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Mammal Research

DOI:

[10.1007/s13364-015-0252-y](https://doi.org/10.1007/s13364-015-0252-y)

Published: 01/01/2016

Other version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Sales, L. P., Hayward, M. W., & Passamani, M. (2016). Local vs landscape drivers of primate occupancy in a Brazilian fragmented region. *Mammal Research*, 61(1), 73-82.
<https://doi.org/10.1007/s13364-015-0252-y>

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Local vs landscape drivers of primate occupancy in a Brazilian fragmented region

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Abstract Understanding the drivers of species distributions in human-dominated landscapes is crucial for proposing sound conservation strategies. Primates are the most studied terrestrial vertebrate taxa, yet still their response to forest loss and fragmentation widely varies among species. In this paper, we assessed the relative influence of local vs landscape features on occupancy of two primate species – the black-fronted titi monkey and the black-pencilled marmoset, in a Brazilian fragmented region. We created detection histories by performing repeated auditory surveys on 25 native vegetation patches. Then we fitted occupancy models using habitat and GIS-based data as site covariates, and weather conditions as detection covariates. We found that forest-like canopy elements are important for the titi monkey, which is a forest-dependent species. Marmoset occupancy was also related to local elements, but in a lesser extent. In addition, we found that ignoring detectability in playback call surveys created a 20% difference in occupancy estimates for the marmoset. We conclude that drivers of primate occupancy at the studied landscape rely mainly on local key habitat elements, so that on-ground conservation actions should not focus on habitat amount alone. Furthermore we reiterate that primate researchers should explicitly account for imperfect detection to avoid substantial detectability bias.

Key words Conservation, Wildlife-habitat, Detection, *Callicebus nigrifrons*, *Callithrix penicillata*.

Introduction

Historically, primate studies have been performed in relatively undisturbed areas, and the emphasis had been placed on studying primates in their native environment (Chapman and Peres 2001; Marsh et al. 2013). Only recently have primatologists focused their attention to primate responses to landscape changes (Arroyo-Rodríguez and Fahrig 2014). Although the amount of habitat is usually related to an increased persistence of primates on fragmented landscapes, other within-patch and matrix type elements also modulate primate distributions within the patch fragments (Benchimol and Peres 2013). Population dynamics in patches depend on landscape context, and responses to habitat loss diverge among species (Sharma et al. 2014). Local and landscape history of anthropogenic disturbances and life-history attributes are also related to primate persistence in Neotropical forest patches (Benchimol and Peres 2014).

Primate responses to habitat loss and fragmentation have been extensively studied (Mandujano et al. 2006; Anderson et al. 2007; Arroyo-Rodríguez and Dias 2010; Pozo-Montuy et al. 2011). However, the drivers of species distribution on fragmented landscapes are still uncertain (Umapathy 2013). In this sense, occupancy-detection modeling is considered one of the most robust methods for assessing the effects of habitat fragmentation on primate populations (Arroyo-Rodríguez and Mandujano 2009). Recently, researchers have also argued that occupancy-detection modeling may be a feasible tool for the continued monitoring of primate populations living in fragmented landscapes (Guillera-Arroita et al. 2010; Hines et al. 2010; Baker et al. 2011; Keane et al. 2012).

Occupancy is defined as the proportion of sampling units in a landscape that are occupied by a target species (MacKenzie et al. 2002). Yet the species may go undetected when present, so it is expected that occupancy estimates will generally be biased to some degree if imperfect detection is disregarded (MacKenzie et al. 2002). Non-detection of a species presence may have several causes, such as small population size, limited sampling effort, or the individuals may display some behavior that inhibits detection (e.g. flee from observer) (Gu and Swihart 2004). It is rarely, if ever possible,

to be completely sure that a species is absent at a site. Not accounting for imperfect detection also reduces inferential and predictive accuracy of species distribution models (Lahoz-Monfort et al. 2014). Therefore disregarding detectability potentially leads to uncertainty in data analysis and implementation of inappropriate management strategies (Wintle et al. 2004).

The main goal of this paper was to evaluate the occupancy drivers, while explicitly accounting for imperfect detection, of two primate species living in a Brazilian fragmented landscape: the black-fronted titi monkey (titi monkey *Callicebus nigrifrons*) and the black-pencilled marmoset (marmoset *Callithrix penicillata*). Titi monkeys are small to medium sized (1-2kg), predominantly frugivorous (Caselli and Setz 2011), arboreal primates that occupy canopy or subcanopy forest levels (Roosmalen et al. 2002; Rylands and Anzenberger 2012). Although they occur in both primary and secondary forests (Trevelin et al. 2007), their remaining populations are generally small and isolated due to extreme forest fragmentation within their range (Roosmalen et al. 2002). The studied species is listed as “Near Threatened (NT)” by IUCN Red List, due to the 20-25% population decline in the past 25 years, as a result of extensive habitat loss (Veiga et al. 2008).

Marmosets of genus *Callithrix* are small-bodied (<500g) primates specialized on chewing tree trunks and branches to feed on tree exudates (Coimbra-Filho and Mittermeier 1976). Gum-chewing specialization enables them to occupy a great variety of habitats and even survive periods of food scarcity (Passamani and Rylands 2000; Norris et al. 2011). The exploitation of abundant gum resource, in addition to their small body size and fast reproduction rate (Sussman and Kinzey 1984; Tardif and Smucny 2003; Mustoe et al. 2012) allows them to persist in habitats virtually inhospitable for other platyrrhine primates (Rylands et al. 2009; Vilela and Del-claro 2011). Differently from titi monkeys, marmosets are listed as “Least Concern (LC)” by IUCN Red List (Rylands and Mendes 2008), regularly use the ground and are not limited by canopy structures (Barros et al. 2004; Júnior and Zara 2007)

Specifically, we looked for local and landscapes characteristics that could explain species-

specific occupancy patterns. We predicted that drivers of occupancy will vary according to species vulnerability to land-use changes. Therefore, vulnerable species may be negatively affected by habitat loss and fragmentation at landscape scale and/or be dependent on key local habitat elements within a fragmented landscape. On the other hand, invasive opportunistic species are predicted to be benefited by habitat loss and fragmentation. We also aimed at observing the effect on not accounting imperfect detection on those estimates.

Materials and methods

This study was carried out on patches of native vegetation in the region of Lavras, Minas Gerais State (Figure 1). Native vegetation is classified as semi-deciduous forest and belongs to geographic domains of the Brazilian Atlantic forest and Cerrado savannas (Oliveira-Filho and Fontes 2000). Soil characteristics make this region extremely profitable for cattle ranching and farming (Oliveira-Filho et al. 1994). Historic fragmentation has occurred since European colonization and created a highly fragmented mosaic of land-use types, which are distributed in the landscape as: 41% of native vegetation, 31% of pasture, 17% of urban areas, 4% of coffee plantations, and 7% of others. Climate is classified as subtropical (Oliveira-Filho et al. 1994). Average annual temperature is 19.4°C and mean annual precipitation is 1493 mm, which is unevenly distributed throughout the year (Dantas et al. 2007).

Survey of primate occurrence

Forest patch was considered our focal spatial unit because it constitutes an easily defined patch for many primate species and is the typical habitat patch in fragmented landscapes. Primate occurrence was surveyed on focal forest patches using playback sampling method, because the studied species are vocally responsive (Melo and Mendes 2000; Miller et al. 2009). Playback technique consists of

broadcasting calls of each studied species separately at sampling points inside the focal forest patches. At each sampling point, we played a species vocalization for one minute and waited for two minutes in silence. We repeated this procedure three times before moving to the next sampling point. We randomized the order of playback calls, to avoid the effect of one species in another. When a species was detected, we ceased the survey of that detected species at that forest patch (and the species was marked as “detected” in that patch). If the species was not detected at that sampling point, we continued the search until the whole forest patch was surveyed (Figure 2).

At each focal forest patch, sampling points were chosen prior to surveys using satellite images. We subdivided each patch into circles of 250m radius, in which center we performed playback calls (Figure 2). That 250m distance was chosen for it is close to the critical distance a human listener can discriminate a titi monkey vocalization (Robinson 1981; Dacier et al. 2011). Other playback-based primate surveys in fragmented landscapes also have used similar approaches (da Silva et al. 2015). That procedure enabled sampling effort to be proportional to patch size. Furthermore, we avoided detectability bias due to differential sampling effort caused by variation in patch size.

However, species may not always be detected when present at a location, so that declaring a species absence is rarely ever possible (MacKenzie et al. 2002; Guillera-Arroita et al. 2014). In this study, we accounted for imperfect detection instead of assuming species absence at sites without detections – the so-called naïve occupancy – to get more realistic estimates of occupancy (Guillera-Arroita et al. 2014). This was achieved by visiting the focal forest patch during three non-consecutive days and modeling the repeated surveys as detection histories, as explained below.

Sampling design

We sampled the two primate species at 51 forest patches, all similar in vegetation, topographic and climatic characteristics. Patch sizes varied from 0.5 up to 150 ha (0-10 ha: 23 patches, 11-50 ha:

18 patches, >50 ha: 10 patches). We tried to randomize the location of sampled patches, but we were constrained by road access. All 51 forest patches were surveyed during three non-consecutive days between January 2013 and March 2013. Each day was considered one survey in detection histories. Therefore, if a species was detected at a forest patch during the first day, but not in the second and third days, resulting detection history would be 100.

An assumption of MacKenzie *et al.*(2002) occupancy model is that sites are “closed” to changes in occupancy during the sampling period, i.e, no sites become unoccupied and no new sites become colonized before cessation of the survey. We tried to achieve that closeness assumption by reducing as much as possible the duration of total survey period. However, we also kept an interval of two consecutive days between surveys, to avoid habituation of animals. Therefore each forest patch was surveyed in a maximum period of 10 days (3 surveys separated by 2 consecutive days). We also avoided neighboring forest patches, and most patches were more than 1 km apart from each other.

Despite our effort to homogenize sampling effort, detection probabilities can still vary among surveys, so we selected some environmental variables that could influence on primate activity and detectability. As acoustic communication of animals depends on propagation of sound in atmosphere (Wiley and Richards 1978), some physical constraints may affect primates calling behavior (Dooley *et al.* 2013). To control for the effect of weather conditions (and associated background noise) on detection probability models, we collected wind speed and atmospheric precipitation from the Brazilian meteorology institute (<http://inmet.gov.br>) for the meteorological station of Lavras, Minas Gerais State.

Local vs landscape predictors

To assess the relative influence of local and landscape elements on primate occupancy, we collected

predictor variables at those different scales. Landscape variables were collected using GIS-based techniques and are related to the amount of native vegetation cover at the studied region and to how fragmented that remaining vegetation is. Local variables were collected inside focal forest patches and are meant to reflect habitat elements important to primate occupancy.

Two landscape variables were considered: habitat amount and fragmentation. Habitat amount was considered the percent of native vegetation cover within a 1km radius buffer. We sampled 51 forest patches but we removed 26 out of the total, because several buffers were overlapping each other and this would lead to pseudo-replication. Therefore we considered only 25 non-overlapping buffers. The inverse number of patches was considered here a proxy of fragmentation, because it indicates how subdivided is that native vegetation. Contiguous landscapes should have values closer to one, while fragmented landscapes values closer to zero. Fragmentation is related to a greater number of small patches, higher edge density and probability of animals crossing non-native matrix. Fragmented landscapes also host smaller populations of edge-sensitive or matrix-avoiding species.

We predict that both titi monkey and marmoset occupancy will be related to landscape-scale predictors, because both species have relatively large daily path lengths (titi monkey = 1.27 km/day (Mittermeier et al., 2013); marmoset = 1.0 km/day (Kinzey, 1997)). However, marmoset occupancy should be positively related to disturbed landscapes because that species is usually found in disturbed and secondary forests and also edge habitats (Vilela & Del-claro, 2011).

We used data from RapidEye sensor from 2011. These images have five meter accuracy and five spectral bands (Red, Green, Blue, RedEdge and Infra-red). The additional RedEdge band allows precise discrimination of vegetation and land-use types (Schuster et al. 2012). These images were classified into main land-use types (native vegetation, arboreal agriculture, pasture, water, exposed soil, urban areas, and roads). We used parametric, supervised and multispectral method used in that classification, executed pixel by pixel. Both habitat amount and fragmentation were quantified in QGIS 2.0.1 (www.qgis.org).

Canopy measures are particularly important habitat elements for arboreal, forest-dwelling primates (Arroyo-Rodríguez and Mandujano 2009). In this study, we hypothesized that titi monkey occupancy would be positively related to canopy elements because they do not systematically utilize the ground or emergent forest levels (Lawler et al. 2006) and are considered dependent on canopy structures (Norconk 2007). Marmoset occupancy is not predicted to rely on canopy elements, but it can be related to disturbed canopy characteristics.

To assess local variables related to tree canopy, we measured canopy height and canopy openness. Canopy height was measured from one 100 m linear transect from each forest patch border. 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 eight mm hemispherical “fish-eye” lens and positioned 1.5m above the ground (Pontin 1962). Canopy openness is a measure that compares the area covered by white (openness) and black pixels (vegetation canopy) and ranges between 0% (total canopy closure) to 100% (no tree cover). This procedure was performed in the software Gap Light Analyzer (GLA) 2.0 (Frazer et al. 1999). 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 patch.

Occupancy modelling

Prior to analysis, all variables were standardized. Two detection predictors (wind velocity and atmospheric precipitation), and four occupancy predictors (habitat amount, fragmentation, canopy height and canopy openness) were analyzed. We also avoided collinearity problems by calculating correlations among variables and deleting highly correlated variables (correlation > 0.5). We fitted a set of single-season occupancy models to detection/non-detection data for each species separately. Single-season models involve estimation of: 1) probability p of detecting the species, given that the

species is present at the site, and 2) occupancy Ψ , which is the probability that a certain species is present in a site (MacKenzie et al. 2002). Models were ranked by their Akaike Information Criterion (Akaike 1974) corrected for small sample sizes (AICc), in which the number of patches was considered the effective sample size. Values within two AICc score from top-ranking model have similar level of support (Burnham and Anderson 2002).

Firstly, we fitted models in which Ψ and p were held constant. Then, we modeled p as a function of detection covariates (wind velocity and atmospheric precipitation). When the constant model was as good as models incorporating a detection covariate ($\Delta\text{AICc} < 2$), we did not include that covariate, in order to avoid unnecessary overparameterization. The detection model with best structure in terms of ΔAICc score was kept and we went on to model the occupancy parameter Ψ as function of local and landscape covariates, as shown in Table 1. Therefore, for each species, we got a set of four candidate detectability models (a constant model, two models including a detection covariate, and a model including both detection covariates), and 8 candidate occupancy models (a constant and a global model, a model including each landscape predictor, a model including both landscape predictors, and the same for local predictors).

We also assessed the fit of global models by comparing the Pearson *chi-square* statistic to a parametric distribution obtained via bootstrap procedure. That procedure estimates the overdispersion parameter called *c-hat*, which is used to evaluate how well the model fits the data, according to the formula (MacKenzie and Bailey 2004)

$$\hat{c} = X_{obs}^2 / X_B^2$$

where X_B^2 is the average of the test statistics obtained from the parametric bootstrap. When *c-hat* > 1, we corrected for data overdispersion by calculating the Quasi-likelihood Akaike information criterion (QAICc).

The AICc or QAICc differences of each model were converted to Akaike weights (w_i). Akaike

weights measure the relative likelihood of a particular model, given the data, (Burnham and Anderson 2002). Because predictors were uncorrelated and standardized, Akaike weights were used to obtain model averaged estimates for covariate parameters. If numerical convergence is not reached, parameter estimation is also not reliable. So when a model did not converge with default parameters (Quasi-Newton optimization method), we changed optimization method for *simulated annealing*, which is a stochastic global optimization method (Bélisle 1992). Figure 3 summarizes modeling procedures. We fitted all models using the *occu* function, available in R package *unmarked* (Fiske and Chandler 2011). Model selection tables and model averaging procedures were performed using R package *AICcmodavg* (Mazerolle 2015), and are described in the R script provided as supplementary material, as well as all data used in this study (Sup11).

Results

There was no correlation among predictors and none of them were removed. Minimum patch size in which titi monkeys were found was 4.48ha. Marmosets were found even in the smallest sampled fragment (0.53 ha). Titi monkey naïve occupancy was 0.64 and detection-corrected occupancy estimate was also 0.64 (SE \pm 0.0961). Mean detection probability for titi monkey was 0.91 (SE \pm 0.04). Conversely, marmoset naïve occupancy was 0.72 and detection-corrected occupancy estimate was 0.88 (SE \pm 0.11). Furthermore, marmoset mean detection probability was 0.39 (SE \pm 0.06).

Contrary to our expectations, our data did not provide evidence of an effect of weather conditions on detectability of either species. The constant detection model performed as well as models with detectability covariates (Table 2). Therefore, detection covariates were not included in subsequent occupancy models.

For the titi monkey, models with local predictors were consistently better than any other models ($\Delta AICc$ or $\Delta QAICc < 2$). For the marmoset, the constant occupancy model performed as well as two models containing local predictors (Table 3). Models containing landscape predictors were less

supported than those with local predictors, for both species.

Canopy height was the most important occupancy predictor for both species, and was positively related to titi monkey occupancy (Figure 4). Canopy openness was also the second most important predictor of both species and was negatively related to titi monkey occupancy. Marmoset occupancy did not exhibit a clear relationship to any predictors, because standard errors of model averaged estimated spanned wide over zero (Figure 4).

There was no evidence of effect of fragmentation or habitat amount on occupancy for any of the studied species. Predictions of whether local, landscape or constant models would better explain occupancy were corroborated only for the titi monkey (Table 4). Specific predictions for relationships with covariates were corroborated in some cases (Table 4).

Discussion

We aimed at identifying the relative importance of local vs landscape variables to explain primate occupancy in a Brazilian fragmented landscape. Contrary to our predictions, models including landscape covariates did not explain occupancy better than local predictors for any studied species. Most supported models for titi monkey included only local predictors, thus suggesting a clear effect of habitat elements in occupancy of that species. For the marmoset, the constant model worked as well as models including local predictors, which could also be an indication of local effects, although in a lesser extent.

A clear relationship between occupancy predictor variables was observed only for the titi monkey, and our initial hypothesis was corroborated. As titi monkeys are an essentially arboreal group, we expected that their occupancy pattern would be explained by local canopy measures. Indeed we found that titi monkey occupancy is positively related to high and closed canopy, thus confirming that this primate requires forest-like environments. Here, we advocate that dependency on canopy structures may inhibit their dispersal ability and thus confine remaining populations in

forest patches where they can survive. This fact has straightforward implications for conservation of titi monkey.

As selective logging damages canopy quality by reducing canopy height and increasing openness in tropical forests (Villela et al. 2006; Broadbent et al. 2008), titi monkeys are likely to be severely affected by that practice. Furthermore, titi monkeys inhabit the most populated region of Brazil, where remaining forest patches are usually small and embedded within agricultural areas (Ribeiro et al. 2009). Long-term persistence of forest-obligate and forest-dependent species is then unlikely to occur (Tabarelli et al. 2010) unless connectivity is restored and key habitat elements, such as canopy quality, is conserved. On-ground conservation actions should therefore not focus on patch area alone but also consider the value of small forest patches on preserving biodiversity, particularly those with forest-like canopy.

Contrary to our expectations, there was small evidence of effect of canopy measures on marmoset occupancy. We caution that results regarding canopy relationship with marmoset occupancy should be interpreted warily, because the model with constant occupancy performed as well as models with local variables. Also the relationship between occupancy and covariate parameters could not be assessed due to wide standard errors related to model-averaged estimates (Figure 4).

The marmosets studied here originally inhabited forest and savanna formations of Brazilian Cerrado (Rylands et al. 2009; Vilela and Del-claro 2011), a fairly dense woody savanna of shrubs and small trees (Oliveira-Filho and Ratter 2002). Deforestation of Brazilian Atlantic forest (and also misguided introductions of confiscated animals) has been favoring expansion of marmoset distribution into areas outside its original distribution (Rylands et al. 2009). We suggest that other local elements not necessarily related to canopy could possibly affect marmoset occupancy in fragmented landscapes. Marmoset home ranges are related to location of gum trees, an essential food resource (Scanlon et al. 1989, M Passamani and Rylands 2000), so we hypothesize that the

patchy distribution of gum trees across real landscapes could affect marmoset occupancy in fragmented regions. However, this effect is yet to be tested.

Primate responses at local scale are expected to vary dramatically in landscapes with different habitat amounts and degrees of fragmentation (Arroyo-Rodríguez et al. 2013; Arroyo-Rodríguez and Fahrig 2014). In this study, local predictors better explained primate occupancy than models containing landscape variables. However, we cannot state that primate occupancy does not rely on any landscape predictors. Ecological, biogeographic and anthropogenic variables are expected to have scale-specific influence on species distribution. We did not observe the effect of a 1km buffer landscape but we advocate that scaling up could lead to potentially different results, as multi-scale models can exhibit divergent results (Nichols et al. 2008).

Contrary to our expectations, weather conditions (and associated background noise) were not important predictors of detectability. Here, primate detection was based on auditory clues, so increased wind velocity and atmospheric precipitation were expected to affect detection due to increased background noise level. Because there are trade-offs between energetic costs of singing displays and benefits from communication (Ryan and Kime 2003), strong background noise should adversely affect singing behavior (Wiley and Richards 1978). In order to achieve occupancy closeness assumptions, we constrained our sampling to a maximum period of 10 consecutive days per site. However, this constraint may have prevented us from capturing a wider range of weather conditions. If weather conditions are rather constant, their effects might not be captured in the data.

Detection probability of titi monkey was high (close to one), indicating that detection of this species was close to perfect in our surveys. On other hand, naïve occupancy was 20% lower than detection-corrected occupancy for the marmoset. Not accounting for imperfect detection of marmoset could lead to alarmist reactions for observed declines in population sizes derived from weak methods (Wintle et al. 2004; Gu and Swihart 2004). Erroneous predictions of a species response to habitat changes can also take place due to poorly formulated wildlife-habitat models

(Gu and Swihart 2004; Lahoz-Monfort et al. 2014).

Inadequate management plans can further waste conservation opportunities and financial resources, which are known to limit management actions especially in developing countries, where most primate species are found. Imperfect detection must therefore be explicitly accounted for. It is no longer sufficient to claim that similar habitats between sites mean equivalent detectability, weather patterns also need to be the same, or methods that account for variable detectability must be used. This has substantial implications for bird, bat, frog and mammal acoustic surveys.

Acknowledgments

We are sincerely thankful to all land-owners who allowed us to work in their rural properties. Special thanks are given to Renan Macedo, Rayssa Faria Pedroso, Tiago Fogaça de Carvalho, and Ismael Aparecido da Silva for their valuable help in fieldwork. We also thank two anonymous referees for their valuable suggestions to the manuscript.

Compliance with Ethical Standards

Data collection was conducted under approval of the Brazilian Institute of the Environment (IBAMA process number 14083-1), and follows the Principles for the Ethical Treatment of Non-Human Primates of the American Society of Primatologists. Co-authors state their participation and agree with the resubmission in Mammal Research. The first author is financed by the Brazilian Federal Agency for Evaluation of Graduate Education (CAPES number 00.889.834/0001-08). The authors also declare that they have no conflict of interest.

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Figure captions

Fig. 1 Study area and location of sampling sites. Top left, there is a Latin America map, highlighting the Brazilian Atlantic forest and the Cerrado distribution. At right, black circles indicate the location of buffers surrounding sampled forest patches. Native vegetation is indicated in green color, coffee plantations are red and urban areas are grey. White color indicates other land-use

types.

Fig. 2 Sampling scheme of each forest patch. In the scheme above, dark grey polygons indicate forest patches. All forest patches were subdivided into circles of 250m radius. At all sampling occasions, we broadcasted playback calls at the center of a circle. We surveyed the whole area of the forest patch or until the species was detected. Therefore, sampling effort was proportional to patch size.

Fig. 3 Summary of modelling procedures. Detection probabilities were modeled as function of weather conditions. The best detection structure was assessed via ΔAIC comparisons and was used in subsequent occupancy models. Goodness-of-fit tests were performed in global models, and $AICc$ was adjusted to overdispersion when necessary (using $QAICc$). Then occupancy models were fitted to data using default parameters (Quasi-Newton optimization method). When model convergence was not reached, simulated annealing optimization method was used. Covariate relevance was assessed by top-ranking models and by analyzing the relationship between occupancy and predictor variables using model averaged parameters.

Fig. 4 Model averaged estimates of covariate parameters and their associated standard errors. A clear relationship was found only for the titi monkey occupancy and local predictors *Canopy openness* (negative relation) and *Canopy height* (positive relation). All estimates for the marmoset had standard errors overlapping zero, so there was no relationship between occupancy and covariates.