

**PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL**  
**FACULDADE DE BIOCÊNCIAS**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA**

**EFEITO DA DISPONIBILIDADE DE ALIMENTO**  
**NA DISTRIBUIÇÃO ESPACIAL DE BUGIOS-RUIVOS**  
**EM UM FRAGMENTO DE MATA ATLÂNTICA**

**Danielle Camaratta**

**DISSERTAÇÃO DE MESTRADO**  
**PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL**  
**Av. Ipiranga 6681 - Caixa Postal 1429**  
**Fone: (051) 3320-3500**  
**CEP 90619-900 Porto Alegre - RS**  
**Brasil**

**2016**

PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL

FACULDADE DE BIOCÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**EFEITO DA DISPONIBILIDADE DE ALIMENTO  
NA DISTRIBUIÇÃO ESPACIAL DE BUGIOS-RUIVOS  
EM UM FRAGMENTO DE MATA ATLÂNTICA**

**Danielle Camaratta**

**Orientador: Dr. Júlio César Bicca-Marques**

**Coorientador: Dr. Óscar M. Chaves**

**DISSERTAÇÃO DE MESTRADO**

**PORTO ALEGRE - RS - BRASIL**

**2016**

## SUMÁRIO

<b>AGRADECIMENTOS</b> .....	VI
<b>RESUMO</b> .....	IX
<b>ABSTRACT</b> .....	X
<b>APRESENTAÇÃO GERAL</b> .....	1
<b>REFERÊNCIAS</b> .....	4
<b>ARTIGO:</b> Fruit availability drives the dispersion of brown howler monkeys within an Atlantic forest remnant.....	10
Abstract.....	12
Introduction.....	13
Methods.....	16
Results.....	21
Discussion.....	22
Acknowledgements.....	25
References.....	26
Tables.....	36
Figure legends.....	37
Figures.....	38
Supporting information.....	40



Morro São Pedro. Crédito: Danielle Camaratta

*“Todos os caminhos são os mesmos, não conduzem a lugar algum. São caminhos que atravessam o mato ou que entram no mato. Em minha vida posso dizer que já passei por caminhos compridos, compridos, mas não estou em lugar algum. A pergunta de meu benfeitor agora tem um significado. Este caminho tem um coração? Se tiver o caminho é bom, se não tiver não presta. Ambos os caminhos não conduzem a parte alguma, mas um tem coração e o outro não. Um torna a viagem alegre, enquanto você o seguir, será um com ele. O outro o fará maldizer sua vida. Um o torna forte, o outro o enfraquece.”*

*Don Juan Matus, em Carlos Castaneda*

## Dedicatória



Bugio-ruivo (*Alouatta guariba clamitans*). Crédito: Danielle Camaratta

*Dedico esta dissertação aos bugios-ruivos,  
que me guiaram até aqui.*

## AGRADECIMENTOS

Primeiramente agradeço ao Morro São Pedro por existir, local que me acolhe desde que nasci. Grata por tua biodiversidade, tuas nascentes, teus encantos e tua guarnição.

Ao meu avô, Horst Hans Beier, que é o precursor deste agradável vínculo com o Morro São Pedro.

Ao meu orientador, Júlio César Bicca-Marques, por oportunizar a realização de um sonho, pela sinceridade, pelo bom humor, pela dedicação e amor à sua profissão.

Ao meu coorientador, Óscar M. Chaves, por acreditar em mim. *Gracias* por me encorajar a fazer este estudo, pela convivência e amizade sincera, por todos os ensinamentos, pelo apoio logístico (incluindo deliciosas marmitas), esforço e dedicação em campo e em laboratório, e em especial pelo refinado auxílio nas análises estatísticas dos dados coletados neste estudo.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico/CNPq pelo essencial apoio financeiro integral para a realização deste estudo.

A João Cláudio Godoy Fagundes, pela amizade fiel e pela disponibilidade em participar da abertura/demarcação de trilhas. O teu trabalho foi essencial para a realização deste estudo.

Aos meus pais, Suzana E. Beier Camaratta e Epifanio Juarez Camaratta, que sempre me incentivam e apoiam a estudar. Grata pelo apoio logístico, pelas caronas e deliciosas marmitas também!

A toda a minha família, que sempre apoia as minhas escolhas e mantém acesa a chama do amor e da união familiar. Em especial ao vô Horst e ao tio Herbert pelas inesperadas caronas.

Aos ajudantes da primeira semana de campo de levantamento de bugios deste estudo: Anamélia de Souza Jesus, Ítalo Mourthe, Luana Melo e Gustav Beier. A presença de vocês me trouxe mais autoconfiança e coragem para seguir adiante. Grata pelo esforço percorrido naqueles dias quentes da primeira semana do ano.

À Renata Souza da Costa, que me acompanhou em diversos campos de levantamento de bugios. Grata pelo companheirismo, pelo esforço, pelas risadas e pela amizade cultivada! A tua presença me trouxe mais segurança para seguir a caminhada.

A todos os demais amigos e ajudantes de campo (em levantamentos botânicos e de bugios) que, independentemente da frequência, juntos, formamos um grande time: Fabiana Corrêa, Monique Costa de Camargo, Pedro Bencke Ermel da Silva, Lívia Machado, Gabriela Pacheco Hass, Kássia Ramos, Paula Miranda Grison Azevedo, Vitor Vieira Chagas e José Antônio Filho.

Aos colegas de laboratório pelo auxílio e coleguismo, em especial a Gabriela Pacheco Hass e a Karine Galisteo Diemer Lopes, pelas conversas descontraídas, pelo carinho e atenção nos momentos mais difíceis.

À Secretaria Municipal do Meio Ambiente (SMAM) por autorizar a condução deste estudo no Refúgio de Vida Silvestre São Pedro.

Ao Centro Espírita Beneficente União do Vegetal e sua respectiva Associação Ecológica Novo Encanto, pelo sublime trabalho que vem realizando no Morro São Pedro e contribuindo essencialmente para a manutenção da biodiversidade. Por permitirem a realização desta pesquisa em sua propriedade e me acolherem de maneira bem especial.

Ao Instituto Econsciência (Felipe Vianna), à Reserva Particular do Patrimônio Natural Costa do Cerro (Nairo Guerisoli), à Associação Macrobiótica (em especial à Sra. Neda), e aos moradores André Jair Oliveira e ao casal Diego e Bárbara (da propriedade dos Lagos) por permitirem a realização desta pesquisa em suas propriedades.

À Sra. Eli, que apoiou este estudo carinhosamente e cedeu muitas vezes o espaço no seu pátio para o estacionamento do veículo.

Às famílias Almeida e Silveira, pelo carinho, receptividade e convivência ao longo desse lindo passeio em que viemos a nos encontrar. Por todas as oportunidades de aprendizado que me apresentaram, transformando pedras em diamantes.

Ao Instituto Nacional de Excelência Humana (INEXH) pelo brilhante trabalho realizado no DL-POA47, contribuindo de maneira bastante pessoal para a conclusão desta pesquisa e agregando ferramentas essenciais para o meu desenvolvimento profissional.



## RESUMO

A compreensão dos fatores ecológicos que influenciam a presença, a abundância e a distribuição das espécies nos ambientes naturais é essencial para a conservação da biodiversidade em longo prazo. No caso dos consumidores primários, como a maioria dos primatas, a riqueza e a disponibilidade de plantas utilizadas na alimentação são considerados fatores-chave que direcionam a densidade populacional em diferentes escalas espaciais. No entanto, pouco se sabe sobre como (e se) essas variáveis influenciam a dispersão das unidades sociais de um táxon em uma escala fina, em nível de parcelas de habitat. Nessa pesquisa investiguei se a riqueza e a disponibilidade espaço-temporal de alimento são bons preditores da distribuição espacial de bugios-ruivos (*Alouatta guariba clamitans*) dentro do habitat em um remanescente de Mata Atlântica (ca. 1.200 ha) no sul do Brasil. Para isso, realizei um censo populacional a cada duas semanas no período de janeiro a junho de 2015, percorrendo um total de 205 km distribuídos em cinco transecções lineares. Além disso, utilizei dados de levantamentos florísticos do estrato arbóreo, realizados em todas as parcelas com avistamento de bugios e parcelas controle, e de amostragem fenológica de 17 espécies principais da dieta para estimar a disponibilidade espaço-temporal de alimento para os bugios-ruivos a cada duas semanas. Foram registrados 95 avistamentos de bugios durante o estudo (2-12 avistamentos/período de amostragem). A disponibilidade de frutos (maduros e imaturos) foi maior nas parcelas com avistamento de bugios do que nas parcelas controle, enquanto a disponibilidade de folhas (jovens e adultas) foi semelhante. Já o número de indivíduos observados em cada ponto de avistamento esteve diretamente (embora marginalmente) relacionado à disponibilidade de frutos maduros, mas não à riqueza de árvores ou à disponibilidade de frutos imaturos, folhas adultas e folhas jovens. Em conclusão, a distribuição e disponibilidade de frutos no Morro São Pedro possuem importante influência no padrão de uso do espaço pelos bugios-ruivos durante o período de estudo.

**Palavras-chave:** disponibilidade de frutos; escala fina; distribuição de primatas; uso do habitat; *Alouatta guariba clamitans*, transecção linear

## ABSTRACT

Understanding the ecological factors that influence the presence, abundance, and distribution of species within their habitats is critical for ensuring their long-term conservation. In the case of primary consumers, such as most primates, the richness and availability of plant foods are considered key drivers of population density at different spatial scales. However, little is known about how (and whether) these variables influence the spacing of social units within a finer, habitat patch level scale. I investigated whether resource richness and spatiotemporal food availability are good predictors of local, within-habitat spatial distribution of brown howler monkeys (*Alouatta guariba clamitans*) in a 1,200 ha Atlantic forest remnant in southern Brazil. I censused the population every two weeks from January to June 2015 by walking 205 km distributed in five line transects. Then, I used data on tree inventories in all sighting and control plots and phenological surveys of 17 top food tree species to estimate bi-weekly food availability for the monkeys. We recorded a total of 95 sightings (2-12 sightings/sampling period) and found that fruit (ripe and unripe) availability was higher in sighting than in control plots. Leaf availability was similar. On the other hand, the number of individuals observed in each sighting was marginally directly related to the availability of ripe fruits, but not to tree richness or the availability of unripe fruits, mature leaves, and young leaves. We concluded that the distribution and availability of fruit sources was an important driver of the pattern of habitat use by brown howler during the study period.

**Key words:** food availability; fine-scale sample; within-habitat monkey distribution; habitat use; *Alouatta guariba clamitans*, distance sampling

## APRESENTAÇÃO GERAL

A presente dissertação de Mestrado é apresentada na forma de artigo científico e está configurada de acordo com as normas do periódico *American Journal of Primatology*. Todas as legendas, figuras e material suplementar estão incluídos no final do artigo, conforme as regras do periódico.

As flutuações na abundância de primatas podem ser afetadas por diversos fatores bióticos como presença, diversidade e abundância de recursos alimentares, predadores, parasitos e doenças [Bicca-Marques, 2009; Strier & Mendes, 2009; Arroyo-Rodríguez & Dias, 2010], assim como por variáveis climáticas [e.g., fotoperíodo e precipitação: Fernandez-Duque et al., 2002; Rudran & Fernandez-Duque, 2003; furacões: Pavelka et al., 2003; Pavelka & Behie, 2005]. Dentre estes fatores, a disponibilidade e/ou riqueza de recursos alimentares tem sido apontada como um dos principais determinantes da presença e/ou abundância populacional de primatas em uma escala espacial ampla [Chapman et al., 2006; Arroyo-Rodríguez & Dias, 2010; Hanya & Chapman, 2013], e em uma escala espacial fina, em nível local [Marshall & Leighton, 2006; Stone, 2007; Potts et al., 2009; Mourthé, 2014], conforme a definição em Chapman et al. [2002].

Apesar da importante contribuição de estudos realizados em escalas espaciais amplas na detecção de diferenças nas variáveis-resposta contrastando populações separadas por longas distâncias (centenas ou milhares de quilômetros), os estudos em escala fina podem ser considerados detectores mais sensíveis de determinantes ecológicos da abundância local de primatas do que os contrastes gerais [Chapman & Chapman, 1999]. Contudo, poucos estudos avaliaram a influência da disponibilidade espaço-

temporal de alimento na distribuição espacial de uma espécie em uma escala fina [Estrada, 1984; Williams-Guillén et al., 2006]. Em geral, a disponibilidade de recursos alimentares para os primatas encontrada em plantas, tais como folhas jovens e frutos, varia amplamente no tempo e no espaço [van Schaik et al., 1993; Chapman et al., 2005; Zimmerman et al., 2007]. Sendo assim, os estudos que examinam a influência da disponibilidade de alimento como determinante ecológico da abundância e distribuição espacial de primatas e que consideram apenas a área basal (bem como comparações entre tipos de vegetação ou diversidade de espécies arbóreas) estão medindo apenas a disponibilidade de recursos alimentares “potencial” das espécies de plantas [veja revisão em Hanya & Chapman, 2013]. Ao realizar uma análise refinada da disponibilidade de itens vegetais (tais como folhas adultas e jovens, frutos maduros e imaturos, flores) podemos estimar a “real” disponibilidade de recursos em um determinado habitat considerando uma escala espacial fina.

O padrão de distribuição dos recursos alimentares (aleatório, agregado ou uniforme) pode influenciar a distribuição espacial dos primatas no habitat [Milton, 1981], uma vez que eles podem focar o forrageio em alimentos de alta qualidade energética, quando disponíveis [Bravo & Sallenave, 2003]. Como os recursos ricos em nutrientes e energia não estão distribuídos homogeneamente e variam temporalmente, estudos indicam que os primatas são capazes de rastrear as principais fontes de alimento com base em uma representação mental, topológica, das rotas espaciais que dão acesso a esses recursos [p. ex. *Alouatta*: Fortes et al. 2015; Hopkins, 2015]. Esta cognição mental está relacionada com a estratégia de “traplining” [Dew & Wright, 1998], que consiste em visitar as principais áreas de alimentação de acordo com a variação da disponibilidade espacial destes itens ao longo do tempo [Anderson, 1983]. Espécies folívoro-frugívoras,

como o bugio-ruivo (*Alouatta guariba clamitans*), forrageiam por frutos e folhas novas quando disponíveis, podendo ser mais facilmente encontradas nas áreas com alta disponibilidade de alimentos ricos em nutrientes durante períodos de produção destes itens [Chaves & Bicca-Marques, 2016].

Os bugios possuem hábitos alimentares flexíveis [Estrada et al., 1999; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Chaves & Bicca-Marques, 2013], sendo capazes de adaptar a dieta a mudanças na vegetação, incluindo principalmente a utilização de espécies exóticas (tais como *Citrus sinensis*, *Eucalyptus* spp., *Psidium guajava*, *Vitis* spp., *Diospyros kaki* e *Malus* spp.) como fonte de alimento durante períodos de escassez de frutos nativos em ambientes antropizados [Bicca-Marques & Calegari-Marques, 1994; Estrada et al., 2012]. Eles apresentam uma dieta composta principalmente por folhas, frutos e flores de acordo com a composição florística e a disponibilidade espaço-temporal de recursos alimentares na área [Bicca-Marques, 2003; Chaves & Bicca-Marques, 2013]. Apesar da flexibilidade alimentar, os bugios, assim como outras espécies de atelídeos, concentram seus hábitos alimentares em um pequeno grupo de espécies denominadas espécies “top” (i.e., espécies que juntas constituem  $\geq 80\%$  dos registros de alimentação) [*Alouatta guariba clamitans*: Chaves & Bicca-Marques, 2013, 2016], as quais podem ser determinantes na presença e/ou abundância desses primatas [*Alouatta palliata mexicana*: Serio-Silva et al., 2002; Arroyo-Rodríguez et al., 2007; *Ateles geoffroyi*: Chaves et al., 2012].

O objetivo deste estudo foi avaliar a influência da disponibilidade e riqueza de recursos alimentares na distribuição espacial de bugios-ruivos em uma escala espacial fina, em nível de parcelas de habitat, em um fragmento de 1200 ha de Mata Atlântica no Morro São Pedro, Porto Alegre, Rio Grande do Sul, Brasil. O Morro São Pedro é o maior

remanescente de Mata Atlântica de Porto Alegre, característica que o qualifica como o fragmento de maior importância para a conectividade funcional entre os remanescentes florestais e para a conservação do bugio-ruivo no município [Alonso, 2010]. O presente estudo poderá contribuir como fundamento científico para planos de manejo para a conservação da população de bugios-ruivos do Morro São Pedro. Além disso, o município apresenta um preocupante cenário de fragmentação devido à crescente urbanização em direção às áreas de paisagem natural mais preservadas [Alonso, 2010; Lokschin, 2012], o que compromete a disponibilidade dos principais recursos alimentares deste atelídeo e, conseqüentemente, a sua distribuição espacial no ambiente e sobrevivência em longo prazo.

## Referências

- Alonso AC. 2010. Delineamento e avaliação de corredores lineares multi-habitat: estudo de caso com bugio-ruivo (*Alouatta clamitans*) em mosaico urbano-rural [dissertação]. Porto Alegre (RS): Universidade Federal do Rio Grande do Sul. 64 p.
- Anderson DJ. 1983. Optimal foraging and the traveling salesman. *Theoretical Population Biology* 24:145–159.
- Arroyo-Rodriguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology* 72:1–16.
- Arroyo-Rodríguez V, Mandujano S, Benitez-Malvido J, Cuende-Fanton C. 2007. The influence of large tree density on howler monkey (*Alouatta palliata mexicana*) presence in very small rain forest fragments. *Biotropica* 39:760–766.

- Bicca-Marques JC. 2003. How do howler monkeys cope with habitat fragmentation? In: Marsh LK, editor. *Primates in fragments: Ecology and conservation*. New York: Kluwer Academics/Plenum Publishers. p 283–303.
- Bicca-Marques JC. 2009. Outbreak of yellow fever affects howler monkeys in southern Brazil. *Oryx* 43:173.
- Bicca-Marques JC, Calegari-Marques C. 1994. Exotic plant species can serve as staple food sources for wild howler populations. *Folia Primatologica* 63:209–211.
- Bravo SP, Sallenave A. 2003. Foraging behavior and activity patterns of *Alouatta caraya* in the northeastern Argentinean flooded forest. *International Journal of Primatology* 24:825–846.
- Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40:215–231.
- Chapman CA, Chapman LJ, Bjørndal KA, Onderdonk DA. 2002. Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology* 23:283–310.
- Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ, Poulsen JR. 2005. A long-term evaluation of fruiting phenology: importance of climate change. *Journal of Tropical Ecology* 21:31–45.
- Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE. 2006. Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology* 131:525–534.
- Chaves OM, Bicca-Marques JC. 2013. Dietary flexibility of the brown howler monkey throughout its geographic distribution. *American Journal of Primatology* 75:16–29.

- Chaves ÓM, Bicca-Marques JC. 2016. Feeding strategies of brown howler monkeys in response to variations in food availability. *PLoS ONE* 11:e0145819.
- Chaves OM, Stoner KE, Arroyo-Rodríguez V. 2012. Differences in diet between spider monkey groups living in forest fragments and continuous forest in Lacandona, Mexico. *Biotropica* 44:105–113.
- Cristóbal-Azkarate J, Arroyo-Rodríguez V. 2007. Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. *American Journal of Primatology* 69:1–17.
- Dew JL, Wright P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30:425–437.
- Estrada A. 1984. Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *International Journal of Primatology* 5:105–131.
- Estrada A, Juan-Solano S, Martinez TO, Coates-Estrada R. 1999. Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology* 48:167–183.
- Estrada A, Raboy BE, Oliveira LC. 2012. Agroecosystems and primate conservation in the tropics: a review. *American Journal of Primatology* 74:696–711.
- Fernandez-Duque E, Rotundo M, Ramirez-Llorens P. 2002. Environmental determinants of birth seasonality in night monkeys (*Aotus azarai*) of the Argentinean Chaco. *International Journal of Primatology* 23:639–656.
- Fortes VB, Bicca-Marques JC, Urbani B, Fernández VA, da Silva Pereira T. 2015. Ranging behavior and spatial cognition of howler monkeys. In: Kowalewski MM, Garber PA, Cortés-



- Ortiz L, Urbani B, Youlatos D, editors. Howler Monkeys: Behavior, ecology, and conservation. New York: Springer. p. 219–255.
- Hanya G, Chapman CA. 2013. Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecology Research* 28:183–190.
- Hopkins ME. 2016. Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. *Animal Cognition* 19:387–403.
- Lockschin LX. 2012. A distribuição espaço-temporal de bugio-ruivo (*Alouatta clamitans*) (Primates, Atelidae) em gradiente urbano-rural no sul do Brasil [dissertação]. Porto Alegre (RS): Universidade Federal do Rio Grande do Sul. 115 p.
- Marshall AJ, Leighton M. 2006. How does food availability limit the population density of white-bearded gibbons? In: Hohmann G, Robbins MM., Boesch C, editors. *Feeding Ecology in Apes and Other Primates*. Cambridge: Cambridge University Press. p 313–335.
- Milton K. 1981. Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist* 83:534–548.
- Mourthé I. 2014. Response of frugivorous primates to changes in fruit supply in a northern Amazonian forest. *Brazilian Journal of Biology* 74:720–727.
- Pavelka MSM, Behie AM. 2005. The effect of Hurricane Iris on the food supply of black howlers (*Alouatta pigra*) in southern Belize. *Biotropica* 37:102–108.
- Pavelka MSM, Brusselers OT, Nowak D, Behie AM. 2003. Population reduction and social disorganization in *Alouatta pigra* following a hurricane. *International Journal of Primatology* 24:1037–1055.

- Potts KB, Chapman CA, Lwanga JS. 2009. Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. *Journal of Animal Ecology* 78:1269–1277.
- Rudran R, Fernandez-Duque E. 2003. Demographic changes over thirty years in a red howler population in Venezuela. *International Journal of Primatology* 24:925–947.
- Serio-Silva JC, Rico-Gray V, Hernandez-Salazar LT, Espinosa-Gomez R. 2002. The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys, *Alouatta palliata mexicana*, released on an island in southern Veracruz, Mexico. *Journal of Tropical Ecology* 18:913–928.
- Stone AI. 2007. Responses of squirrel monkeys to seasonal changes in food availability in an Eastern Amazonian forest. *American Journal of Primatology* 69:142–157.
- Strier KB, Mendes SL. 2009. Long-term field studies of South American primates. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier K, editors. *South American primates: Comparative perspectives in the study of behavior, ecology, and conservation*. New York: Springer Press. p 139–155.
- van Shaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forest: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–77.
- Williams-Guillén K, McCann C, Martinez Sanchez JC, Koontz F. 2006. Resource availability and habitat use by mantled howling monkeys in a Nicaraguan coffee plantation: can agroforests serve as core habitat for a forest mammal? *Animal Conservation* 9:331–338.

Zimmerman JK, Wright SJ, Calderon O, Pagan MA, Paton S. 2007. Flowering and fruiting phenologies of seasonal and aseasonal Neotropical forests: the role of annual changes in irradiance. *Journal of Tropical Ecology* 23:231–251.

**Artigo Científico**

Fruit availability drives the spatial distribution of brown howler monkeys  
within a large Atlantic forest remnant

Danielle Camaratta<sup>1\*</sup>, Óscar M. Chaves, and Júlio César Bicca-Marques

*Artigo no formato de submissão ao periódico*

*American Journal of Primatology*

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23

**Short title:** Fruit availability drives howler monkey dispersion

**Fruit availability drives the spatial distribution of brown howler monkeys within a large Atlantic forest remnant**

Danielle Camaratta<sup>1\*</sup>, Óscar M. Chaves, and Júlio César Bicca-Marques

<sup>1</sup>Departamento de Biodiversidade e Ecologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil

Correspondence to: Danielle Camaratta, Laboratório de Primatologia, Faculdade de Biociências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, 90619-900, Brazil. Email: danielle.camaratta@gmail.com

Phone: 55-51-3353.4742

FAX: 55-51-3353.4742

**Competing interests:** The authors declare that they have no competing interests.

24 **ABSTRACT**

25           Understanding the ecological factors that influence the presence, abundance, and  
26 distribution of species within their habitats is critical for ensuring their long-term  
27 conservation. In the case of primary consumers, such as most primates, the richness and  
28 availability of plant foods are considered key drivers of population density at different  
29 spatial scales. However, little is known about how (and whether) these variables  
30 influence the spacing of social units within a finer, habitat patch level scale. We  
31 investigated whether resource richness and spatiotemporal food availability are good  
32 predictors of local, within-habitat spatial distribution of brown howler monkeys  
33 (*Alouatta guariba clamitans*) in a 1,200 ha Atlantic forest remnant in southern Brazil.  
34 We censused the population every two weeks from January to June 2015 by walking  
35 205 km distributed in five line transects. Then, we used data on tree inventories in all  
36 sighting and control plots and phenological surveys of 17 top food tree species to  
37 estimate bi-weekly food availability for the monkeys. We recorded a total of 95  
38 sightings (2-12 sightings/sampling period) and found that fruit (ripe and unripe)  
39 availability was higher in sighting than in control plots. Leaf availability was similar.  
40 On the other hand, the number of individuals observed in each sighting was marginally  
41 directly related to the availability of ripe fruits, but not to tree richness or the availability  
42 of unripe fruits, mature leaves, and young leaves. We concluded that the distribution  
43 and availability of fruit sources was an important driver of the pattern of habitat use by  
44 brown howler during the study period.

45

46 **Key words:** food availability; fine-scale sample; within-habitat monkey distribution;  
47 habitat use; *Alouatta guariba clamitans*, distance sampling

## 48 INTRODUCTION

49 Plant species distribution and phenology may vary widely in space and time [van  
50 Schaik et al., 1993; Chapman et al., 2005; Zimmerman et al., 2007]. Climatic variables  
51 (e.g., rainfall and photoperiod) and extreme meteorological phenomena (e.g.,  
52 hurricanes) may also have strong influences on plant phenology [Richardson et al.,  
53 2013], thereby promoting increases [Wright & Calderón, 2006] or decreases [Harrison,  
54 2000] in food availability for primary consumers (e.g., young leaves and fruits). These  
55 dynamic and sometimes unpredictable changes in food availability may directly  
56 influence the survival, abundance and/or spatial distribution of animals at a broad scale  
57 [Hanya et al., 2013], or at a fine, local scale [Marshall et al., 2014; Schwartzberg et al.,  
58 2014]. Whereas studies at the broad (or large) spatial scale compare areas widely  
59 separated (sometimes by hundreds or thousands of kilometers), those at the fine (or  
60 small) spatial scale focus on understanding the ecological characteristics of areas within  
61 a single habitat patch or of a single site over time [Chapman et al., 2002].

62 At the broad spatial scale, plant species richness and food availability in tropical  
63 forests [Janson & Chapman, 1999] are major drivers of vertebrate density [e.g., reptiles:  
64 Wasko & Sasa, 2012; birds: Mulwa et al., 2013; primates: Janson & Chapman, 1999;  
65 Chapman et al., 2004; Marshall & Leighton, 2006; Marshall et al., 2009; other  
66 terrestrial mammals: Carbone & Gittleman, 2002] and richness [primates: Kay et al.,  
67 1997; Stevenson, 2001]. In this respect, the carrying capacity of a given habitat is likely  
68 to be set particularly by lean periods because of their negative influence on individual  
69 fecundity, growth, health, and/or survival [Goldizen et al., 1988; Lee & Hauser, 1998;  
70 Altmann & Alberts, 2005; Chapman et al., 2006; Marshall & Leighton, 2006; Foerster  
71 et al., 2012].

72           Although these broad scale studies allow detecting differences in the abundance  
73 of individuals between widely separated populations, studies at finer spatial scales are  
74 more sensitive for detecting important local ecological determinants of species  
75 abundance [primates: Chapman & Chapman, 1999; Potts et al. 2009; Jung et al., 2015].  
76 Despite this advantage, little is known about whether and how spatiotemporal variations  
77 in food availability influence the dispersion of individuals or social units of a species at  
78 a finer habitat scale [e.g., *Ateles belzebuth*: Mourthé, 2014; *Pan troglodytes*: Potts et al.,  
79 2009]. For instance, the dispersion of the highly frugivorous *Ateles belzebuth* was more  
80 strongly related to seasonal variations in fruit supply than the dispersion of the less  
81 frugivorous species [*Cebus olivaceus*, *Alouatta macconnelli*; Mourthé, 2014]. Similarly,  
82 the density of *Pan troglodytes* in two sites separated by only 12 km was related to the  
83 availability of fruits during lean periods [Potts et al., 2009]. The positive influence of  
84 the protein-to-fiber ratio in leaves on the biomass of folivorous African colobines was  
85 also found at the fine scale level [Chapman et al., 2002; Wasserman & Chapman, 2003].

86           Consumers may show a dispersion similar to that of the resources that they  
87 depend upon. Therefore, in general terms both plant species and their primate  
88 consumers may show a random (or aleatory), clustered (or clumped) or uniform (or  
89 homogeneous) distribution within a given habitat patch [Krebs, 1999]. This seems to be  
90 particularly true for primate species that feed on highly seasonal and clumped plant  
91 foods such as ripe fruits and/or young leaves [van Schaik et al., 1993; Zimmerman et  
92 al., 2007]. Additionally, consumer dispersion may vary temporally in response to  
93 spatiotemporal shifts in resource availability (as described above) and the presence of  
94 competitors that forage for the same limited resources [Milton, 1981; Chapman, 1988].  
95 For instance, *Alouatta palliata* spent up to 14 days near a clump of food trees before



96 travelling to new feeding sites when in syntopy with *Ateles geoffroyi* and *Cebus*  
97 *capucinus* [Chapman, 1988]. Similarly, *Lagothrix lagothricha* reduced the competition  
98 with three other primate species by feeding on unripe fruit when ripe fruits were scarce  
99 [Stevenson et al., 2000].

100         In addition to their rarity, most studies at a fine spatial scale have employed  
101 indirect estimators of food availability, such as comparisons of vegetation type, tree  
102 species diversity, and basal area of preferred food sources [e.g., Thomas, 1991;  
103 Anzures-Dadda & Manson, 2007; Gómez-Posada et al., 2007; Hopkins, 2011], instead  
104 of actual food availability [for a review see Hanya & Chapman, 2013; Marshall et al.,  
105 2009]. A more robust and informative analysis of the influence of within-site  
106 differences in habitat quality on primate abundance and dispersion at a fine spatial scale  
107 must integrate data on spatiotemporal shifts in food availability. *Syagrus romanzoffiana*  
108 (Arecaceae) helps to illustrate this point. This palm is an important food source for  
109 brown howler monkeys (*Alouatta guariba clamitans*) in southern Brazil. However, it is  
110 only exploited for food when fruiting or flowering because its leaves are not eaten by  
111 howlers [Chaves & Bicca-Marques, 2013]. Therefore, its importance to the diet of  
112 howler monkeys varies through time. The same variation is real for all sources of  
113 seasonal resources.

114         Here we test the hypothesis that the availability of plant foods within a large  
115 Atlantic forest remnant drives the spatial distribution and abundance of brown howlers  
116 at a fine spatial scale. Based on the aforementioned heterogeneity of the spatial  
117 distribution and phenology of plants and the reliance of brown howlers on highly  
118 seasonal plant items [Chaves & Bicca-Marques, 2013, 2016], particularly those items  
119 rich in energy and/or protein [e.g., mature fruit and young leaves; Lambert, 2011;

120 Lambert & Rothman, 2015], we predict that the distribution of brown howler social  
121 groups is driven by the availability of mature fruits and young leaves (prediction 1).  
122 Furthermore, as spatiotemporal availability of plant foods may positively affect primate  
123 group size [Chapman et al., 1995; Chapman & Chapman, 2000] and overall primate  
124 abundance [Oates, 1990; Hanya et al., 2011], we also predict that the abundance of  
125 brown howlers is directly related to the availability of their preferred plant items [e.g.,  
126 mature fruits and young leaves: Chaves & Bicca-Marques, 2016] (prediction 2).

127

## 128 **METHODS**

### 129 **Study Species**

130 Howler monkeys are folivorous-frugivorous primates that have the largest  
131 distribution and occupy the widest range of forest types among Neotropical primates  
132 [Crockett & Eisenberg, 1987]. The brown howler monkey, *Alouatta guariba clamitans*,  
133 occurs from the state of Minas Gerais to the state of Rio Grande do Sul in Brazil and in  
134 the province of Misiones in Argentina [Gregorin, 2006]. The taxon is endemic to the  
135 Atlantic forest, a world's biodiversity hotspot [Myers et al., 2000] that is currently split  
136 into 245,000 forest fragments [83% <50 ha; Ribeiro et al., 2009]. Diet composition  
137 includes primarily leaves and fruits from Leguminosae, Lauraceae, Moraceae and  
138 Myrtaceae species [Chaves & Bicca-Marques, 2013, 2016].

139

### 140 **Study Site**

141 The study was conducted in Morro São Pedro (hereafter MSP; 30°8'34"N -  
142 30°12'6,4"S, 51°5'26"E - 51°8'7,5"W, 35-289 m a.s.l.), the largest Atlantic forest  
143 remnant (ca. 1,200 ha of forest) in the municipality of Porto Alegre, state of Rio Grande  
144 do Sul, Brazil (Fig. 1). The site is covered by a mosaic of mature and secondary

145 subtropical semideciduous forests and natural grasslands surrounded by tree plantations  
146 (*Eucalyptus* spp. and *Pinus taeda*), human settlements, pastures, and cultivated lands. A  
147 total of 123 tree species distributed in 41 families were found in MSP in this study.  
148 Most of these species (109 spp. or 89%) provide food sources for brown howlers (Table  
149 SI). Twenty-five of them are considered top food species (i.e., those species that  
150 together contribute  $\geq 80\%$  of total feeding records) according to Chaves & Bicca-  
151 Marques [2013, 2016]. A small portion of MSP is legally protected in one public  
152 (Refúgio de Vida Silvestre São Pedro, 136 ha) and two private (Instituto Econsciência,  
153 142 ha; Reserva Particular do Patrimônio Natural Costa do Cerro, 12 ha) nature  
154 reserves. However, most of its area experiences strong human pressures, especially via  
155 urbanization, deforestation, illegal selective logging, fire, water contamination, and  
156 motocross practicing [Velez et al., 1998; Overbeck et al., 2011].

157         According to our meteorological records for MSP, average monthly temperature  
158 between 2012 and 2014 was 22°C. Daily temperatures ranged between 7°C and 26°C in  
159 the Winter and between 22°C and 34°C in the Summer. Average total annual rainfall  
160 was 1,130 mm for these years.

161         The brown howler monkey is the only primate inhabiting the site and the largest  
162 surviving arboreal frugivorous species of the original regional fauna. Therefore, it is  
163 unlikely that any of the other remaining arboreal frugivores are capable of outcompeting  
164 brown howlers at food sources via contest competition. This absence of “stronger”  
165 competitors qualifies the study site as an adequate scenario for testing the influence of  
166 food availability on howler monkey distribution because interspecific spatial  
167 segregation is probably null. We estimated a population of 1,662 brown howlers (=1.4  
168 inds/ha; 95% confidence interval: 1,225-2,256) for MSP (Table SII, Fig. S1).

## 169 **Howler Monkey Surveys**

170 We established five line transects (2.6-4.3 km long, Fig. 1) marked with colored  
171 flagging tape at 3-m intervals (removed after the study) from August to December 2014.  
172 DC (eventually accompanied by one assistant) walked transects from 7:00 to 13:00 and  
173 from 13:30 to 18:30 at an average speed of ca. 1 km/h as suggested by Buckland et al.  
174 [2010a]. Each transect was walked once in periods of three days every two weeks from  
175 January to June 2015 (sampling effort per transect=12 surveys). Therefore, a total of ca.  
176 205 km was walked during 36 days of sampling. The starting point (south or north of  
177 transect) was alternated between consecutive surveys to reduce sampling bias. Because  
178 the rain critically compromises visibility and animal detection, no survey was carried  
179 out during rainy days.

180 DC collected the following data during each sighting of a howler monkey group  
181 or solitary individual: date, time, transect number, number of animals, sex-age  
182 composition [*sensu* Mendes, 1989], perpendicular distance from the transect to the  
183 center of the group using a 30-m measuring tape [Buckland et al., 2010a, 2010b], and  
184 geographic positioning using a GPS device (Garmin Oregon 550t). The center of the  
185 sighting location was marked with a flagging tape. We used the number of brown  
186 howlers recorded in each sighting location [i.e., cluster size, *sensu* Thomas et al., 2010]  
187 as an estimate of abundance at the fine spatial scale.

188

## 189 **Spatiotemporal Food Availability**

190 We carried out vegetation surveys from January to September 2015 to estimate  
191 local food availability. In each sighting location (whose center was marked with a  
192 flagging tape) we established 20 m x 20 m tree survey plots (hereafter sighting plots)

193 and identified and measured all trees with diameter at breast height (DBH)  $\geq 5$  cm.  
194 OMC identified the trees based on taxonomic keys of the flora of the state of Rio  
195 Grande do Sul [Sobral et al., 2006]. Botanical vouchers of trees that could not be  
196 identified in the field were collected for later identification in the laboratory and/or the  
197 Herbarium of the Museum of Science and Technology of the Pontifical Catholic  
198 University of Rio Grande do Sul, Brazil. Twenty-five 20 m x 20 m additional tree  
199 survey plots were established 120 m SE of 25 randomly selected sighting plots (five  
200 sighting plots per line transect) to estimate food availability at control sites. Overall, we  
201 sampled one hundred and twenty 20 m x 20 m plots (=4.8 ha).

202 DC and OMC monitored the phenology of 1 to 11 adult trees (mode and  
203 median=10) of 17 native top food species for brown howlers [according to Chaves &  
204 Bicca-Marques, 2013] in the central transect (T3, Fig. 1) the day before the beginning of  
205 each three-day howler monkey survey period. The availability of ripe and unripe fruit,  
206 mature and young leaves, and flowers of the 132 adult trees was estimated by the semi-  
207 quantitative method of Fournier [1974]. A Phenological Index for the Species (PIS) was  
208 obtained by averaging the scores of each phenophase of the individual trees of each top  
209 food species at the respective sampling period. Following Agostini et al. [2010], we  
210 calculated the Food Availability Index (FAI) by multiplying the dominance (total basal  
211 area of a given species in the 400-m<sup>2</sup> plot) by its PIS. Then, we summed up FAI (for  
212 each phenophase) of each species found in each plot for calculating an overall FAI of  
213 each phenophase per plot during a given period sampled.

214

## 215 **Statistical Analyses**

216           We tested whether the availability of ripe fruits, unripe fruits, young leaves, and  
217 mature leaves affect the distribution of brown howlers by comparing the FAI of the  
218 same number of sighting and control plots per sampling period via one-tailed Mann-  
219 Whitney tests using the function ‘wilcox.test’ in R [R CoreTeam, 2015]. The subset of  
220 control plots matching the number of sightings in a given sampling period was  
221 randomly chosen using the function ‘sample’. We tested the relative influence of food  
222 availability (ripe fruits, unripe fruits, young leaves, mature leaves, and tree richness) on  
223 brown howler cluster size (i.e., the number of individuals observed in each sighting) by  
224 performing a Generalized Linear Mixed Model with Poisson error distribution [GLMM;  
225 Zuur et al., 2009] using the R package nlme [R CoreTeam, 2015]. We reduced the effect  
226 of multicollinearity between predictor variables by selecting those variables with  
227 Variance Inflation Factor (VIF)  $< 2$  as suggested by Zuur et al. [2009]. We identified  
228 these variables by using the ‘VIF’ function of the R package car [R CoreTeam, 2015].  
229 Unlike other linear models, GLMMs account for temporal and/or spatial pseudo-  
230 replication problems by simultaneously assessing the influence of random factors (i.e.,  
231 the repeated variables) and fixed factors on the model [Zuur et al., 2009]. We specified  
232 the line transect and the sampling period as random factors and the availability of each  
233 plant item as fixed factors. We determined the minimal adequate (i.e., the most  
234 parsimonious) model by the model simplification process described by Crawley [2012].  
235 In this procedure, the model containing all factors, interactions and covariates of interest  
236 (i.e., the maximal model) is simplified until a model that produces the least unexplained  
237 variation or the lowest AIC is achieved [see Crawley, 2012]. All statistical analyses  
238 were ran in Rv.3.2.1 [R CoreTeam, 2015].

239 This research was approved by the Scientific Committee of the Faculty of  
240 Biosciences of the Pontifical Catholic University of Rio Grande do Sul (project SIPESQ  
241 #5933). It met all Brazilian animal care policies and adhered to the ethical and legal  
242 requirements established by the American Society of Primatologists and the Ethical  
243 Committee of the Zoological Society of London for research with nonhuman primates.

244

## 245 **RESULTS**

246 A total of 95 howler monkey sightings were recorded during the 205 km walked  
247 (transect 1=28 sightings, 2=12, 3=27, 4=17, 5=11). The number of sightings per  
248 sampling period varied from 2 to 12 (mean  $\pm$  S.D.= $8 \pm 3$ ;  $G$ -test=13.8, d.f.=11,  $P=0.2$ ).

249 The availability of unripe and ripe fruits was significantly higher in sighting  
250 plots (median=4.4 and 1.1, respectively) than in control plots (unripe fruits:  
251 median=2.1,  $W=5572$ ,  $P=0.0009$ ; ripe fruits: median=0.4,  $W=5347$ ,  $P=0.006$ ).  
252 However, the availability of young (median=13.7 vs. 13.3,  $W=4345$ ,  $P=0.5781$ ) and  
253 mature leaves (median=276.4 vs. 194.8,  $W=4844$ ,  $P=0.127$ ) did not differ between  
254 sighting and control plots (Fig. 2). Prediction 1 was supported in relation to the role of  
255 ripe fruits, but not in relation to young leaves.

256 On the other hand, the abundance of howler monkeys (number of individuals  
257 recorded) in each sighting location was positively related to the availability of ripe  
258 fruits, although its effect only approached significance ( $\beta=0.02$ ,  $P = 0.06$ , Table I).  
259 However, unripe fruits, young leaves, mature leaves, and tree richness or the  
260 interactions between these variables did not influence brown howler abundance (Table  
261 I). Therefore, we found only weak support to prediction 2.

262

263 **DISCUSSION**

264 We found that the availability of fruit of top food species was the most likely  
265 driver of the spatial distribution and abundance of brown howlers within the 1,200 ha  
266 Atlantic forest fragment in south Brazil. This importance of fruits can be explained, at  
267 least in part, by their key role in satisfying the nutritional demands of primates [Milton,  
268 1998; Lambert, 2011; Behie & Pavelka, 2015; Righini et al., 2015]. Overall, ripe fruits  
269 are high quality foods (i.e., easily digestible foods with a high content of carbohydrates  
270 and minerals compared with other plant items exploited by primates, such as mature  
271 leaves and flowers [Lambert, 2011; Behie & Pavelka, 2015; Lambert & Rothman,  
272 2015]. This critical role was clearly highlighted by Silver et al.'s [1998] description of  
273 howler monkeys as “as frugivorous as possible, as folivorous as necessary.”

274 Contrasting with fruits, mature leaves are more abundant resources that are rich  
275 in protein, but that are also high in fiber and secondary metabolites against herbivory  
276 [Dias & Rangel-Negrín, 2015; but see Righini et al., 2015]. Therefore, the exploitation  
277 of a more frugivorous diet is expected to result in a higher energy intake than that of a  
278 more folivorous one. Compatible with this expectation, brown howlers tend to cover  
279 longer day ranges when feeding heavily on fruit [Limeira, 1996; Agostini et al., 2010].  
280 These findings give support to the adoption of a high cost-high reward strategy during  
281 periods of higher frugivory and a low cost-low reward strategy during periods of higher  
282 folivory [*sensu* Zunino, 1986]. However, these patterns may not hold true when  
283 consumers exploit abundant, but clumped, fruit species. Under these circumstances,  
284 frugivores may camp during several days near productive fruiting sources [Zunino,  
285 1986]. This strategy has been reported for other frugivores [Unruh, 1990], including



286 *Brachyteles hypoxanthus* [Strier, 1987; Tabela & Lee, 2010] and *Alouatta seniculus*  
287 [Palacios & Rodrigues, 2001].

288         Although such camping behavior is compatible with our findings, it is also  
289 possible that the strong relationship between howler monkey distribution and fruit  
290 availability resulted from its limited supply during the study period. The FAI of fruit,  
291 particularly ripe ones, was much lower than that of leaves. Although data from a recent  
292 3-year study on two brown howler groups at the same site showed that the availability  
293 of these items does not vary widely throughout the year, the production of ripe fruit  
294 tended to be higher in the first half of the year (the period covered by this study),  
295 whereas the yield of young leaves tended to be higher in the second half of the year  
296 [Chaves & Bicca-Marques, 2016]. However, there is reliable evidence that the  
297 availability of ripe fruit and young leaves of most top food species is indeed higher in  
298 the Spring (particularly in September and October; Chaves & Bicca-Marques, 2016), a  
299 period that was not covered by this study.

300         In fact, MSP brown howlers intensively exploited abundant sources of young  
301 leaves during their 1 to 2-mo long flushing [Chaves & Bicca-Marques, 2016].  
302 Therefore, it is reasonable to expect that this heavy exploitation of young leaves may  
303 significantly influence the spatial distribution of brown howlers in a similar way at these  
304 times. Whether the most limiting or the most profitable of these seasonal resources play  
305 a major role in driving the distribution of consumers during lean and wealth periods by  
306 directly influencing their pattern of space use is an interesting open question for future  
307 research.

308         The fact that howlers feed on a limited number of plant species per day [mean  $\pm$   
309  $SD=7 \pm 2$ ,  $N=12$ ; Bicca-Marques, 2003] is compatible with the adoption of a

310 “traplining” strategy [Dew & Wright, 1998]; that is, a strategy by which consumers  
311 travel between consecutive target resources of the same species [see Bicca-Marques,  
312 2005]. The consecutive heavy exploitation of a small set of trees of species that fruit  
313 asynchronously throughout the year in the study region [e.g., *Syagrus romanzoffiana*,  
314 *Areaceae*, and *Ficus* spp., *Moraceae*: Marques, 2001; Chaves & Bicca-Marques, 2016]  
315 is a good example of this strategy. This strategy is also compatible with evidence that  
316 howlers are capable of keeping a mental map of the distribution of important food trees  
317 [Fortes et al., 2015]. Therefore, if howlers are traplining fruit sources of a few species  
318 during a given period, they are more likely to be found near them instead of in areas of  
319 the home range where these species are absent. Understanding which resources brown  
320 howlers are exploiting in these food sources may better qualify us to evaluate their  
321 potential contribution to the distribution of these animals at a finer spatial scale.

322         While stronger interspecific competitors are absent from MSP, the site presented  
323 a high population density of brown howlers. This high density of conspecifics might  
324 force social groups to explore small home ranges where they travel shorter distances  
325 [Fortes et al., 2015]. Both the absence of interspecific food competitors and a higher  
326 availability of potential sources of high quality foods support this high howler monkey  
327 density. The difference in the availability of fruit between sighting and control plots  
328 gives support to the contention that howler monkey clumped distribution at MSP is  
329 centered on fruit sources.

330         In sum, we found that the spatial distribution and availability of fruit sources  
331 seem to play a critical role in the pattern of habitat use by this high density population  
332 of brown howlers of Morro São Pedro, at least during part of the year. Understanding  
333 the proximate cause(s) of this relationship would require an examination of the

334 nutritional content of food items exploited throughout the year together with a longer (at  
335 least one year) phenology sampling and the identification of the species that drive their  
336 ranging behavior. An increase in the number of control plots would also potentially  
337 increase the reliability of the comparisons with sighting plots. Nevertheless, we  
338 highlight the importance of spatiotemporal fine scale studies in detecting determinants  
339 of primate spatial distribution and abundance.

340

#### 341 **ACKNOWLEDGMENTS**

342         We thank Felipe Vianna (Instituto Econsciência), the Private Reserve of Natural  
343 Heritage (RPPN) Costa do Cerro, the Beneficent Spiritual Center União do Vegetal and  
344 other local residents for giving us permission to conduct this research in their properties.  
345 The Municipal Secretariat for the Environment in Porto Alegre (SMAM) giving us  
346 permission to conduct this research in the Wildlife Refuge São Pedro. Claudio Godoy,  
347 Renata Souza, Anamelia Jesus, Fabiana Corrêa, Monique Costa, Ítalo Mourthé, Gustav  
348 Beier, Luana Melo, Pedro Bencke, Lívia Machado, Gabriela Hass, Kássia Ramos, Paula  
349 Grison, Vitor Vieira for field assistance. Suzana E.B. Camaratta and Epifanio Juarez  
350 Camaratta for logistical support. Cristiane Follmann J. helped in botanical voucher  
351 identification. Secretaria de Arquitetura e Urbanismo (SMURB) of Porto Alegre  
352 municipality provided land cover data. Regis A. Lahm and Everton L. Quadros  
353 (Laboratório de Tratamento de Imagens e Geoprocessamento/PUCRS) assisted to  
354 prepared the map of the Morro São Pedro. The study was supported by a grant from the  
355 Programa Nacional de Pós-Doutorado of the Brazilian Higher Education  
356 Authority/CAPES (PNPD grant # 2755/2010). D.C. was supported by the Brazilian  
357 National Council for Scientific and Technological Development/CNPq. O.M.C. was

358 supported by a PNPd postdoctoral fellowship. JCBM thanks the Brazilian National  
359 Council for Scientific and Technological Development/CNPq for a research fellowship  
360 (PQ#303306/2013-0).

361

## 362 REFERENCES

- 363 Agostini I, Holzmann I, Di Bitetti MS. 2010. Are howler monkey species ecologically  
364 equivalent? Trophic niche overlap in syntopic *Alouatta guariba clamitans* and  
365 *Alouatta caraya*. *American Journal of Primatology* 72:173–186.
- 366 Altmann J, Alberts SC. 2005. Growth rates in a wild primate population: ecological  
367 influences and maternal effects. *Behavioral Ecology and Sociobiology* 57:490–501.
- 368 Anzures-Dadda A, Manson RH. 2007. Patch-and landscape-scale effects on howler  
369 monkey distribution and abundance in rainforest fragments. *Animal Conservation*  
370 10:69–76.
- 371 Behie AM, Pavelka MSM. 2015. Fruit as a key factor in howler monkey population  
372 density: Conservation implications. *Howler monkeys*: Springer. p 357–382.
- 373 Bicca-Marques JC. 2003. How do howler monkeys cope with habitat fragmentation? In:  
374 Marsh LK, editor. *Primates in fragments*. New York: Kluwer Academics/Plenum  
375 Publishers. p 283–303.
- 376 Bicca-Marques JC. 2005. The win-stay rule in foraging decisions by free-ranging titi  
377 monkeys (*Callicebus cupreus cupreus*) and tamarins (*Saguinus imperator imperator*  
378 and *Saguinus fuscicollis weddelli*). *Journal of Comparative Psychology* 119:343–  
379 351.
- 380 Buckland ST, Plumptre AJ, Thomas L, Rexstad EA. 2010a. Design and analysis of line  
381 transect surveys for primates. *International Journal of Primatology* 31:833–847.

- 382 Buckland ST, Plumptre AJ, Thomas L, Rexstad EA. 2010b. Line transect sampling of  
383 primates: can animal-to-observer distance methods work? *International Journal of*  
384 *Primateology* 31:485–499.
- 385 Carbone C, Gittleman JL. 2002. A common rule for the scaling of carnivore density.  
386 *Science* 295:2273–2276.
- 387 Chapman C. 1988. Patterns of foraging and range use by three species of Neotropical  
388 primates. *Primates* 29:177–194.
- 389 Chapman CA, Chapman LJ. 1999. Implications of small scale variation in ecological  
390 conditions for the diet and density of red colobus monkeys. *Primates* 40:215–231.
- 391 Chapman CA, Chapman LJ. 2000. Constraints on group size in red colobus and red-  
392 tailed guenons: examining the generality of the ecological constraints model.  
393 *International Journal of Primatology* 21:565–585.
- 394 Chapman CA, Chapman LJ, Bjorndal KA, Onderdonk DA. 2002. Application of  
395 protein-to-fiber ratios to predict colobine abundance on different spatial scales.  
396 *International Journal of Primatology* 23:283–310.
- 397 Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, Mcdowell LR. 2004.  
398 Predicting folivorous primate abundance: validation of a nutritional model. *American*  
399 *Journal of Primatology* 62:55–69.
- 400 Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ, Poulsen JR. 2005. A  
401 long-term evaluation of fruiting phenology: importance of climate change. *Journal of*  
402 *Tropical Ecology* 21:31–45.
- 403 Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler  
404 TE. 2006. Do food availability, parasitism, and stress have synergistic effects on red

- 405 colobus populations living in forest fragments? *American Journal of Physical*  
406 *Anthropology* 131:525–534.
- 407 Chapman CA, Wrangham RW, Chapman LJ. 1995. Ecological Constraints on Group-  
408 Size: an Analysis of Spider Monkey and Chimpanzee Subgroups. *Behavioral*  
409 *Ecology and Sociobiology* 36:59–70.
- 410 Chaves ÓM, Bicca-Marques JC. 2013. Dietary flexibility of the brown howler monkey  
411 throughout its geographic distribution. *American Journal of Primatology* 75:16–29.
- 412 Chaves ÓM, Bicca-Marques JC. 2016. Feeding strategies of brown howler monkeys in  
413 response to variations in food availability. *PLoS ONE* 11:e0145819.
- 414 Crawley MJ. 2012. *The R book*. New Jersey: John Wiley & Sons. 1051 p.
- 415 Crockett CM, Eisenberg JF. 1987. Howlers: variations in group size and demography.  
416 In: Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors.  
417 *Primate societies*. Chicago: University of Chicago Press. p 54–68.
- 418 Dew JL, Wright P. 1998. Frugivory and seed dispersal by four species of primates in  
419 Madagascar's eastern rain forest. *Biotropica* 30:425–437.
- 420 Dias PAD, Rangel-Negrín A. 2015. Diets of howler monkeys. In: Kowalewski MM,  
421 Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D, editors. *Howler monkeys:*  
422 *behavior, ecology, and conservation*. New York: Springer. p 21–56.
- 423 Foerster S, Cords M, Monfort SL. 2012 Seasonal energetic stress in a Tropical forest  
424 primate: proximate causes and evolutionary implications. *PLoS ONE* 7:e50108.
- 425 Fortes VB, Bicca-Marques JC, Urbani B, Fernández VA, da Silva Pereira T. 2015.  
426 Ranging behavior and spatial cognition of howler monkeys. In: Kowalewski MM,  
427 Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D, editors. *Howler monkeys:*  
428 *behavior, ecology, and conservation*. New York: Springer. p. 219–255.

- 429 Fournier L. 1974. Un método cuantitativo para la medición de las características  
430 fenológicas en árboles. *Turrialba* 24:422–423.
- 431 Goldizen AW, Terborgh J, Cornejo F, Porras DT, Evans R. 1988. Seasonal food  
432 shortage, weight-loss, and the timing of births in saddle-back tamarins (*Saguinus*  
433 *fuscicollis*). *Journal of Animal Ecology* 57:893–901.
- 434 Gómez-Posada C, Martínez J, Giraldo P, Kattan GH. 2007. Density, habitat use, and  
435 ranging patterns of red howler monkeys in a Colombian Andean forest. *Neotropical*  
436 *Primates* 14:2–10.
- 437 Gregorin R. 2006. Taxonomy and geographic variation of species of the genus *Alouatta*  
438 *Lacepede* (Primates, Atelidae) in Brazil. *Revista Brasileira De Zoologia* 23:64–144.
- 439 Hanya G, Chapman CA. 2013. Linking feeding ecology and population abundance: a  
440 review of food resource limitation on primates. *Ecological Research* 28:183–190.
- 441 Harrison RD. 2000. Repercussions of El Nino: drought causes extinction and the  
442 breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London B:*  
443 *Biological Sciences* 267:911–915.
- 444 Hopkins ME. 2011. Mantled howler (*Alouatta palliata*) arboreal pathway networks:  
445 relative impacts of resource availability and forest structure. *International Journal of*  
446 *Primateology* 32:238–258.
- 447 Janson CH, Chapman CA. 1999. Resources and primate community structure. In:  
448 Fleagle JG, Janson CH, Reed KE, editors. *Primate communities*. New York:  
449 Cambridge University Press. p 237–267.
- 450 Jung L, Mourthe I, Grelle CEV, Strier KB, Boubli JP. 2015. Effects of local habitat  
451 variation on the behavioral ecology of two sympatric groups of brown howler  
452 monkey (*Alouatta clamitans*). *PLoS ONE* 10:e0129789.

- 453 Kay RF, Madden RH, Van Schaik C, Higdon D. 1997. Primate species richness is  
454 determined by plant productivity: implications for conservation. Proceedings of the  
455 National Academy of Sciences 94:13023–13027.
- 456 Krebs CJ. 1999. Ecological methodology. Menlo Park: Addison Wesley Longman. 620  
457 p.
- 458 Lambert JE. 2011. Primate nutritional ecology: feeding biology and diet at ecological  
459 and evolutionary scales. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M,  
460 Bearder SK, Stumpf R, editors. Primates in perspective. Oxford: Oxford University  
461 Press. p 512–522.
- 462 Lambert JE, Rothman JM. 2015. Fallback foods, optimal diets, and nutritional targets:  
463 primate responses to varying food availability and quality. Annual Review of  
464 Anthropology 44:493–512.
- 465 Lee P, Hauser M. 1998. Long-term consequences of changes in territory quality on  
466 feeding and reproductive strategies of vervet monkeys. Journal of Animal Ecology  
467 67:347–358.
- 468 Limeira VLAG. 1996. Comportamento alimentar, padrão de atividades e uso do espaço  
469 por *Alouatta fusca* (Primates, Platyrrhini) em um fragmento degradado de Floresta  
470 Atlântica no estado do Rio de Janeiro [MSc dissertation]. Rio de Janeiro (RJ):  
471 Universidade Federal do Rio de Janeiro. 135 p.
- 472 Marques AAB. 2001. Estratégias de uso do espaço por *Alouatta guariba clamitans*  
473 Cabrera, 1940 em habitats temperado e subtropical no sul do Brasil [PhD  
474 dissertation]. Minas Gerais (BH): Universidade Federal de Minas Gerais. 147 p.



- 475 Marshall AJ, Beaudrot L, Wittmer HU. 2014. Responses of primates and other  
476 frugivorous vertebrates to plant resource variability over space and time at Gunung  
477 Palung National Park. *International Journal of Primatology* 35:1178–1201.
- 478 Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M. 2009. Defining fallback  
479 foods and assessing their importance in primate ecology and evolution. *American*  
480 *Journal of Primatology* 140:603–614.
- 481 Marshall AJ, Leighton M. 2006. How does food availability limit the population density  
482 of white-bearded gibbons? In: Hohmann G, Robbins MM, Boesch C, editors.  
483 *Feeding ecology in apes and other primates*. Cambridge: Cambridge University  
484 Press. p 313–335.
- 485 Mendes SL. 1989. Estudo ecológico de *Alouatta fusca* (Primates: Cebidae) na Estação  
486 Biológica de Caratinga, MG. *Revista Nordestina de Biologia* 6:71–104.
- 487 Milton K. 1981. Distribution patterns of tropical plant foods as an evolutionary stimulus  
488 to primate mental development. *American Anthropologist* 83:534–548.
- 489 Milton K. 1998. Physiological ecology of howlers (*Alouatta*): Energetic and digestive  
490 considerations and comparison with the colobinae. *International Journal of*  
491 *Primatology* 19:513–548.
- 492 Mourthé I. 2014. Response of frugivorous primates to changes in fruit supply in a  
493 northern Amazonian forest. *Brazilian Journal of Biology* 74:720–727.
- 494 Mulwa RK, Neuschulz EL, Böhning-Gaese K, Schleuning M. 2013. Seasonal  
495 fluctuations of resource abundance and avian feeding guilds across forest–farmland  
496 boundaries in tropical Africa. *Oikos* 122:524–532.
- 497 Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J. 2000. Biodiversity  
498 hotspots for conservation priorities. *Nature* 403:853–858.

- 499 Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Dasilva GL, Mole S.  
500 1990. Determinants of variation in tropical forest primate biomass: new evidence  
501 from West Africa. *Ecology* 71:328–343.
- 502 Overbeck G, Muller SC, Pillar V, Setubal RB. 2011. Propostas de manejo e  
503 conservação para os campos. In: Setubal RB, Boldrini IL, Ferreira PM, editors.  
504 Campos dos morros de Porto Alegre. Porto Alegre, Rio Grande do Sul, Brazil:  
505 Secretaria Municipal do Meio Ambiente. p 95–98.
- 506 Palacios E, Rodriguez A. 2001. Ranging pattern and use of space in a group of red  
507 howler monkeys (*Alouatta seniculus*) in a southeastern Colombian rainforest.  
508 *American Journal of Primatology* 55:233–251.
- 509 Potts KB, Chapman CA, Lwanga JS. 2009. Floristic heterogeneity between forested  
510 sites in Kibale National Park, Uganda: insights into the fine-scale determinants of  
511 density in a large-bodied frugivorous primate. *Journal of Animal Ecology* 78:1269–  
512 1277.
- 513 R CoreTeam. 2015. R: a language and environment for statistical computing. Vienna,  
514 Austria: R Foundation for Statistical Computing.
- 515 Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian  
516 Atlantic forest: how much is left, and how is the remaining forest distributed?  
517 Implications for conservation. *Biological Conservation* 142:1141–1153.
- 518 Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M. 2013.  
519 Climate change, phenology, and phenological control of vegetation feedbacks to the  
520 climate system. *Agricultural and Forest Meteorology* 169:156–173.

- 521 Righini N, Garber PA, Rothman JM. 2015. The effects of plant nutritional chemistry of  
522 food selection of mexican black howler monkeys (*Alouatta pigra*): The role of lipids.  
523 American Journal of Primatology (in press). doi: 10.1002/ajp.22524.
- 524 Schwartzberg EG, Jamieson MA, Raffa KF, Reich PB, Montgomery RA, Lindroth RL.  
525 2014. Simulated climate warming alters phenological synchrony between an  
526 outbreak insect herbivore and host trees. *Oecologia* 175:1041–1049.
- 527 Silver SC, Ostro LET, Yeager CP, Horwich R. 1998. Feeding ecology of the black  
528 howler monkey (*Alouatta pigra*) in northern Belize. *American Journal of*  
529 *Primatology* 45:263–279.
- 530 Sobral M, Jarenkow JA, Brack P. 2006. Flora arbórea e arborescente do Rio Grande do  
531 Sul. Brasil. São Carlos: RiMa. 350 p.
- 532 Stevenson PR. 2001. The relationship between fruit production and primate abundance  
533 in Neotropical communities. *Biological Journal of the Linnean Society* 72:161–178.
- 534 Stevenson PR, Quiñones MJ, Ahumada JA. 2000. Influence of fruit availability on  
535 ecological overlap among four Neotropical primates at Tinigua National Park,  
536 Colombia. *Biotropica* 32:533–544.
- 537 Strier KB. 1987. Ranging behavior of woolly spider monkeys, or muriquis, *Brachyteles*  
538 *arachnoides*. *International Journal of Primatology* 8:575–591.
- 539 Talebi MG, Lee PC. 2010. Activity patterns of *Brachyteles arachnoides* in the largest  
540 remaining fragment of Brazilian Atlantic forest. *International Journal of Primatology*,  
541 31:571–583.
- 542 Thomas SC. 1991. Population densities and patterns of habitat use among anthropoid  
543 primates of the Ituri Forest, Zaire. *Biotropica* 23:68–83.

- 544 Unruh JD. 1990. Iterative increase of economic tree species in managed swidden-  
545 fallows of the Amazon. *Agroforestry Systems* 11:175–197.
- 546 van Shaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forest:  
547 adaptative significance and consequences for primary consumers. *Annual Review of*  
548 *Ecology and Systematics* 24:353–77.
- 549 Velez E, Meira J, Oliveira P. 1998. Avaliação dos morros com base no uso do solo. In:  
550 Menegat R, Porto M, Carraro C, Fernandes L, editors. *Atlas ambiental de Porto*  
551 *Alegre*. Porto Alegre: Universidade Federal do Rio Grande do Sul. p 62–63.
- 552 Wasko DK, Sasa M. 2012. Food resources influence spatial ecology, habitat selection,  
553 and foraging behavior in an ambush-hunting snake (Viperidae: *Bothrops asper*): an  
554 experimental study. *Zoology* 115:179–187.
- 555 Wasserman MD, Chapman CA. 2003. Determinants of colobine monkey abundance: the  
556 importance of food energy, protein and fibre content. *Journal of Animal Ecology*  
557 72:650–659.
- 558 Wright S, Calderón O. 2006. Seasonal, El Niño and longer term changes in flower and  
559 seed production in a moist Tropical forest. *Ecology Letters* 9:35–44.
- 560 Zimmerman JK, Wright SJ, Calderon O, Pagan MA, Paton S. 2007. Flowering and  
561 fruiting phenologies of seasonal and aseasonal Neotropical forests: the role of annual  
562 changes in irradiance. *Journal of Tropical Ecology* 23:231–251.
- 563 Zunino GE 1986. Algunos aspectos de la ecología y etología del mono aullador negro  
564 (*Alouatta caraya*) en habitats fragmentados [PhD dissertation]. Buenos Aires (BA):  
565 Universidad de Buenos Aires. 152 p.
- 566 Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed effects models and  
567 extensions in ecology with R. New York: Springer. 574 p.

568 **SUPPORTING INFORMATION**

569           Additional supporting information may be found in the online version of this  
570 article at the publisher's web-site.

**Table I. Results of the GLMM for the three best models examining the influence of food availability and tree richness on brown howler cluster size in Morro São Pedro, Rio Grande do Sul, Brazil.**

Variable <sup>a</sup>	AIC <sup>c</sup>	<i>B</i>	S.E.	<i>t</i>	d.f.	<i>P</i> -value
<i>Model 1</i> <sup>b</sup>		458.2				
Intercept		4.16	0.33	12.80	48	<0.0001
Ripe fruit		0.02	0.01	1.90		0.06
<i>Model 2</i>		463.7				
Intercept		3.53	1.17	3.02	47	0.004
Ripe fruit		0.02	0.01	1.93		0.06
Tree richness		0.03	0.06	0.56		0.58
<i>Model 3</i>		474.8				
Intercept		3.55	1.17	3.02	46	0.004
Ripe fruit		0.02	0.01	1.91		0.06
Tree richness		0.03	0.06	0.52		0.61
Young leaves		0.0005	0.004	0.13		0.89

<sup>a</sup>We specified the line transect and the sampling week as random factors and the availability of ripe fruits, unripe fruits, mature leaves, and young leaves as fixed factors (see Methods).

<sup>b</sup>Minimal adequate model or best model.

<sup>c</sup>Akaike's Information Criterion.

## Figure legends

**Fig. 1** Satellite image of the study site (Morro São Pedro) showing the length and location of line transects and sampling plots where tree surveys were performed (see Methods). Circles represent sighting plots and squares represent control plots. Adapted from Google Earth©.

**Fig. 2** Availability of vegetative and reproductive structures of the top food tree species exploited by brown howler monkeys. Comparisons between sighting (S) and control (C) plots are shown. Boxes represent the first and third interquartiles (IQR) of Food Availability Index (FAI), whiskers represent the IQR multiplied by 1.5, the black line within each box represents the median of FAI, whereas the small red line represents the mean FAI. Dots represent the FAI of each plot. Different letters indicate significant differences according to the Mann-Whitney test ( $P < 0.05$ ).

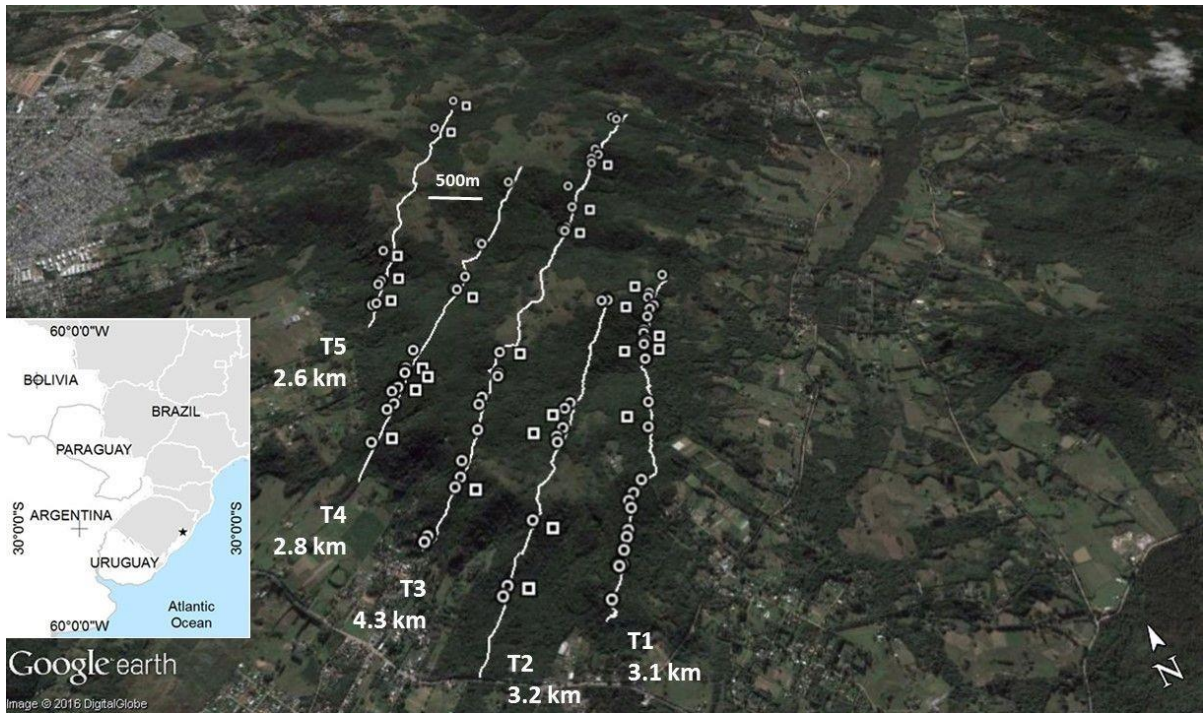
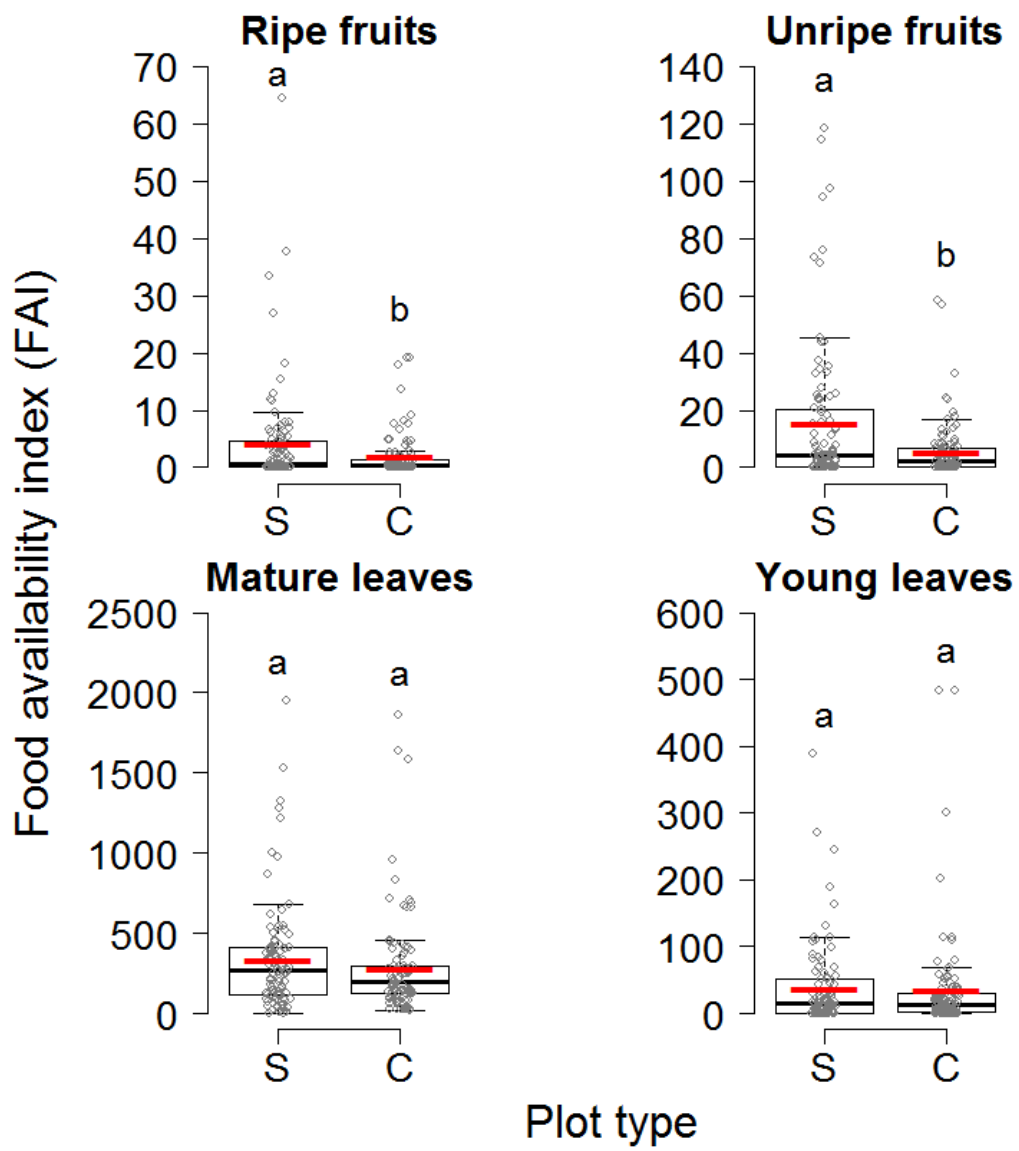


Fig. 1





**Fig. 2**

## Supporting Information

Camaratta D, Chaves ÓM, Bicca-Marques JC. 2016. Fruit availability drives the spatial distribution of brown howler monkeys within a large Atlantic forest remnant.

**Table SI.** List of tree species found in Morro São Pedro, Rio Grande do Sul, Brazil. Data based on plant surveys of trees  $\geq 5$  cm diameter at breast height (DBH) in one-hundred-and-twenty 20 m x 20 m plots (=4.8 ha).

Family	Species <sup>1</sup>	Food source? <sup>2</sup>	Basal area (m <sup>2</sup> )	IVI
Euphorbiaceae	<i>Sebastiania serrata</i>	yes	15313.94	56.4
Nyctaginaceae	<i>Guapira opposita</i>	<b>yes</b>	7013.79	26.4
Primulaceae	<i>Myrsine umbellata</i>	yes	3804.09	18.4
Salicaceae	<i>Casearia sylvestris</i>	yes	2780.37	17.4
Anacardiaceae	<i>Lithraea brasiliensis</i>	<b>yes</b>	3843.86	15.7
Euphorbiaceae	<i>Actinostemon concolor</i>	no	1159.13	12.8
Sapotaceae	<i>Chrysophyllum marginatum</i>	yes	1475.98	10.7
Meliaceae	<i>Trichilia clausenii</i>	yes	1211.38	10.5
Sapindaceae	<i>Allophylus edulis</i>	<b>yes</b>	1086.92	8.87
Ebenaceae	<i>Diospyros inconstans</i>	<b>yes</b>	823.71	7.76
Moraceae	<i>Sorocea bonplandii</i>	<b>yes</b>	320.07	7.31
Sapindaceae	<i>Cupania vernalis</i>	yes	566.86	6.42
Salicaceae	<i>Casearia decandra</i>	yes	249.20	6.08
Moraceae	<i>Ficus cestrifolia</i>	<b>yes</b>	1330.21	5.77
Fabaceae	<i>Enterolobium contortisiliquum</i>	<b>yes</b>	654.50	4.57
Malvaceae	<i>Luehea divaricata</i>	<b>yes</b>	399.01	4.54
Lauraceae	<i>Ocotea porosa</i>	yes	497.78	3.86
Myrtaceae	<i>Myrciaria cuspidata</i>	yes	113.52	3.7
Urticaceae	<i>Coussapoa microcarpa</i>	<b>yes</b>	455.90	3.55
Fabaceae	<i>Machaerium stipitatum</i>	<b>yes</b>	108.59	3.17
Salicaceae	<i>Banara parviflora</i>	<b>yes</b>	137.52	3.14
Rubiaceae	<i>Faramea montevidensis</i>	yes	44.74	2.94
Rutaceae	<i>Zanthoxylum rhoifolium</i>	<b>yes</b>	26.04	2.75
Clusiaceae	<i>Garcinia gardneriana</i>	yes	42.57	2.55
Myrtaceae	<i>Annona sylvatica</i>	<b>yes</b>	31.10	2.54
Annonaceae	<i>Myrcianthes pungens</i>	yes	76.38	2.54
Boraginaceae	<i>Cordia americana</i>	yes	102.67	2.4
Lauraceae	<i>Ocotea pulchella</i>	yes	97.15	2.32
Myrtaceae	<i>Myrcia glabra</i>	yes	32.21	2.23
Lauraceae	<i>Nectandra megapotamica</i>	<b>yes</b>	65.09	2.19
Meliaceae	<i>Calabrea canjerana</i>	no	153.57	2.14

Rubiaceae	<i>Chomelia obtusa</i>	yes	17.83	2.13
Meliaceae	<i>Trichilia elegans</i>	yes	11.50	1.99
Fabaceae	<i>Inga striata</i>	<b>yes</b>	158.65	1.9
Myrtaceae	<i>Campomanesia xanthocarpa</i>	yes	33.21	1.75
Erythroxylaceae	<i>Erythroxylum argentinum</i>	<b>yes</b>	49.42	1.63
Sapotaceae	<i>Chrysophyllum gonocarpum</i>	<b>yes</b>	12.98	1.59
Euphorbiaceae	<i>Sebastiania brasiliensis</i>	yes	6.40	1.39
Rubiaceae	<i>Guettarda uruguensis</i>	yes	3.29	1.39
Myrtaceae	<i>Eugenia rostrifolia</i>	<b>yes</b>	5.98	1.35
Myrtaceae	<i>Eugenia</i> sp. <sup>2</sup>	yes	5.84	1.22
Sapotaceae	<i>Chrysophyllum inornatum</i>	<b>yes</b>	11.54	1.1
Arecaceae	<i>Syagrus romanzoffiana</i>	<b>yes</b>	12.04	0.96
Fabaceae	<i>Mimosa bimucronata</i>	yes	12.22	0.91
Primulaceae	<i>Myrsine glomerata</i>	yes	15.44	0.89
Myrtaceae	<i>Myrcianthes gigantea</i>	yes	5.43	0.83
Moraceae	<i>Ficus luschnatiana</i>	<b>yes</b>	11.01	0.75
Sapindaceae	<i>Matayba elaeagnoides</i>	yes	12.63	0.73
Euphorbiaceae	<i>Pachystroma longifolium</i>	yes	14.98	0.73
Araliaceae	<i>Dendropanax cuneatus</i>	yes	4.00	0.71
Cannabaceae	<i>Trema micranta</i>	yes	4.35	0.62
Euphorbiaceae	<i>Sebastiania commersoniana</i>	yes	1.04	0.58
Myrtaceae	<i>Psidium cattleianum</i>	yes	1.03	0.53
Rutaceae	<i>Esenbeckia grandiflora</i>	yes	1.11	0.52
Primulaceae	<i>Myrsine guianensis</i>	yes	2.24	0.49
Salicaceae	<i>Xylosma ciliatifolia</i>	yes	0.54	0.44
Chrysobalanaceae	<i>Hirtella hebeclada</i>	yes	2.86	0.44
Rosaceae	<i>Prunus myrtifolia</i>	yes	3.63	0.43
Rubiaceae	<i>Randia ferox</i>	yes	0.23	0.43
Myrtaceae	<i>Eugenia bacopari</i>	yes	0.44	0.42
Myrtaceae	<i>Eugenia involucrata</i>	yes	1.11	0.41
Fabaceae	<i>Inga marginata</i>	<b>yes</b>	2.38	0.38
Myrtaceae	<i>Eugenia uniflora</i>	yes	0.87	0.35
Symplocaceae	<i>Symplocos uniflora</i>	yes	0.80	0.35
Urticaceae	<i>Cecropia pachystachya</i>	yes	2.29	0.34
Quillajaceae	<i>Quillaja brasiliensis</i>	yes	1.40	0.33
Primulaceae	<i>Myrsine coriacea</i>	yes	0.93	0.33
Meliaceae	<i>Guarea macrophylla</i>	yes	0.08	0.32
Musaceae	<i>Musa acuminata</i> *	no	0.67	0.31
Anacardiaceae	<i>Schinus terebinthifolius</i>	yes	1.07	0.31
Sapotaceae	<i>Sideroxylon obtusifolium</i>	yes	1.87	0.26
Moraceae	<i>Maclura tinctorica</i>	yes	1.09	0.26
Rhamnaceae	<i>Hovenia dulcis</i> *	yes	2.06	0.25
Rutaceae	<i>Zanthoxylum caribaeum</i>	yes	0.47	0.24
Myrtaceae	<i>Eugenia</i> sp. <sup>3</sup>	yes	0.24	0.24

Aquifoliaceae	<i>Ilex dumosa</i>	yes	0.15	0.24
Styracaceae	<i>Styrax leprosus</i>	yes	0.13	0.24
Verbenaceae	<i>Citharexylum myrianthum</i>	yes	5.60	0.24
Myrtaceae	<i>Eugenia</i> sp.5	yes	0.22	0.21
Lamiaceae	<i>Vitex megapotamica</i>	<b>yes</b>	0.28	0.2
Euphorbiaceae	<i>Alchornea triplinervia</i>	yes	1.01	0.19
Boraginaceae	<i>Cordia ecalyculata</i>	yes	0.74	0.18
Rhamnaceae	<i>Colubrina glandulosa</i>	yes	0.47	0.18
Anacardiaceae	<i>Manguifera indica</i>	no	2.77	0.16
Euphorbiaceae	<i>Sapium</i> c.f. <i>haematospermum</i>	no	1.49	0.15
Anacardiaceae	<i>Schinus molle</i>	yes	0.25	0.14
Malvaceae	<i>Ceiba speciosa</i>	yes	1.95	0.13
Myrtaceae	<i>Eucalyptus grandis</i> *	no	4.16	0.12
Lauraceae	<i>Ocotea acutifolia</i>	yes	0.11	0.12
Rosaceae	<i>Eriobotrya japonica</i> *	yes	0.03	0.12
Lauraceae	<i>Ocotea</i> sp.2	yes	0.02	0.12
Euphorbiaceae	<i>Sapium glandulosum</i>	no	0.02	0.12
Myrtaceae	<i>Blepharocalyx</i> sp.2	yes	0.02	0.12
Pinaceae	<i>Pinus taeda</i> *	no	1.31	0.1
Myrtaceae	<i>Psidium guajava</i>	<b>yes</b>	0.51	0.09
Myrtaceae	<i>Syzygium jambos</i>	yes	1.27	0.08
Moraceae	<i>Ficus adhatodifolia</i>	yes	0.46	0.06
Asteraceae	<i>Gochnatia polymorpha</i>	no	0.26	0.06
Lauraceae	<i>Nectandra</i> sp.2	yes	0.22	0.06
Ebenaceae	<i>Diospyros kaki</i> *	<b>yes</b>	0.08	0.06
Lauraceae	<i>Ocotea</i> sp.1	yes	0.05	0.06
Oleaceae	<i>Chionanthus trichotomus</i>	no	0.04	0.06
Rutaceae	<i>Zanthoxylum</i> sp.2	no	0.03	0.06
Proteaceae	<i>Roupala brasiliensis</i>	yes	0.03	0.06
Solanaceae	<i>Solanum</i> sp.1	yes	0.03	0.06
Rutaceae	<i>Zanthoxylum</i> sp.1	no	0.01	0.06
Myrtaceae	<i>Eugenia</i> sp.6	yes	0.01	0.06
Lauraceae	<i>Ocotea</i> sp.3	yes	0.009	0.06
Bignoniaceae	<i>Handroanthus pulcherrimus</i>	yes	0.008	0.06
Solanaceae	<i>Solanum</i> sp.2	yes	0.008	0.06
Myrtaceae	<i>Myrcia</i> sp.1	yes	0.007	0.06
Cardiopteridaceae	<i>Citronella paniculata</i>	no	0.005	0.06
Myrtaceae	<i>Eugenia</i> sp.1	yes	0.005	0.06
Lauraceae	<i>Nectandra</i> sp.1	yes	0.005	0.06
Myrtaceae	<i>Blepharocalyx</i> sp.1	yes	0.004	0.06
Rutaceae	<i>Citrus reticulata</i>	yes	0.004	0.06
Chrysobalanaceae	<i>Hirtella</i> sp.1	yes	0.004	0.06
Sapindaceae	<i>Matayba</i> sp.1	yes	0.004	0.06
Lauraceae	<i>Nectandra oppositifolia</i>	yes	0.004	0.06

Moraceae	<i>Morus nigra</i> *	yes	0.003	0.06
Myrtaceae	<i>Eugenia</i> sp.4	yes	0.003	0.06
Euphorbiaceae	<i>Sebastiania</i> sp.1	no	0.003	0.06
Fabaceae	<i>Schizolobium parahyba</i>	yes	0.002	0.06
<b>No. families = 41</b>		<b>No. species = 123</b>	<b>No. TFS = 25</b>	

<sup>1</sup> Alien species are marked with an asterisk.

<sup>2</sup> Top food species (TFS) for brown howlers according to Chaves & Bicca-Marques [2013, 2016] are highlighted in bold.

IVI=Importance Value Index

### Estimation of brown howler density

We estimated the density of brown howler monkeys implementing the Conventional Distance Sampling (CDS) method in Distance v.6.0 [Thomas et al., 2010]. This method uses a set of flexible semi-parametric functions to model a detection function, which represents the probability of detecting an animal as a function of the animal-transect distance [Thomas et al., 2010]. We tested the hazard-rate, half-normal, and uniform detection function models using a cosine adjustment. For each model, we truncated both 5% of data and outliers, and selected the best model based on the Akaike's Information Criterion corrected (AICc) as recommended for small sample sizes [Buckland et al., 2001]. We determined the expected cluster size (number of individuals in each sighting) using size-biased regression methods (natural log of cluster or group size against estimated  $g(x)$ ) to account for the fact that large groups are easier to detect at greater distances than small groups [Thomas et al., 2010]. The detection probability decreased at greater distances from the transect (Fig. S1). However, as most sightings were grouped near transects, the fit of the data to the model was poor, limiting the prediction value of the model.

**Table SII.** Results of the density function models tested for brown howlers in the Morro São Pedro, Rio Grande do Sul, Brazil.

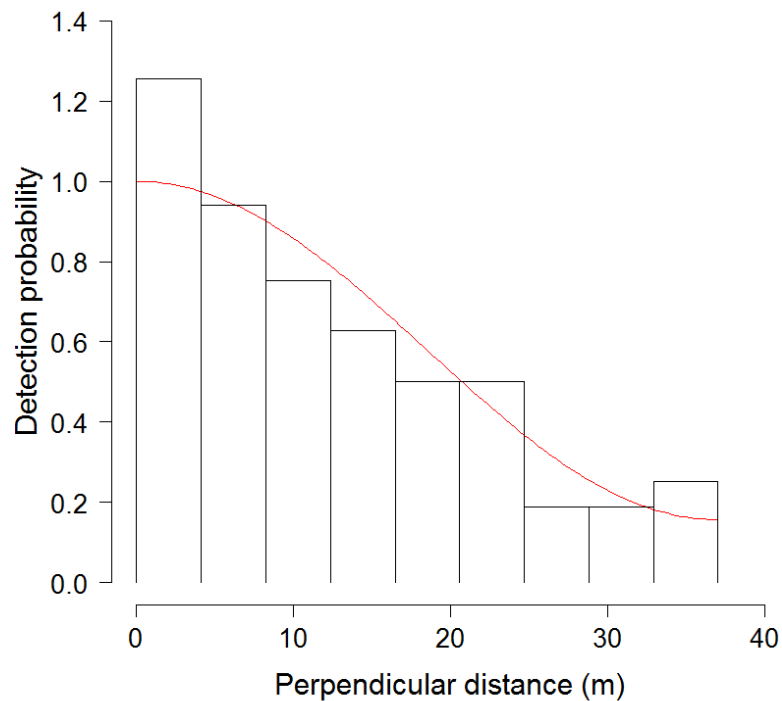
Model description			No. ind/ha	Density <sup>c</sup>
Key function <sup>a</sup>	Truncation	AICc <sup>b</sup>		
Uniform	5%	575.5	1.4 (1.0-1.8)	1662 (1225-2256)
Half-normal	5%	576.1	1.4 (1.0-1.9)	1683 (1229-2303)
Negative-exponential	outliers	630.4	2.2 (1.5-3.1)	2618 (1835-3737)
Half-normal	outliers	636.3	1.3 (0.9-1.8)	1601 (1160-2211)

<sup>a</sup>The adjustment term was Cosine for all the models.

<sup>b</sup>Akaike's Information Criterion corrected (AICc).

<sup>c</sup>Density of individuals in the entire study area (*i.e.*, 1200 ha).

In parentheses 95% confidence intervals for the best density function model.



**Fig. S1.** Detection probability plot for brown howlers sighted from five line transects during the study period in Morro São Pedro, southern Brazil.

## REFERENCES

Buckland ST, Anderson DR, Brunham KP, Laake JL, Borchers DL, Thomas L. 2001.

Introduction to distance sampling: estimating abundance of biological populations. New York: Oxford University Press. 448 p.

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JR,

Marques TA, Burnham KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.