilum spineeis* | - | 9.6 (3) | 3.6 (4) | 4.6 (4) | - | **8.6** | 3.6 | 4.3 | - | 0 | 0 | 0 | - | 1.0 | 0 | 0.4 |
| *Lithraea brasiliensis* | 2.0 (1) | 1.0 (2) | 0.7 (2) | 1.1 (4) | 2.0 | 1.0 | 0.7 | 1.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Casearia decandra* | - | - | 1.7 (4) | 0.6 (4) | - | - | 0.0 | 0.0 | - | - | 0 | 0 | - | - | 1.7 | 0.6 |
| *Myrcianthes gigantea* | 1.9 (3) | 0.3 (1) | - | 0.6 (3) | 1.1 | 0.3 | - | 0.4 | 0.8 | 0 | - | 0.2 | 0 | 0 | - | 0 |
| *Xylosma pseudosalzmanii* | - | - | 0.6 (3) | 0.2 (3) | - | - | 0.0 | 0.0 | - | - | 0 | 0 | - | - | 0.6 | 0.2 |
| *Ilex brevicuspis* | - | - | 0.6 (3) | 0.2 (3) | - | - | 0.6 | 0.2 | - | - | 0 | 0 | - | - | 0 | 0 |
| *Esenbeckia grandiflora* | 2.5 (2) | - | - | 1.4 (2) | 2.5 | - | - | 1.4 | 0 | - | - | 0 | 0 | - | - | 0 |
| *Chrysophyllum gonocarpum* | 2.3 (2) | - | 1.8 (1) | 1.2 (2) | 2.3 | - | 1.8 | 1.2 | 0 | - | 0 | 0 | 0 | - | 0 | 0 |
| *Allophyllus edulis* | - | - | 1.1 (2) | 0.4 (2) | - | - | 1.1 | 0.4 | - | - | 0 | 0 | - | - | 0 | 0 |
| *Miconia rigidiuscula* | 0.2 (1) | 0.2 (1) | - | 0.1 (2) | 0.2 | 0.2 | - | 0.1 | 0 | 0 | - | 0 | 0 | 0 | - | 0 |
| *Myrcia glabra* | 0.2 (1) | 0.1 (1) | - | 0.1 (2) | 0.2 | 0.1 | - | 0.1 | 0 | 0 | - | 0 | 0 | 0 | - | 0 |
| *Ocotea pulchella* | - | - | 1.6 (1) | 0.6 (1) | - | - | 1.6 | 0.6 | - | - | 0 | 0 | - | - | 0 | 0 |
| *Sloanea monosperma* | 2.0 (1) | - | 0.1 (1) | 0.5 (1) | 2.0 | - | 0.1 | 0.5 | 0 | - | 0 | 0 | 0 | - | 0 | 0 |
| *Campomanesia xanthocarpa* | 0.2 (1) | 0.6 (1) | - | 0.5 (1) | 0.2 | 0.6 | - | 0.4 | 0 | 0 | - | 0 | 0 | 0 | - | 0.1 |
| *Solanum peseudo-quina* | - | - | 1.0 (1) | 0.4 (1) | - | - | 1.0 | 0.4 | - | - | 0 | 0 | - | - | 0 | 0 |
| *Inga uruguensis* | - | 0.9 (1) | - | 0.3 (1) | - | 0.9 | - | 0.3 | - | 0 | - | 0 | - | 0 | - | 0 |
| *Myrsine coreaceae* | 0.3 (1) | 0.5 (1) | - | 0.3 (1) | 0.3 | 0.5 | - | 0.3 | 0 | 0 | - | 0 | 0 | 0 | - | 0 |
| *Psidium cattleianum* | 1.0 (1) | - | - | 0.2 (1) | 1.0 | - | - | 0.2 | 0 | - | - | 0 | 0 | - | - | 0 |
| *Matayba elaeagnoides* | - | 0.4 (1) | 0.4 (1) | 0.2 (1) | - | 0.4 | 0.4 | 0.2 | - | 0 | 0 | 0 | - | 0 | 0 | 0 |
| *Cytharexyllum myrianthum* | 0.7 (1) | - | - | 0.2 (1) | 0.0 | - | - | 0.0 | 0.7 | - | - | 0.2 | 0 | - | - | 0 |
| *Cabralea canjerana* | - | 0.2 (1) | - | 0.1 (1) | - | 0.2 | - | 0.1 | - | 0 | - | 0 | - | 0 | - | 0 |
| *Ilex dumosa* | - | - | 0.3 (1) | 0.1 (1) | - | - | 0.3 | 0.1 | - | - | 0 | 0 | - | - | 0 | 0 |
| *Erythroxylum argentinum* | - | 0.2 (1) | - | 0.1 (1) | - | 0.2 | - | 0.1 | - | 0 | - | 0 | - | 0 | - | 0 |
| TOTAL | 100 (74) | 100 (72) | 100 (145) | 100 (239) | 64.9 | 49.7 | 64.0 | 58.3 | 34.0 | 32.7 | 13.6 | 26.1 | 1.2 | 17.6 | 22.7 | 15.6 |