



LILIAN PATRÍCIA SALES SILVEIRA

**OCUPAÇÃO E DETECTABILIDADE DE
CALLICEBUS nigrifrons E *CALLITHRIX
penicillata* EM FRAGMENTOS FLORESTAIS DE
MATA ATLÂNTICA BRASILEIRA**

LAVRAS – MG

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestre.

Dr. Marcelo Passamani

Orientador

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A Deus que sempre está comigo,

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“Isso também passa.” – Chico Xavier

RESUMO GERAL

A detectabilidade de uma espécie depende da interação entre suas características ecológicas, do habitat em que ela vive e do método usado para averiguar sua presença. Ignorar o impacto da detectabilidade de uma espécie é uma das maiores fontes de erro e viés em pesquisas com populações selvagens, principalmente quando se busca estimar a proporção de uma paisagem que é ocupada pela espécie. A nova abordagem proposta por Mackenzie et al. (2002) incorpora explicitamente a probabilidade de detecção na modelagem da ocupação de uma área por certa espécie e, por isso, gera parâmetros não-enviesados em suas estimativas. Neste estudo, nós modelamos as probabilidades de ocupação e de detecção de dois primatas (*Callicebus nigrifrons* e *Callithrix penicillata*) em função de covariáveis específicas de sítio e de covariáveis específicas de amostragem, respectivamente. Com isso nós avaliamos o impacto do habitat e da paisagem na ocupação de fragmentos florestais, e também verificamos de que maneira as condições climáticas do momento da amostragem influenciam na detecção de espécies vocalmente responsivas, através do uso de chamados de conspecíficos via *playback*. Constatamos que as características ecológicas das espécies explicam as diferenças no padrão de ocupação de fragmentos florestais. Dessa forma, a ocupação da espécie especialista florestal é principalmente afetada pelo tamanho e pela qualidade do habitat e, portanto, requer habitats com características florestais (dossel alto e fechado). Além disso, a ocupação da espécie generalista é explicada pela conectividade da paisagem em uma relação contra intuitiva, em que o aumento da conectividade reduz a probabilidade de ocupação. Isso sugere que a ocupação de espécies generalistas pode não ter um padrão óbvio. A detectabilidade das espécies também relaciona-se a aspectos biológicos das espécies, de modo que a espécie mais abundante é também a de maior probabilidade de detecção. Apesar disso, fatores intrínsecos à amostragem, como as condições climáticas ou a eficiência do equipamento usado nas buscas, também podem afetar a detectabilidade de uma espécie. Dessa forma, o desenho amostral em pesquisas com diversas espécies deve ser ajustado de modo a compensar as diferenças de detecção entre as espécies.

Palavras-chave: Modelagem. Ocupação. Fragmentação. Monitoramento.

GENERAL ABSTRACT

The detectability of a species relies on the interaction between its ecological characteristics, its habitat and on the method used to determine its presence. Detectability is also one of the greatest sources of bias in wild population surveys, specially in the estimation of the proportion of a landscape occupied by a target species. The new approach developed by Mackenzue et al. (2002) allows the explicit incorporation of detection probabilities, and thus results in non-biased parameter estimates. In the present study, we modeled the detection and occupancy probabilities for two primates (*Callicebus nigrifrons* and *Callithrix penicillata*) as a function of site-specific covariates and survey-specific covariates. Then, we evaluated the impact of habitat and the surrounding landscape on forest fragment occupancy, and we also checked how weather conditions affect the detection of vocally responsive species at the moment of the survey, via playback. We observed that the ecological characteristics of the species can explain the differences in the forest fragment occupancy pattern. Therefore, the occupancy of a forest specialist species is mainly explained by habitat quality and size, and thus requires forest-like habitats (closed and tall canopy). Furthermore, the occupancy of a habitat-generalist species is explained by landscape connectivity, but in a counter-intuitive way. This suggests that the occupancy pattern of a generalist species is not obvious. The detectability of a species is also related to its biological features, such as population densities. However, survey-specific weather conditions and the effectiveness of the survey equipment also influence the detectability of a species. Therefore, the sampling design of multispecies surveys must be adjusted, in order to compensate detection differences between the species.

Keywords: Modeling. Occupancy. Fragmentation. Monitoring.

LISTA DE ILUSTRAÇÕES

Figura 1	Área de estudo e localização dos pontos amostrais.....	46
Tabela 1	Resumo da seleção de modelos para <i>Callicebus nigrifrons</i> e <i>Callithrix penicillata</i>	47
Tabela 2	Modelos de ocupação para o Sauá (<i>Callicebus nigrifrons</i>) e o Sagui (<i>Callithrix penicillata</i>) em fragmentos de Mata Atlântica brasileira, com valor de ΔAIC menor do que duas unidades, a partir do melhor modelo.....	47
Tabela 3	Somatório do peso do AIC a partir do conjunto de melhores modelos para o Sauá (<i>Callicebus nigrifrons</i>).....	48

SUMÁRIO

PRIMEIRA PARTE		
1	INTRODUÇÃO.....	13
2	REFERENCIAL TEÓRICO.....	17
2.1	Perda de habitat.....	17
2.2	Impactos da perda de habitat em primatas.....	18
2.3	Modelagem de ocupação.....	19
3	CONSIDERAÇÕES GERAIS.....	20
	REFERÊNCIAS.....	21
	SEGUNDA PARTE – ARTIGO.....	23
	ARTIGO On the use of occupancy modeling for monitoring wild primate populations in fragmented landscapes: a case study in the Brazilian Atlantic forest.....	24

PRIMEIRA PARTE

1 INTRODUÇÃO

Algumas das questões mais interessantes em Ecologia e Conservação requerem estudos em larga escala ou replicações temporais ao longo de vários anos. O monitoramento de espécies de ciclo de vida longo, por exemplo, tem como requisito o acompanhamento das populações durante tempo o suficiente para se verificar alterações em seus parâmetros populacionais (CHAPMAN; PERES, 2001). Some-se a isso o atraso na resposta biológica às mudanças ambientais, denominado “débito de extinção” por Tilman (TILMAN et al., 1994), e temos um *trade-off* em que as ações efetivas de manejo e conservação são urgentes, mas dependem de resultados de décadas de pesquisa.

Além disso, a fragmentação de habitats é um processo que ocorre na escala da paisagem. Por isso, sugere-se que o monitoramento de populações remanescentes em fragmentos florestais deva também ser efetuado na escala da paisagem (ARROYO-RODRÍGUEZ; MANDUJANO, 2009). Porém, os custos de amostragem de algumas variáveis biológicas nessa escala podem ser proibitivos. Monitorar, por exemplo, taxas vitais e/ou abundância de certas espécies ao longo do tempo e na escala da paisagem geralmente não é possível.

Em resposta a esses problemas, uma das ferramentas de monitoramento de populações selvagens que tem ganhado muito destaque em publicações recentes é a modelagem de ocupação de sítios, proposta inicialmente por Mackenzie (MACKENZIE et al., 2002). A grande vantagem dessa metodologia em relação às demais é o uso de dados do tipo presença/ausência, além da correção das estimativas pela probabilidade de detecção das espécies. Tais fatores reduzem o custo das amostragens em larga escala e ainda permitem estimativas não-enviesadas dos parâmetros.

O conceito de ocupação de sítios é definido como a proporção de unidades amostrais ocupadas por certa espécie em uma região

(MACKENZIE et al., 2002). Essa ideia tem sido amplamente utilizada em Ecologia. Em meados nos anos de 1970, a probabilidade de ocorrência de espécies de aves em diferentes fragmentos florestais foi estimada em função de características do habitat (DIAMOND, 1975). As chamadas “funções de incidência” foram largamente usadas em estudos metapopulacionais. No início dos anos 1990, Ilkka Hanski descreveu como a fração de unidades de habitat é dependente da área do fragmento e do isolamento (HANSKI; GILPIN, 1991).

Porém, as espécies podem não ser detectadas, mesmo quando presentes em uma área, de modo que a maioria das funções de incidência provavelmente são enviesadas negativamente em algum grau (MACKENZIE et al., 2002). A não-deteccção de uma espécie pode ser causada por diversos fatores. Populações pequenas, comportamentos e/ou morfologias crípticas, e/ou esforço amostral limitado reduzem a chance de se encontrar pelo menos um indivíduo da espécie por unidade amostral. Raramente pode-se estar completamente seguro de que uma espécie será sempre detectada quando presente, e as falsas ausências ocorrem quando a deteção é imperfeita. Ignorar a detectabilidade das espécies gera, então, a incerteza na análise dos dados, a alocação desnecessária de esforços amostrais, além da imprecisão de estratégias de manejo (WINTLE et al., 2004).

A abordagem desenvolvida por Mackenzie et al. (2002) provê um arcabouço teórico flexível que permite estimar as taxas de ocupação de sítios, mesmo quando a probabilidade de deteção é menor do que um. Além disso, o método de máxima verossimilhança, usado nessa abordagem, foi considerado o estimador de probabilidades de ocupação e detectabilidade menos enviesado em uma série de metodologias alternativas (WINTLE et al., 2004). Ademais, tal abordagem ainda prevê a inclusão de não observações, devido a problemas em campo, e permite a inclusão de covariáveis explicativas.

Nesta dissertação foram modeladas as probabilidades de ocupação e de detecção dos primatas *Callicebus nigrifrons* e *Callithrix penicillata*. Os primatas são considerados prioridade de conservação em todo o mundo devido a sua vulnerabilidade à fragmentação de habitats. Em se tratando de primatas brasileiros, compreendem 40% dentre todos os grupos ameaçados e 74% das espécies consideradas alta prioridade de conservação pertencem a esse grupo (COSTA et al., 2005).

Além do preocupante grau de ameaça, algumas características dos primatas podem reduzir sua detectabilidade. Por exemplo, algumas espécies são crípticas, alguns animais são muito pequenos, ocupam grandes áreas de vida e/ou fogem do observador. Esses fatores dificultam a detecção dos indivíduos e podem levar a resultados enviesados negativamente. Por isso, é necessário usar métodos que considerem explicitamente a detectabilidade das espécies em estudos com primatas.

A modelagem de ocupação tem sido considerada uma excelente ferramenta de monitoramento de populações selvagens de primatas. Essa técnica inclusive foi considerada o método mais acurado para elucidar o efeito da fragmentação de habitats em populações de primatas (ARROYO-RODRÍGUEZ; MANDUJANO, 2009).

Por isso, em primeiro lugar modelamos as probabilidades de detecção das duas espécies de primatas, em condições de tempo bom e de tempo ruim. Com isso, apresentamos uma técnica de calibração de esforço amostral para ser usada em pesquisas que envolvam mais de uma espécie. Além disso, modelamos a probabilidade de ocupação em função de características de habitat: tamanho e abertura de dossel. E também modelamos a ocupação em função de características da paisagem: área do fragmento e conectividade da paisagem do entorno dos fragmentos.

Portanto, ao utilizarmos a abordagem de Mackenzie et al. (2002) para modelarmos a ocupação de populações naturais de primatas em fragmentos florestais de Mata Atlântica, estamos na vanguarda das tendências mundiais de pesquisa. Até o momento, esta é a primeira iniciativa de modelagem explícita da probabilidade de detecção e, conseqüentemente, de estimativas não-enviesadas da ocupação de primatas em ambientes fragmentados no Brasil.

O artigo oriundo desta dissertação foi submetido na revista *Biodiversity and Conservation* e possui o título “**On the use of occupancy modeling for monitoring wild primate populations in fragmented landscapes: a case study in the Brazilian Atlantic forest**”. Nesse artigo, o enfoque é a probabilidade de ocupação e de detecção das espécies *Callicebus nigrifrons* e *Callithrix penicillata*. A ocupação foi modelada em função de características da paisagem e do habitat no interior do fragmento. A detecção foi modelada em função de características climáticas no momento da amostragem. A partir dos modelos resultantes, sugestões de manejo das espécies são apresentadas, levando em consideração tanto o resultado das análises quanto a ecologia das espécies.

2 REFERENCIAL TEÓRICO

2.1 Perda de habitat

Perda de habitat e de fragmentação estão entre as ameaças mais relevantes à biodiversidade na atualidade. Estes processos reduzem a quantidade de habitat disponível, aumentam o isolamento entre os fragmentos e geram ambientes caracterizados por manchas de habitat. Isso pode forçar as espécies a sobreviver em populações locais menores e isoladas umas das outras por matrizes de habitat inóspito. Entender os efeitos desses fatores em populações-alvo é fundamental para a correta proposição de estratégias de conservação (BOSCOLO; PAUL METZGER, 2011).

A fragmentação do habitat geralmente é definida como um processo que deve ser medido na escala da paisagem, envolvendo tanto a perda do habitat quanto a separação do habitat remanescente. Estudos empíricos sugerem que a perda do habitat apresenta um considerável efeito negativo sobre a biodiversidade local, e que a fragmentação *per se* pode apresentar efeitos tanto negativos quanto positivos em relação à riqueza e abundância de espécies. Os efeitos negativos da fragmentação são devidos basicamente a duas grandes causas. Primeiro, a fragmentação *per se* implica em um número maior de fragmentos de menor tamanho. Em algum ponto, cada fragmento de habitat será muito pequeno para sustentar uma população local ou talvez até um território individual. Espécies que não podem atravessar a porção não-habitat da paisagem (a matriz) serão confinadas a um grande número de fragmentos muito pequenos, o que deve reduzir o tamanho populacional geral e sua probabilidade de persistência. A segunda grande causa do efeito negativo da fragmentação *per se* são os efeitos de borda; paisagens mais fragmentadas contêm mais borda, para

uma quantidade fixa de habitat. Isto aumenta a probabilidade de indivíduos deixarem o habitat e entrarem na matriz (FAHRIG, 2003).

Paisagens fragmentadas podem ser particularmente desfavoráveis para especialistas florestais que raramente usam habitats de entorno de fragmentos florestais (ARROYO-RODRÍGUEZ; MANDUJANO, 2009). Além disso, os efeitos da fragmentação podem ser imediatos ou apenas evidentes após certo período de tempo, sendo que este tempo, ou o necessário para se obter uma resposta aos efeitos da fragmentação, dependem da habilidade de dispersão do taxon analisado e do tamanho do fragmento em questão (TILMAN et al., 1994).

2.2 Impactos da perda de habitat em primatas

O Brasil é o país que apresenta a maior diversidade de primatas não-humanos. Os primatas neotropicais são prioridade de conservação em todo o mundo e correspondem a 31% de todos os primatas conhecidos. Essencialmente arborícolas, os primatas neotropicais são particularmente vulneráveis aos efeitos da fragmentação porque os distúrbios antropogênicos exercem um forte impacto negativo na sustentabilidade de suas populações. Na atualidade, os primatas compreendem cerca de 40% de todos os táxons ameaçados no Brasil e a mais recente lista de espécies ameaçadas publicada pelo Instituto Brasileiro de Meio Ambiente e Recursos Renováveis apresenta 26 espécies de primatas ameaçados de extinção. Além disso, a maioria dessas espécies é endêmica à Mata Atlântica, um dos habitats mais explorados do planeta e um *hotspot* de biodiversidade (COSTA et al., 2005; RYLANDS; MITTERMEIER, 2009).

A Mata Atlântica possui cerca de 11,4% de sua cobertura original, e a maioria dos remanescentes florestais é pequena e medem menos de 50 ha. Nesse bioma, a maioria das populações animais está restrita a diminutos fragmentos florestais distribuídos em paisagens agrícolas, onde é pequena a

probabilidade de persistência de longo-prazo de espécies especialistas em habitat florestal (TABARELLI et al., 2010).

2.3 Modelagem de ocupação

Mackenzie et al. (2002) desenvolveram um modelo que permite corrigir detecções imperfeitas através do uso de estimativas de máxima verossimilhança dos parâmetros de ocupação. Considerando-se espécies cujas probabilidades de detecção sejam inferiores a 1 visita múltipla aos mesmos sítios geram padrões de detecção e não detecção (chamados de históricos de detecção). Tais históricos permitem estimar as probabilidades de detecção e o parâmetro de interesse, que é a proporção de sítios ocupados ou a probabilidade de ocupação.

Esses dados coletados sobre presença/ausência de uma espécie em fragmentos “discretos” podem ser usados para derivar probabilidades de extinção e colonização, numa perspectiva metapopulacional. Outros dados, como a taxa de substituição, podem ser calculados e as relações entre a persistência de uma população e as características do fragmento (como tamanho ou qualidade do habitat) podem ser postulados. Em modelagem de habitat, a intenção é geralmente construir um modelo que relacione a distribuição das espécies a certas características do habitat e, a partir daí, inferir se a espécie exibe preferência por alguma característica do habitat ou identificar outras áreas de habitat potencialmente adequado.

3 CONSIDERAÇÕES GERAIS

Neste trabalho utilizamos a metodologia proposta por Mackenzie et al. (2002) e modelamos as probabilidades de ocupação e detecção de duas espécies de primatas em fragmentos florestais do sudeste da Mata Atlântica brasileira. As conclusões do trabalho apontam para sugestões de manejo das populações dessas espécies e porventura de outras com ecologia similar. Além disso, nos dois manuscritos apresentados são discutidas adaptações na metodologia de busca usada, de modo a evitar possíveis erros em trabalhos futuros.

Com isso, concluímos que o uso de modelagem de ocupação de sítios, aliada às estimativas de detectabilidade, provê resultados robustos e permite a implementação de ações de manejo de forma direta. Além disso, tal metodologia reduz os custos das coletas em campo, uma vez que são usados dados de presença e ausência. Também permite que estudos de longa duração e larga escala sejam realizados de forma logisticamente viável. Dessa forma, sugerimos seu uso em programas de monitoramento de populações selvagens.

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SEGUNDA PARTE - ARTIGO

ARTIGO 1

On the use of occupancy modeling for monitoring wild primate populations in fragmented landscapes: a case study in the Brazilian Atlantic forest

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Abstract Monitoring primates in tropical forests can be challenging because visibility is usually poor, animals are cryptic and/or flee from the observer, occur in low population densities and/or occupy large home ranges. Occupancy modeling has, therefore, been seen as a surrogate for other biological variables (e.g. abundance, vital rates) in order to assess the conservation status of wild populations within a landscape. We modeled the occupancy and detection probabilities of the Black-fronted Titi Monkey (*Callicebus nigrifrons*) and the Black-tufted-ear Marmoset (*Callithrix penicillata*) within an Atlantic forest fragmented landscape of Southeastern Brazil. Both the occupancy and the detection estimates greatly varied between the species. The less abundant species presented the lower detection probability. Also, bad weather conditions reduced the detection probabilities. The occupancy of the species that is not a forest-specialist was mainly explained by the connectivity of the landscape, and the occupancy of the forest-specialist also depends on the quantity and the quality of the available habitat. We recommend the use of occupancy modeling in the monitoring of wild populations living in fragmented landscapes due to the low costs, straightforward results and the logistic facilities of the presence/absence data.

Keywords: *Callicebus nigrifrons*, *Callithrix penicillata*, Brazilian Atlantic forest, conservation, wildlife-habitat.

INTRODUCTION

Habitat loss is one of the main threats to general biodiversity conservation but forest-dwelling mammals such as primates can be particularly vulnerable to habitat fragmentation (Chapman and Peres 2001). Studies of primates in fragments usually conclude that fragmentation has negative effects on some aspect of their biology or ecology, although there may be no consensus regarding fragmentation concepts. Primates are, therefore, a worldwide conservation priority. Unsurprisingly, they are the most endangered group among all Brazilian mammals, comprising 40% of the threatened taxa, and correspond to 74% of the mammal species that are considered high conservation priority (Costa et al. 2005).

Historically, primate studies have been performed in relatively undisturbed areas, and the emphasis has been placed on studying primates in their native environment (Chapman and Peres 2001). Indeed, protected tropical forests in parks and nature reserves are meant to preserve plant and animal populations and are becoming the final refuge for threatened species. Yet few tropical forests worldwide are legally protected, so small fragments may offer opportunities of conservation of the remaining populations. Besides, conservation efforts must also look for long-term opportunities of documenting patterns of change on biological responses and habitat variables in order to increase the future persistence of fragmented populations (Chapman and Peres 2001).

Long-living species, often endangered, require large sample sizes for studies to be conducted at the appropriate spatial and temporal scales, which is logistically very difficult. Also, the biological responses to environmental

changes may be slow (Tilman et al. 1994), which requires long-term monitoring in order to assess the biological changes. Furthermore, as fragmentation is a landscape-scale process, the monitoring of populations within forest fragments should be conducted at that scale of analysis. Finally, it is important to consider multiple anthropogenic effects of land-use types in the persistence of species on fragmented tropical forest landscapes (Arroyo-Rodríguez and Mandujano 2009).

Recent researchers argue that site-occupancy modeling may be a feasible surrogate tool for the continued monitoring of wild primate populations. Accordingly, site-occupancy modeling is considered one of the most accurate methods for assessing the effects of habitat fragmentation on primate populations (Arroyo-Rodríguez and Mandujano 2009). Occupancy is defined as the proportion of sampling units in a landscape that is occupied by a target species and is an extensively used concept in ecology (Mackenzie et al. 2002).

In the 1970's the probability of occurrence of bird species in different forest patches was described as a function of habitat characteristics, such as size (Diamond 1975)□. The so called “incidence functions” were widely used in metapopulation studies. Later in the 1990's Ilka Hanski described how the fraction of occupied habitat units is dependent on patch area and isolation (Hanski and Gilpin 1991). Yet species may go undetected when present, so it is expected that most incidence function estimates to be negatively biased to some degree (Mackenzie et al. 2002).

The approach developed by Mackenzie et al. (2002) provides a flexible framework that allows the estimation of site occupancy rates when detection probabilities are less than one, accounting explicitly for detection probabilities. The non-detection of a species' presence may be caused by small population size, individuals may be difficult to sample, or sampling effort may be limited. It is rarely if ever possible to be completely sure that a species is absent, and false absences may occur when detection probabilities are less than one. This may

lead to uncertainty in the data analysis and unnecessary allocation of survey efforts, plus the imprecision of management strategies (Wintle et al. 2004).

Wintle et al. (2004) compared six approaches to estimating detection probabilities and the proportion of sites occupied from binary observation data. Their findings suggest that maximum likelihood methods, such as that proposed by Mackenzie et al. (2002), are the least biased estimators of occupancy and detectability rates. Moreover that approach enables covariate information to be included and it also accepts missing observations.

The goal of this research is to answer the following questions 1) The forest fragments occupancy pattern differs between the species? 2) Can that occupancy pattern be explained by habitat and/or landscape characteristics? 3) The climatic conditions, and associated background noise, affect detection probabilities? 4) Is occupancy modeling an efficient tool to monitor populations remaining in fragmented landscapes?

METHODS

Study área

This study was carried out in Atlantic forest fragments in the region of Lavras, Minas Gerais, southeastern Brazil (Fig. 1). Vegetation is classified as semideciduous forest and it belongs to the Atlantic Forest Domain in southeastern Brazil and the soil characteristics of this region makes it extremely profitable for cattle ranching and farming (Oliveira-Filho and Fontes 2000). The historic fragmentation that has been occurring since colonization created a highly fragmented mosaic of land-use types, with a high proportion of coffee culture and pasture (Assis et al. 2013). The climate is classified as Subtropical, i.e., temperate with a mild summer and a dry winter. The average annual

temperature is 19.4°C and the average annual precipitation is 1493 mm which is unevenly distributed throughout the year (Oliveira-Filho and Fontes 2000).

Animal sampling

We performed three surveys in 51 forest fragments. The sampled fragments were all similar in vegetation, topographic and climatic characteristics, and their size varied from 0.5 up to 478 ha. The detection of the species was based on vocal responses to playback calls and visual encounters were used to confirm the identification of the species.

We conducted surveys of the Black-fronted Titi Monkey (*Callicebus nigrifrons*) and the Black-tufted-ear Marmoset (*Callithrix penicillata*) in forest fragments between January 2013 and March 2013. The audio files used in the playback calls were recorded from groups of *C. nigrifrons* belonging to Serra do Caraça (Minas Gerais state, Brazil) and *C. penicillata* from Caratinga (Minas Gerais state, Brazil) and were edited in the Audacity software version 2.0.

We used a CSR megaphone (model HMP1501) attached to a portable MP3 player with the vocalization of the Black-fronted Titi Monkey in each playback session. The amplification of the Black-tufted-ear Marmoset's audio file produced strong background noise, so we performed their playback sessions without the megaphone. We placed the sound equipment onto some tree branch at about 1.5 m above the ground. At each survey point, an audio session was performed. Each audio session was composed of 10 minutes, in which we played the vocalization of both species in sound blocks of 1 minute each, separated by 2 minutes of silence. We kept an interval of at least two consecutive days between surveys in order to avoid habituation of the animals. The procedures regarding data collection were conducted under the legal approval and consent of the Brazilian Federal Authority (IBAMA process number 14083-1) and follow the guidelines of the American Society of

Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Weather covariates

In order to determine if weather conditions affect detection probability models, we also collected data on the main weather conditions, which were roughly categorized as “good weather” or “bad weather.” Bad weather conditions are those that might prejudice auditory detection, in which the background noise is expressive (e.g., strong rain and/or wind), and good weather is considered the absence of bad weather conditions (e.g., rainless moments and the absence of strong wind or other natural background noise). That simplification was necessary because we did not have access to any equipment that could properly measure the background sound intensity.

Habitat covariates

In order to assess habitat variables related to the tree canopy, we used one 100 m line transect from the border of each forest fragment. Each transect was then divided into 10 points, and at each point canopy height was measured with a clinometer. In addition, we took 10 pictures of the canopy above each point transect using a Nikon D40 digital camera equipped with an 8 mm hemispherical “fish-eye” lens and positioned 1.5m above the ground. It allowed us to quantify canopy openness as the ratio of black pixel – vegetation – and white pixel – openness, in the software Gap Light Analyzer (GLA) 2.0. The mean values obtained from each transect were used as predictor variables, so that there was one single value of both canopy height and canopy openness for every forest fragment.

Landscape covariates

The image classification used in this paper was obtained from Assis et al. (2013). The landscape variables we evaluated were fragment size and the amount of suitable habitat within buffers. Fragment size was obtained as the area, measured in hectares, of each polygon of native vegetation. The amount of suitable habitat within buffers was used as a proxy of the landscape connectivity because the concept of landscape connectivity includes both the landscape structure and the species' ability to move among patches.

We used the amount of suitable native vegetation within buffers of 1000m, which is the mean day range of the *Callicebus spp.* (Norconk 2007), from the border of each forest fragment as a proxy of landscape structural connectivity. Both fragment size and connectivity were analyzed in QuantumGis 2.0.1.

Occupancy modeling

We fitted a set of single-season occupancy models to the presence/absence data for each species separately. The single-season models involve the estimation of two parameters: the occupancy ψ , which is the probability that a certain species is present in a site, and the probability p_i of detecting the species in survey i , given that the species is present in the site (Mackenzie et al. 2002). The estimation of those parameters is done by performing multinomial maximum likelihood procedures that allow estimation of occupancy probabilities even when the species is imperfectly detected.

At first, we ran models in which ψ and p were held constant. Then, we modeled ψ as function of different combinations of the habitat and landscape covariates. The detection probabilities were modeled as function of weather conditions. Therefore, we got a set of 16 candidate occupancy models, and 3 candidate detectability models for each species. The resulting models were

ranked by their Akaike Information Criterion (AIC), determined by $-2\text{Loge}L + 2N$ in which L is the maximum likelihood of obtaining one particular model and N is the number of estimated parameters. The AIC approach is embedded in the concept of parsimony because it involves a trade-off between model fit and complexity, with more complex models being selected only if they provide a sufficiently superior fit (McCarthy 2007).

The AIC differences of each model were converted to Akaike weights (w_i). The AIC weights measure the likelihood of the data given the model (McCarthy 2007). When there are R candidate models, the Akaike weights are:

$$w_i = \exp(-\Delta_i / 2) / \sum \exp(-\Delta_r / 2)$$

This equation indicates that the Akaike weights are obtained by the transformation of the AIC differences (Δ_i) using $\exp(-\Delta_i / 2)$ and then re-scaling the subsequent values so that they add up to 1.

We also assessed the goodness-of-fit of the most parameterized model and that of the top-ranking model. It was done by comparing the X^2 statistics of the history probabilities of the model to histories randomly estimated from the model parameters. That procedure is performed via parametric bootstraps (MacKenzie and Bailey 2004).

In order to assess the relative contribution of each covariate on the occupancy probabilities, we summed the AIC weights of the top-ranking models that include the covariate.

We also calculated the minimum number of visits necessary to declare that the species is absent. It was done considering two levels of confidence (95% and 90%). If visits are comparable and independent, and the detection probability is p , then the probability F of not detecting the species after N visits is:

$$F = (1-p)N$$

Therefore, if we want to be 95% confident that the species is absent, then $F = 0.05$ (Pellet and Schmidt 2005). That equation can be solved for the minimum number of visits required to be 95% confident that a species is absent, which gives us:

$$N_{\min} = \log(0.05) / \log(1-p)$$

The untransformed estimates of coefficients for the covariates (Beta's) were used to verify the behavior of the occupancy and probabilities as functions of the covariates.

RESULTS

Detectability

The minimum detection probability estimated for *C. nigrifrons* is approximately 0.84 (95% CI = 0.65 - 0.94) and the maximum is up to 0.92 (95% CI = 0.73 - 0.98). The estimated values for *C. penicillata* range from 0.33 (95% CI = 0.19 - 0.50) up to 0.46 (95% CI = 0.29 - 0.64). The comparison of AIC values indicates that at least one of the top-ranking models includes the weather covariates (Table 1). The best model for *C. nigrifrons* considers the detection probabilities as a function of weather conditions, and *C. penicillata* has two top-ranking models: the null model and the weather model.

In good weather, the detection probabilities for *C. nigrifrons* are 0.91 (95% CI = 0.81 - 0.96), and bad weather conditions reduce those estimates to 0.81 (95% CI = 0.36 - 0.97). The same behavior is observed for *C. penicillata*, in

which the detection probabilities in good weather are 0.42 (95% CI = 0.30 - 0.56) and decrease to 0.35 (95% CI = 0.13 - 0.67) in bad weather conditions.

Occupancy

During our surveys, we heard the Black-fronted Titi Monkey at least once in 26 out of 51 forest fragments, and the Black-tufted-ear Marmoset was heard at least once in 33 out of 51 fragments. Therefore, naïve (non-corrected) occupancy estimate of the Black-fronted Titi Monkey was 0.51 and the naïve occupancy estimate of the Black-tufted-ear Marmoset was 0.67. Yet the corrected occupancy estimate for the Black-fronted Titi Monkey was 0.51 (SD \pm 0.07) and for the Black-tufted-ear Marmoset it was 0.85 (SD \pm 0.11).

The minimum number of visits required to achieve 95% or 99% of confidence that the species is detected when present, given the estimated detection probability, varied between the species. For the Black-fronted Titi Monkey (whose detection probability was 0.88) only 1.40 visits per site is necessary, considering a confidence level equals to 0.05. If the confidence level equals 0.01, the minimum number of site visits is 2.16.

On the other hand, the Black-tufted-ear Marmoset had a detection probability of 0.41 and the minimum number of visits required to be 95% confident that the species will be detected when present, using our sampling methodology, was 5.71 visits (confidence level 0.05) and 8.78 (confidence level 0.01).

We found no evidence of lack of fit for the Black-fronted Titi Monkey's models, neither for the most parameterized model (6 parameters, \hat{c} = 0.90) nor for the top-ranking model (4 parameters, \hat{c} = 0.95) because \hat{c} values are nearly one (Burnham and Anderson 2002). The difference between the top-ranking model indicates the relative support of the set of models, so that Δ AIC values less than two AIC scores from the top-ranking model denotes high level

of support. Three models had $\Delta AIC < 2$, thus the set of best models of the Black-fronted Titi Monkey contained three models (Table 2).

Canopy height (ch) and fragment size (size) were the strongest predictors of the occupancy probability for the Black-fronted Titi Monkey, as demonstrated by the sum of the adjusted AIC weights from all models in the top-ranking set containing this covariate (Table 3).

The untransformed estimates of coefficients for the covariates canopy height, fragment size and landscape connectivity on the occupancy models of the Black-fronted Titi Monkey were positive. As ψ was also positive, the occupancy probabilities increase with canopy height, fragment size and landscape connectivity. However, the coefficients for the covariate canopy openness were negative, thus suggestive that occupancy probabilities of the Black-fronted Titi Monkey decrease with canopy openness.

The Black-tufted-ear Marmoset models also showed a good fit to the data, for both the most parameterized model (6 parameters, $c\text{-hat} = 1.17$) and the top-ranking model (3 parameters, $c\text{-hat} = 1.15$). Therefore, the Black-tufted-ear Marmoset presented two best models (Table 2).

Connectivity (con) was the strongest predictor of the occupancy probabilities for the Black-tufted-ear Marmoset. It was the only covariate indicated by the top-ranking models (AIC wgt = 0.18). Although ψ estimates were positive, the coefficient for the covariate connectivity was negative, hence occupancy probabilities decrease with the increase of the landscape connectivity.

DISCUSSION

We modeled the occupancy probabilities of the Black-fronted Titi Monkey (*Callicebus nigrifrons*) and the Black-tufted-ear Marmoset (*Callithrix penicillata*) as functions of habitat and landscape covariates. The species had

markedly different forest fragments occupancy patterns, and detectability greatly varied between them. Hence the species whose detection probability was higher required a smaller sampling effort in order to check for the absence of this species.

Detectability

The detection probability of the Black-fronted Titi Monkey was at least two times higher than that of the Black-tufted-ear Marmoset. It means that it was twice as easy to find a Black-fronted Titi Monkey than to find a Black-tufted-ear Marmoset, using our sampling scheme. It also indicates that playback calls are an efficient research method for the Black-fronted Titi Monkey and, therefore, should be used in species surveys and monitoring of this species. The Black-tufted-ear Marmoset, on the other hand, had a lower detection probability using this method, and some adjustments, such as increasing the number of sampling points, should be made.

The observed differences in detectability may be linked to species-specific parameters, such as population size. The Black-fronted Titi Monkey has an average population density of 10-12 ind/km² in continuous forests (Trevelin et al. 2007) and up to 24 ind/km² in forest fragments (Costa et al. 2012). There are no records of population densities of the Black-tufted-ear Marmoset in protected areas, but the Buffy-tufted-ear Marmoset (*Callithrix aurita*) exhibit average population densities of 7.5 ind/km² in continuous forest (Norris et al. 2011) and the Black-tufted-ear Marmoset reaches 0.4-0.8 ind/km² in Cerrado fragments (Miranda and Faria 2001).

Those differences in population densities may be the cause of the detection probabilities contrasts between the sampled species because the variation in abundance induces variation in detection probabilities. That is,

higher population densities increase the chance of detecting at least one individual of the species per sampling unit. There is also a general tendency that locally abundant species are more widely distributed in space than rare species, which forms a positive occupancy-abundance relationship.

We also observed evidence that bad weather conditions reduce detection probabilities as compared with good weather conditions. As the detection of primates in this work was based on auditory clues, it was expected that bad weather conditions would increase the level of background noise and, thus, reduce detection probabilities. This interference of weather on vocal/auditory communication is not something new. (Wiley and Richards 1978) previously postulated that acoustic communication relies on detection and discrimination of signal differences and that optimal placement within the habitat and optimal weather conditions increase the effectiveness of the transmission of acoustic signals. Therefore, detection probabilities may be affected by bad weather conditions either because of the reduced singing behavior of monkeys at those moments or because background noise prevents the researchers from detecting the responses to playback calls.

The detectability of a species is also one of the most important sources of uncertainty in determining the proportion of landscape units occupied by a species (Wintle et al. 2004). Our data shows strong bias in the Black-tufted-ear Marmoset's naïve occupancy estimate, which is the observed proportion of occupied sites, not corrected by the detection probability. The naïve estimate is at least 25% lower than the detection-corrected occupancy estimate. This discrepancy could lead to inadequate conservation plans, or alarmist reactions to observed declines in population sizes, besides inducing erroneous predictions of a species' response to habitat changes due to poorly formulated wildlife-habitat models.

Those differences in detection probabilities also lead to unequal sampling effort in order to declare that a species is absent from a sampling site. The number of visits necessary to declare a species is absent was markedly different between the primate species sampled in the present study. Thus, multispecies surveys may be inefficient (Pellet and Schmidt 2005), so that some adjustments should be made. Rare species require more visits in order to declare their absence, and multispecies surveys should only be done for those that are ecologically similar, or have similar population densities. Also, methodology calibration should be conducted in order to maximize the detectability of the less conspicuous species. The present study indicates that at least 2 more visits would be necessary in order to declare the Black-tufted-ear Marmoset is absent.

Occupancy

In addition to those differences in detectability, the top-ranking occupancy models of the Black-fronted Titi Monkey and the Black-tufted-ear Marmoset also revealed variation, which is related to their ecological characteristics. For the Black-fronted Titi Monkey, the best predictor variables of occupancy were fragment size (size) and canopy height (ch), but only connectivity (con) was important according to the Black-tufted-ear Marmoset top-ranking model.

Titi Monkeys are small to medium in size, arboreal quadrupeds, that occupy the canopy or subcanopy forest levels. Accordingly, *Callicebus* spp. do not systematically utilize the ground or emergent forest levels and are considered “habitat specialists” (Norconk 2007). As the Titi Monkeys are an essentially arboreal group, it is expected that their occupancy pattern be explained by canopy measures. Indeed, canopy height (ch) is one of the strongest predictor variables of the Black-fronted Titi Monkey occupancy, and

higher canopy height values corresponded to higher occupancy values. The opposite behavior is observed in the canopy openness values, so that closed canopies are related to higher occupancy probabilities. Therefore, habitats in which the canopy is higher and more closed have greater occupancy probability for the Black-fronted Titi Monkey, thus suggesting that this primate requires forest-like environments.

Actually, the occupancy of other forest-specialist primates is probably linked to forest-like habitat variables. Other studies also suggest that the occurrence of forest-specialist primates is positively linked to canopy height and canopy cover or that forest-habitat measures, such as density of high trees, are the best predictors of some primate species occupancy (Arroyo-Rodríguez and Mandujano 2009). Therefore, the quality of the habitat seems to have major importance for the forest-specialist primate species, so that the observed patterns of occupancy of the Black-fronted Titi Monkey, which are related to canopy height and openness, may reflect the specialization of this group to the life in canopy and sub-canopy habitats.

Another equally important predictor of the Black-fronted Titi Monkey occupancy is fragment size. This result may be caused by the greater habitat diversity, larger population sizes, smaller stochastic extinction rates, higher colonization rates, larger concentration of trophic and/or structural resources, and smaller edge effects (Connor and McCoy 2001). The effect of patch size on biodiversity ultimately reflects the effect of the amount of habitat available for the species (Fahrig 2003), so that small fragments have a lower occupancy probability due to the reduced quantity of habitat.

However, the Black-tufted-ear Marmoset did not respond to any of the covariates that are important for the Black-fronted Titi Monkey. The top-ranking models of the Black-tufted-ear Marmoset showed no relation to fragment size, canopy height nor to canopy openness. The best predictor of the Black-tufted-ear

Marmoset was actually the worst predictor of the Black-fronted Titi Monkey, which is the connectivity of the fragments across its surrounding landscape. The landscape connectivity was therefore a better predictor of the Black-tufted-ear Marmoset occupancy than fragment size, thus suggesting that the landscape-scale may be more appropriate than the fragment-scale for the comprehension of its occupancy patterns.

The marmosets of the genus *Callithrix* are small-bodied (<500g) primates specialized on chewing tree trunks and branches to feed on the tree exudates. As gum tree are patchily distributed across real landscapes and the home range of the Black-tufted-ear is directly related to the location of the gum, the marmosets probably exploit this resource by moving into patches. Therefore, an increase in landscape connectivity could allow the better exploitation of gum trees distributed in patches, which would enhance their permanence in small and highly seasonal forest patches (Passamani and Rylands 2000). But our results are counter-intuitive because occupancy probabilities decrease with landscape connectivity. Forest fragments surrounded by a greater proportion of tree crops are supposed to maintain a higher number of terrestrial mammals (Garmendia et al. 2013).

Some authors suggest that the response of primates to the fragmentation process is not obvious, because studies use different metrics and results are not comparable (Arroyo-rodríguez et al. 2013). Perhaps the incorporation of the gum tree distribution as a site-covariate would explain that relationship.

Our study shows that the occupancy pattern of a forest-specialist primate, the Black-fronted Titi Monkey, is explained by both the amount of habitat and the quality of the habitat within the forest fragment. The Titi Monkeys rarely uses the ground and the dependency of canopy structures may inhibit the dispersal ability of forest-specialist primates and thus confines the remaining populations in forest fragments containing suitable habitat. In this

case, fragmentation processes and habitat loss that occurred several years ago isolated them in forest patches, so that the stochastic processes that threaten small and isolated populations must already have taken place. Therefore, these populations must be prone to extinction due to historical habitat loss, so that the next generations will have to pay for this extinction debt.

On the other hand, the occupancy of a primate that is not a forest-specialist, the Black-tufted-ear Marmoset, is mainly explained by the landscape connectivity. The marmosets regularly use the ground in several situations, such as predation-avoiding behavior or in foraging above army ant swarms (Passamani and Rylands 2000). That ability to move within diverse forest strata and the efficient habitat exploitation must increase the dispersal ability of the marmosets, allowing them to cross the anthropogenic landscape matrix that surrounds the forest fragments. It also explains why the Black-tufted-ear Marmosets occupied a greater proportion of the landscape than the Black-fronted Titi Monkeys.

The Black-fronted Titi Monkeys studied in the present study, therefore, seem to be more vulnerable to fragmentation and habitat loss than the Black-tufted-ear Marmosets, because of the difference in their ecological characteristics. Those differences are reflected by their occupancy patterns of forest remnants within a fragmented landscape. Several questions arise from those conclusions and future studies should investigate the existence of a metapopulation of the Black-fronted Titi Monkey in the region, and to verify the extent to which their populations are isolated from each other. Moreover, modeling the occupancy of the Black-tufted-ear Marmoset as a function of the patchy distribution of tree gum should improve the knowledge about the ecology and conservation of primates living in fragmented landscapes.

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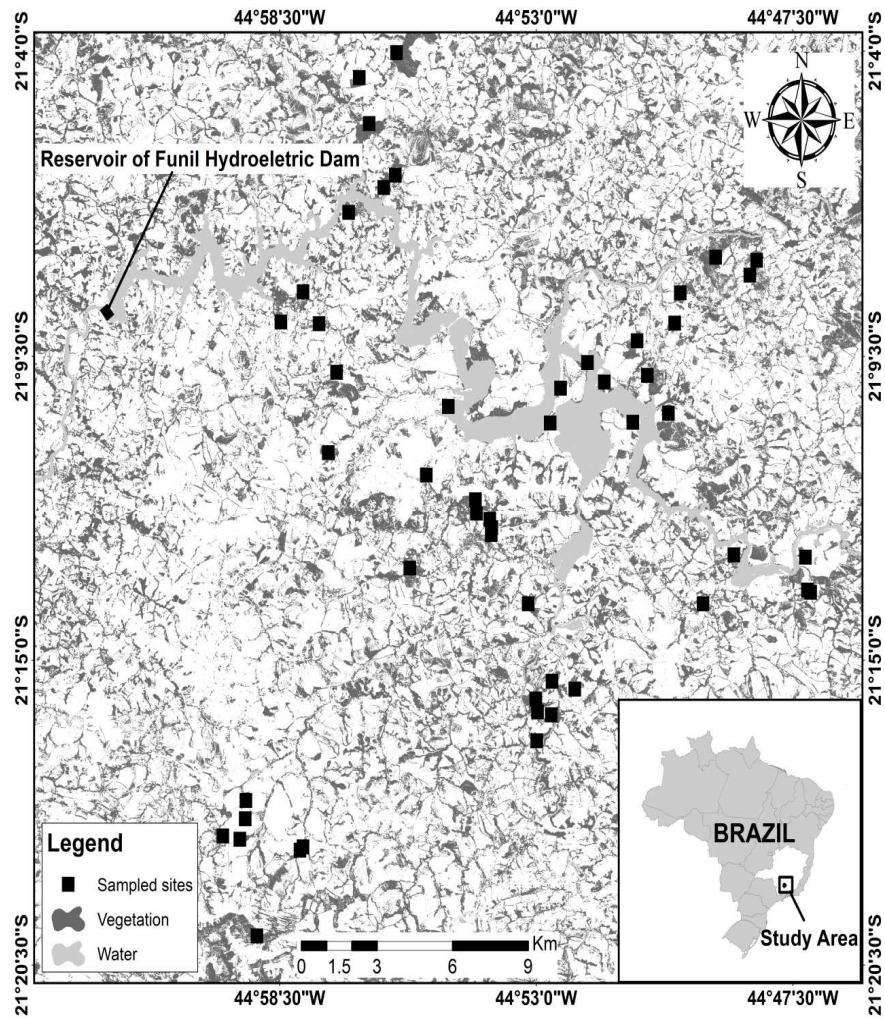


Fig. 1 Study area and the location of sampling sites. The black quadrates indicate the location of the sampled forest fragments. The dark grey color polygons indicates native vegetation, the light grey color indicates water and the white color indicates other land-use types. The reservoir of Funil hydroelectric dam is also showed in the picture.

Table 1 Summary of model selection for *Callicebus nigrifrons* and *Callithrix penicillata*.

Species	Model	ΔAIC	AICw	<i>c-hat</i>
<i>C. nigrifrons</i>	$\psi(\cdot), p(\text{weather})$	0	0.66	0.97
	$\psi(\cdot), p(\cdot)$	2.55	0.28	0.84
	$\psi(\cdot), p(\text{full_identity})$	4.93	0.06	1.16
<i>C. penicillata</i>	$\psi(\cdot), p(\cdot)$	0	0.54	1.17
	$\psi(\cdot), p(\text{weather})$	1.03	0.32	1.17
	$\psi(\cdot), p(\text{full_identity})$	2.81	0.13	1.28

Table footnote: In the model specifications ψ the occupancy and p is the detection probability. The notation (\cdot) indicates that the parameter is kept constant, while (weather) indicates that the parameter is modeled as a function of weather conditions. The notation (full identity) indicates that detection probabilities are allowed to vary throughout the surveys without any survey-specific covariate; *c-hat* is the overdispersion parameter.

Table 2 Occupancy models for the black-fronted titi monkey and the black-tufted era marmoset in fragments of the Brazilian Atlantic forest, with AIC values within 2 units from the top-ranking model.

Species	Model	AIC	ΔAIC	AIC <i>wgt</i>	C-hat
Black-tufted ear marmoset	$\psi(\text{con}), p(\cdot)$	195.20	0.00	0.18	1.15
	$\psi(\cdot), p(\cdot)$	195.20	0.22	0.16	1.17
Black-fronted titi monkey	$\psi(\text{size}+\text{ch}), p(\cdot)$	116.00	0.00	0.32	0.95
	$\psi(\text{size}+\text{ch}+\text{cop})$	117.13	1.13	0.18	0.91
	$\psi(\text{size}+\text{ch}+\text{con})$	117.65	1.65	0.14	0.96

Table footnote: In the model specifications ψ is the occupancy. The notation (\cdot) indicates that the parameter is held constant while the acronyms inside the brackets are the predictor covariates. *Size* is the area (ha) of the forest fragment; *ch* is the average canopy height; *cop* is the average canopy openness and *con* is the connectivity of the fragment. AIC indicates the Akaike Information Criteria. ΔAIC is the difference in AIC units between the top-ranking model and model. AIC *wgt* is the weight of evidence in favor of model being the best model for the situation, given the data and the set of models. *C-hat* is the overdispersion parameter.

Table 3 Sum of AIC weights from the set of best models for the titi monkey.

Predictor covariates	\sum AIC <i>wgt</i>
Canopy height	0.64
Fragment size	0.64
Canopy openness	0.18
Connectivity	0.14

Table footnote: \sum AIC *wgt* is the sum of the Akaike Information Criteria weights of all the models containing each of the predictor variables.