Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade
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Influência de variáveis locais, descritoras da qualidade da floresta e do recurso alimentar, na dieta e uso do espaço do ouriço-preto (*Chaetomys subspinosus* Olfers, 1818), um folívoro arborícola ameaçado e endêmico da Mata Atlântica, Brasil.

KENA FERRARI MOREIRA DA SILVA

Ihéus - Bahia

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Orientador: Profª Dr. Deborah Maria de Faria

Co-Orientador: Prof. Dr. Gastón Andrés Fernandez Giné

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Dedico esta tese às minhas queridas, Irmã e Mãe

Luiza Elisabeth & Bete

in memorian

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Índice

Resumo

Esta tese tem o objetivo avaliar e discutir diferentes aspectos do comportamento e ecologia de mamíferos folívoros arborícolas utilizando como foco o ouriço-preto (*Chaetomys subspinosus* Olfers 1818), um pequeno roedor endêmico da Mata Atlântica. O primeiro capítulo traz uma revisão do número e quais são as espécies de mamíferos do mundo que podem ser classificadas como “folívoras arborícolas”. De acordo com a literatura, 386 mamíferos arborícolas (inclui espécies de primatas, roedores, marsupiais, preguiças, hyraxes e colugos) podem consumir alguma quantidade de folhas, mas somente 98 espécies puderam ser verificadas quanto ao grau de folivoria em suas dietas, o que corresponde a uma lacuna de informações quantitativas para 288 spp. (74.8%). Além disto, o primeiro capítulo traz uma revisão de trabalhos científicos com informações sobre orçamento de atividade (especificamente, o tempo em repouso) e a proporção de folhas consumidas na dieta. A porcentagem de folhas na dieta foi um importante fator para explicar a variação no tempo diário despendido para o repouso nestas espécies. O segundo capítulo estuda a dieta do ouriço-preto e verifica se a diversidade das espécies de plantas consumidas é influenciada pelo tamanho do fragmento em que o indivíduo se encontra. Avalia também se a frequência de consumo de sete espécies de sua dieta pode ser explicada pela concentração de metabólitos secundários (taninos condensados e fenóis totais) e aspectos nutricionais (proteína total e fibra em detergente ácido). Nossos resultados indicam que a riqueza e diversidade da dieta são maiores em grandes fragmentos do que em pequenos e que poucas espécies de plantas forrageiras são compartilhadas entre estas duas categorias de tamanho, mas são estas que estão entre as espécies com a maior frequência de consumo entre todos os porcos-espinhos estudados. As concentrações de taninos condensados, fenóis totais e fibra em detergente ácido influenciam a frequência de consumo de sete espécies de plantas forrageiras dos ouriços-preto. No terceiro capítulo desta tese estudamos os efeitos de uma série de características conectadas à qualidade do habitat, como distância à borda do fragmento florestal, estrutura local da floresta, abundância e conteúdos nutricionais dos recursos alimentares, nos padrões de uso do habitat do ouriço-preto. Nós também avaliamos se nutricionalmente, a qualidade de duas espécies forrageiras varia conforme sua localização no habitat florestal (borda x interior), e se essa diferença pode explicar um viés no uso do habitat pelo ouriço-preto. Utilizamos a abordagem que utiliza a estimativa de distribuição de utilização (UD), definida como frequência relativa com que um animal usa várias partes de sua área de vida, para quatro animais adultos monitorados por radiotelemetria em pequenos fragmentos do sul da Bahia. Identificamos que a área basal total, densidade de cipós, abundância das espécies de alimento, distância ao centro da área de vida e a distância à borda do fragmento juntas são importantes variáveis que guiam o uso do habitat. Embora não tenhamos encontrado diferenças marcantes nas características nutricionais entre borda e interior dos fragmentos, a abundância local e sua distribuição foram de extrema importância para determinar a UD dos animais. Nossos dados sugerem que múltiplos fatores ambientais, provavelmente de uma forma complexa, agem juntos para determinar os movimentos destes animais e consequentemente influenciam o uso do espaço em pequenos fragmentos dominantes ao longo da restrita distribuição geográfica do ouriço-preto.

Palavras-chave: Mata Atlântica; Mamífero; Rodentia; Porco-espinho; Folívoro; Dieta; Metabólitos secundários; Fragmentação; Efeito de borda; Ecologia do movimento; Uso do habitat.

Abstract

This thesis aims to evaluate and discuss different aspects of the behavior and ecology of arboreal folivorous mammals using as a focus the thin-spined porcupine (*Chaetomys subspinosus* Olfers 1818), a small rodent endemic to the Atlantic Forest. The first chapter provides a review of the number and what are the mammal species of the world that can be classified as "arboreal folivores". According to the literature, 386 arboreal mammals (including primates, rodents, marsupials, sloths, hyraxes and colugos) may consume some leaves, but only 98 species could be verified on the degree of folivory in their diets that corresponds to a quantitative information gap for 288 *spp*. (74.8%). In addition, the first chapter presents a review of scientific papers with information about activity budget (specifically, resting time) and the proportion of leaves consumed in the diet. The percentage of leaves in the diet was an important factor to explain the variation in daily time spent for rest in these species. The second chapter studies the diet of the thin-spined porcupine and verifies if the diversity of the species of plants consumed is influenced by the size of the fragment in which the individual is. It is also evaluated if the consumption frequency of seven species of its diet can be explained by the concentration of secondary metabolites (condensed tannins and total phenols) and nutritional aspects (total protein and acid detergent fiber). Our results indicate that diet richness and diversity are greater in large fragments than in small ones and that few species of forage plants are shared between these two size categories, but these are among the species with the highest consumption frequency between all the porcupines studied. The concentrations of condensed tannins, total phenols and acid detergent fiber influence the frequency of consumption of seven species of forage plants of the thin-spined porcupines. In the third chapter of this thesis we study the effects of a series of characteristics connected to habitat quality, such as distance to the forest fragment edge, local forest structure, abundance and nutritional content of the porcupines´ food resources, and habitat use patterns. We also evaluated whether nutritional quality of two forage species varies according to their location in the forest habitat (edge x interior), and whether this difference may explain a bias in habitat use by the thin-spined porcupines. We used the use utilization distribution (UD) estimate approach, defined as the relative frequency with which an animal uses several parts of its home range, for four adult animals monitored by radiotelemetry in small fragments of southern Bahia. We identified that the total basal area, density of lianas, abundance of food species, distance to the center of the homer range, and the distance to the edge of the fragment together are important variables that drive porcupines´ habitat use. Although we did not find significant differences in the nutritional characteristics between the edge and the interior of the forest fragments, the local abundance and its distribution were of extreme importance to determine the UD of the animals. Our data suggest that multiple environmental factors, probably in a complex way, act together to determine the movements of these animals and consequently influence the use of space in small dominant fragments along the restricted geographic distribution of the thin-spined porcupine.

Keywords: Atlantic Forest; Mammalian; Rodentia; Porcupine; Folivore; Diet; Secondary Metabolites; Forest Fragmentation; Edge effect; Movement ecology; Habitat use.

Introdução Geral

Para se tentar compreender o valor do habitat para os animais deve-se primeiro descrever a qualidade e quantidade dos recursos nele contido e em segundo, sua distribuição espacial em uma escala de forrageamento relevante para a espécie estudada (Moore et al., 2010). O ouriço-preto (*Chaetomys subspinosus*) é um pequeno roedor folívoro, arborícola, vulnerável e endêmico da porção central da Mata Atlântica (Catzeflis et al. 2008). Esta espécie pode ser um bom modelo para testar estas questões, pois há alguns anos, estudos começaram a desvendar importantes aspectos de seu comportamento, ecologia e conservação no sul da Bahia e Espírito Santo (Giné 2009; Giné et al. 2010, 2012, 2015; Souto Lima et al. 2010; Faria et al. 2011; Oliveira et al. 2012).

Esta espécie possui um alto grau de folivoria e uma tendência a consumir uma grande quantidade de poucas espécies de plantas, pioneiras e com uma ampla distribuição (de Souto Lima et al., 2010; Giné et al, 2010). O alto valor protéico das folhas consumidas foi um importante fator na seleção alimentar, mas não explicou sozinho a seletividade na dieta desta espécie (Giné et al, 2010). Outros fatores não investigados anteriormente como metabólitos secundários de defesa das plantas podem estar agindo na seletividade alimentar do ouriço-preto, como por exemplo os níveis de compostos fenólicos, incluindo os taninos condensados das folhas consumidas.

Outra questão ainda não investigada é a possibilidade de que em fragmentos florestais do sul da Bahia ocupados por esta espécie, a abundância e os níveis de proteína e metabólitos secundários de defesa das folhas de plantas forrageiras estejam sendo alterados nas áreas de borda com relação ao interior dos fragmentos florestais. Isto por sua vez, pode estar influenciando o movimento e uso do espaço pelos ouriços-pretos. Seu comportamento alimentar pode seguir uma lógica de custo-benefício ("trade off’), pois os indivíduos ao selecionarem poucas espécies forrageiras próximas taxonomicamente, estão provavelmente detoxificando específicos tipos e níveis de metabólitos secundários para em troca obter um recurso alimentar de alta qualidade nutricional, abundante e previsível no tempo e espaço.

Entretanto, a seleção de poucas espécies para compor a dieta pode ser um efeito do fato dos ouriços-pretos previamente estudados ocuparem somente pequenos fragmentos florestais, locais onde se espera um efeito de borda mais pronunciado e como consequência com uma maior simplificação florística. Portanto não sabemos se teriam uma dieta mais rica e diversificada se estivessem em fragmentos maiores, uma questão que poderia revelar padrões de seleção ainda não entendidos para a espécie. Além disso, a dieta desta espécie foi estudada apenas para 4 animais da Bahia (Giné et al. 2010) e 3 animais do Espirito Santo (Souto Lima et al. 2010).

Desta forma esta tese tem o objetivo geral de investigar a influência de fatores locais descritores da qualidade da floresta (efeito de borda e estrutura) e dos recursos alimentares (conteúdos nutricionais e metabólitos secundários de folhas) sobre o comportamento alimentar e uso do habitat de uma população de ouriço-preto (*Chaetomys subspinosus*) do sul do estado da Bahia, região central da Mata Atlântica. Esta tese está dividida em três capítulos escritos em forma de artigo científico na língua inglesa: o primeiro capítulo trata de uma revisão sobre a influência do consumo de folhas no tempo gasto em repouso diário em mamíferos arborícolas, discutindo a influência deste tipo de dieta nas restrições energéticas que este grupo possui. Além disto, este capítulo traz uma lista das espécies de mamíferos arborícolas do mundo com dados sobre a proporção (em relação a itens alimentares) de folhas na dieta, complementada por espécies potencialmente comedoras de folhas, ou seja sem dados quantitativos sobre sua dieta. O segundo capítulo procura entender em específico, utilizando o ouriço-preto como modelo, quais características, sejam elas nutricionais ou de defesa das plantas (metabólitos secundários) que estão guiando o consumo de folhas por estes animais. Esta questão já foi relativamente bem investigada para outras espécies de mamíferos folívoros arborícolas, como exemplo alguns marsupiais na Austrália (Moore et al. 2005, 2010; Jensen et al. 2014), enquanto que para mamíferos folívoros da Mata Atlântica, os estudos apenas estão se iniciando (Giné et al. 2010). Outro ponto investigado é se o ouriço-preto estando em um pequeno fragmento possui uma dieta menos diversificada, com um "cardápio" mais pobre de espécies de plantas do que em relação a um fragmento maior e consequentemente mais bem conservado. O terceiro capítulo verifica quais variáveis ambientais influenciam o uso de porções da floresta pelos ouriços-preto em uma escala dentro da área de vida destes animais. Neste contexto, verificamos se o efeito de borda está afetando a composição química (nutricional e metabólitos secundários) de duas espécies de árvores muito consumidas pelo ouriço-preto. Foi investigado também, a partir do estudo do movimento dos ouriços-pretos, se a estrutura da floresta, a distância à borda do fragmento florestal e a abundância e distribuição do alimento (árvores forrageiras) são importantes para explicar a intensidade de uso de porções dentro de suas áreas de vida.

Desta forma, além de elucidar questões básicas da ecologia e comportamento do ouriço-preto, esta tese pode nos auxiliar a compreender melhor as respostas que os mamíferos folívoros arborícolas têm frente à fragmentação, degradação e perda dos habitats naturais em florestas tropicais, especialmente na Mata Atlântica. Com isto esperamos subsidiar possíveis ações de conservação, não só para esta espécie, mas para toda a fauna de mamíferos dependente destes remanescentes florestais.

Referências Bibliográficas

CATZEFLIS, F., J. PATTON, A. PERCEQUILLO, C. BONVICINO AND M. WEKSLER. 2008. Chaetomys subspinosus. *The IUCN Red List of Threatened Species*. .

FARIA, D. M., G. A. F. GINÉ AND M. L. REIS. 2011. Plano de ação nacional para conservação do ouriço-preto (ICMBio/MMA). Série Espécies Ameaçadas 17:36p.

GINÉ, G. A. F. 2009. Ecologia e comportamento do ouriço-preto (Chaetomys subspinosus, Olfers 1818) em fragmento de Mata Atlântica do municipio de Ilhéus, sul da Bahia.

GINÉ, G. A. F., E. H. DE BARROS, J. M. B. DUARTE AND D. FARIA. 2015. Home Range and Multiscale Habitat Selection of Threatened Thin-Spined Porcupine in the Brazilian Atlantic Forest. Journal of Mammalogy 96:1095–1105.

GINÉ, G. A. F., J. M. B. DUARTE AND D. FARIA. 2010. Feeding ecology of a selective folivore, the thin-spined porcupine (Chaetomys subspinosus) in the Atlantic forest. Journal of Mammalogy 91:931–941.

GINÉ, G. A. F., J. DUARTE, T. MOTTA AND D. FARIA. 2012. Activity, movement and secretive behavior of a threatened arboreal folivore, the thin-spined porcupine , in the Atlantic forest of southern Bahia, Brazil. Journal of Zoology 286:131–139.

JENSEN, L. M., I. R. WALLIS, K. J. MARSH, B. D. MOORE, N. L. WIGGINS AND W. J. FOLEY. 2014. Four species of arboreal folivore show differential tolerance to a secondary metabolite. Oecologia 176:251–258.

MOORE, B. D., W. J. FOLEY, I. R. WALLIS, A. COWLING AND K. A. HANDASYDE. 2005. Eucalyptus foliar chemistry explains selective feeding by koalas. Biology Letters 1:64–67.

MOORE, B. D., I. R. LAWLER, I. R. WALLIS, C. M. BEALE AND W. J. FOLEY. 2010. Palatability mapping: A koala's eye view of spatial variation in habitat quality. Ecology 91:3165–3176.

OLIVEIRA, P. A., R. B. S. LIMA AND A. G. CHIARELLO. 2012. Home range, movements and diurnal roosts of the endangered thin-spined porcupine, Chaetomys subspinosus (Rodentia: Erethizontidae), in the Brazilian Atlantic Forest. Mammalian Biology - Zeitschrift für Säugetierkunde 77:97–107.

SOUTO LIMA, R. B., P. A. OLIVEIRA AND A. G. CHIARELLO. 2010. Diet of the thin-spined porcupine (Chaetomys subspinosus), an Atlantic forest endemic threatened with extinction in southeastern Brazil. Mammalian Biology 75:538–546.

Capítulo 1: The arboreal folivore mammals of the world and the influence of leaf consumption on the percentage of daily time spend in rest: a review.

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Abstract

Many mammalian arboreal folivores live close to the limit of their energy budget due to the little availability of soluble carbohydrates and low digestibility of its diet. Mainly due to this energetic constraint, these mammal species commonly show low levels of activity, small home range size, short and slow movements among other strategies and adaptations in order to avoid unnecessary energetic expenditure. My aim in this revision was to identify and list the species of arboreal folivores mammals of the world and investigate the influence of leaf consumption on the daily time spend in rest by arboreal mammal. For this last, I expected a positive relationship between degree of folivory (percentage of the leaves in the diet) and the daily inactivity budget of the arboreal folivore mammal species. If I compare with a Eisenberg´s seminal review of 1978 that ranked mammal genera simultaneously for herbivory and arboreality (identified 58 genera in 7 orders with the greatest adaptations to herbivory and arboreality), in this review, with the aid of new information from new global compilations and scientific papers it was possible to identify 83 genera in 6 orders (49 new genera), totaling 386 arboreal mammal species with potential to eat leaves. Quantitative diet data were available for 98 species, which 73 may be considered folivores (>30% of the diet composed by leaves), including 12 strictly folivores (>90% of the diet composed by leaves). With quantitative resting and diet data, and controlling the effect of phylogeny, the results indicated that the activity levels declined significantly with the increasing of the proportion of leaves in the species' diet. Thus, I confirmed that the time dedicated to rest is positively associated with the degree of folivory of arboreal mammals.

Keywords: Activity budgets, Folivory, Resting time, Diet, Arboreal mammals.

Introduction

Time allocation decisions in different activities (e.g. activity budgets), and the knowledge of factors and mechanisms that influence and determine this variation, is relevant to understand species behaviour and ecology (Schoener 1971; Kronfeld-Schor and Dayan 2003).

The daily time allocated for rest (i.e., percentage of time resting per day) is an important component of activity budgets and it is often related to energy saving (Milton 1998), waiting to put in more useful activities like recovery, predator avoidance, digestion and thermoregulation (Herbers 1981). Resting time can be splited in two basic forms: the enforced resting time for digestive and thermoregulatory purposes, and uncommitted resting, related to time available for conversion into additional feeding, travel or social interactions (Dunbar 1996).

The quantity of leaves in the diet and the mean annual temperature were important factors known to influence the resting time in primates, particularly the enforced resting time (Korstjens et al. 2010). It may impose significant limits on primates' geographic distribution by making it difficult for animals to allocate sufficient time to other essential activities (Korstjens et al. 2010). In folivores primates, the enforced resting time requirements are in part set by the time needed for digestion, mainly imposed by the processes of leaf fermentation. Thus, folivores need to devote more time to resting purely to allow fermentation of leaf material (Korstjens et al. 2010), and then, the adoption of this life history strategy may also impose energetic constraints associated with caloric and nutritionally poor food resources (Eisenberg 1978).

Leaves are generally a low energetically and quality food resource, consisting of cellulose and fiber rich content, as well as secondary metabolites, such as essential oils, tannins and phenols (Freeland and Jansen 1974; McNab 1978). Besides having few energy available due to low soluble carbohydrate content, the detoxification and elimination of these compounds is energetically expensive for herbivorous (Freeland et al. 1985; Sorensen et al. 2005). It may also influence the activity budgets and mobility of arboreal mammals.

If arboreal folivory is constrained by nutritional energetics, increasing specialization should be accompanied by reduced energetic needs and energy-saving strategies (McNab 1978). In fact, mammals occupying this feeding niche share some adaptations signing reduced energetic needs and energy-saving strategies, as low muscle-mass ratio (McNab 1978), upper-limited body size to allow arboreal habits, and bottom-limited body size to enable plant matter digestion (Parra 1978; Cork and Foley 1991). It is also common that these species have reduced basal metabolic rates (Mcnab 1986), small litter sizes (Eisenberg 1978), anatomical specializations related to digestion (Cork and Foley 1991), thermoregulation strategies (Briscoe et al. 2014; Giné et al. 2015), short and slow movements (Eisenberg 1978), small home ranges (Eisenberg 1978) and low activity levels (Urbani and Bosque 2007; Caselli and Setz 2011; Giné et al. 2012, 2015; Ryan et al. 2013). Arboreal folivores usually have lower BMRs and FMRs (basal and field metabolic rates, respectively) than other mammals. However, as specialization increases only FMR decreases, which suggest that reduced energetic expenditure in more specialized species is the result of thermoregulatory and behavioral strategies, rather than simply a linear reduction in BMR (Pauli et al. 2016).

My first aim in this revision was to identify and list the species of arboreal folivores mammals of the world, following the classification scheme made by Eisenberg (1978). Due to the long time of this seminal review, new information on leaf consumption and arboreal habits are available, providing an update and filling gaps on this specific guild. I also investigated the influence of leaf consumption on the activity level of arboreal mammal species of the world. There is a wide variation in dietary specialization in arboreal mammals (Eisenberg 1978) that allow us to look at the effect of diet on resting time. We expected a positively linear relationship between leaf consumption and the ratio of daily time spend to rest. Some studies reinforce this relationship, as shown by Boonratana (2003), for species level. Here, I provide a review on a guild perspective, searching this relation considering the potential arboreal folivore species with quantitative data available in the current literature.

Methods

Species (or genus) of arboreal folivore mammals of the world

In order to assess and list the potential species of arboreal folivore mammals of the world we performed a review in the published literature from 1978 to 2017 for obtain data on the percentage of leave in the diet for all arboreal mammals that eats some amount of leaves. I used as a starting point a previous review about the diet of terrestrial mammals worldwide (Kissling et al. 2014), in order to obtain semi-quantitative information on degree of leaf consumption. In addition, I used the Elton Traits 1.0 global species-level diet attributes compilation (Wilman et al. 2014) to review which of these mammals use arboreal foraging stratum (excluding scansorial and terrestrial species). From these two compilations I obtained a list of arboreal folivores mammals that I have some information of food habits and list all species recognized in these genera that have at least one species that eats leaves using Wilson and Reeder (2005) taxonomy and PanTHERIA species level life-history database (Jones et al. 2009). I classified species, when I have quantitative information, in four categories following Eisenberg's rating (Eisenberg 1978): low (<30%), medium (30 to 50%), high (50 to 90%) and very high (>90%) folivory specialization. Such as Eisenberg (1978), the species of these categories were considered “non folivores”, “occasional folivores”, “predominant folivores” and “strict folivores”, respectively. When a species was qualitatively considered as arboreal folivore in previous literature but no quantitative data of their diet was found, I listed as “likely folivore”.

Folivory and resting time relation

For all mammalian species foraging on leaves at some extent, I searched in the published literature for quantitative data on leaf consumption and daily resting ratio (summarized in the Appendix) focused on behavior long-term studies of mammal’s diet and activity budgets. I used web databases of Google Scholar and Scopus, combining as search terms the genus *or* scientific species names *and* the word “diet” *or “*activity patterns”. Search terms were applied to the title, followed by the keywords and subsequently by the whole article. After obtaining a final article set output, filtering each content to assure its relation with the issue studied here, I extracted the following quantitative information: (1) the proportion of feeding time dedicated to eat leaves, as a proxy of the proportion of leaves in the diet, and; (2) the proportion of resting time or frequency in the daily activity budget of each species. Studies were choice for subsequent analysis if one of the behavioral parameters of interest was measured. Ideally, observations had to be carried out over at least 8 months and/or data had to be available for multiple seasons, as well as data obtained by scan sampling or focal animal sampling (as recommended by Dias and Rangel-Negrín 2015 and Korstjens et al. 2010). The differences between these sampling methods of behavioral record may introduce additional error variance into the analyses, but I assumed that this should only act conservatively by reducing significance levels. When I obtained more than one valid variable record for each species, I calculated average of the values to generate species-specific ‘typical’ value.

Finally, I performed a nested linear mixed-effects model analysis in order to evaluated the relationship between the percentage of leaves in the diet and the percentage of daily time spend in rest. As fixed effects, I entered the percentage of leaves in the diet into the model. As nested random effects, I had intercepts for genus within families (Bolker et al. 2009). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. I used Wald t-tests to obtain *p*-value for the linear model, and we provided an absolute value for the goodness-of-fit of a model (R^2) using 'r.squareGLMM r' function, as proposed by Nakagawa and Schielzeth (2013). Statistical analyses were performed on the software environment R (R Core Team 2015) using lme4 package (Bates et al. 2014).

Results

Potential species (or genus) of arboreal folivore mammals of the world

In this review, with the aid of new information from global species-level compilations and literature, it was possible to identify 83 genera in 6 orders (49 new genera in relation to Eisenberg´s seminal list), totaling 386 arboreal mammalian species (36.4% in total of 1060 extant mammals arboreal species) that may eats some amount of leaves (Appendix A). This new list includes monkeys (Primates; n = 238), rodents (Rodentia, n = 79), marsupials (Diprotodontia; n = 58), sloths (Pilosa, n = 6), tree hyraxes (Hyracoidea; n = 3), and colugos (Dermoptera; n = 2).

There is quantitative information gap for 288 spp. of arboreal mammals that can potentially feed on leaves, what I am calling the "likely folivores" (Supplemental Material - S1). In other words, 74.8% of potential arboreal folivorous species do not have quantitative data on their leaves diet, only semi-quantitative information (Kissling, 2014). I confirmed the folivory degree for 98 arboreal mammalian species

(Supplemental Material - S1). Of those, 25 species may be considered as “non folivore” (<30% of leaves in the diet), 23 as “occasional folivore” (30-50% of leaves in the diet), 38 as “predominant folivore” (>50-90% of leaves in the diet), and 12 as “strict folivore” (>90% of leaves in the diet). Few species may be considered “strict folivores”, *sensu* Eisenberg (1978), which are: two monkeys (*Avahi laniger* and A. *meridionalis*); sloths (*Bradypus torquatus, B. tridactylus*, *B. variegatus*); a rodent porcupine (*Chaetomys subspinosus*); a colugo (*Cynocephalus volans*), a tree hyrax (*Dendrohyrax arboreus*), and four marsupials (*Dendrolagus lumholtzi, Hemibelideus lemuroides, Phascolarctos cinereus*, and *Pseudochirops archeri*).

Relation among degree of folivory and resting time

I found quantitative data for both the proportion of leaves in the diet and the proportion of resting in daily activity for 77 species from five taxonomic families. Primates accounted for 83.0% (n = 65) of the sample. Linear mixed models show a positive relationship between the degree of folivory and the percentage of daily time spend in the rest, indicating that species with higher proportion of leaves in the diet tend to spend more time in rest. The regression slope of resting time on the proportion of leaves in diet for all the data combined was 0.398 (SE ± 0.047). When we controlled the random effect of phylogeny by nested genus and family, the linear model with variable leaves explained 69.62% (R^2= 69.62, p < 0.001, d.f. = 76, r = 76.4, Fig. 1) of the observed variation in resting time of arboreal mammals. The model with nested random effects is significant different from the model without this effect (p < 0.01, d.f. = 2, χ^2 = 11.03), which suggests great dependence of diet strategy on phylogenetic background.

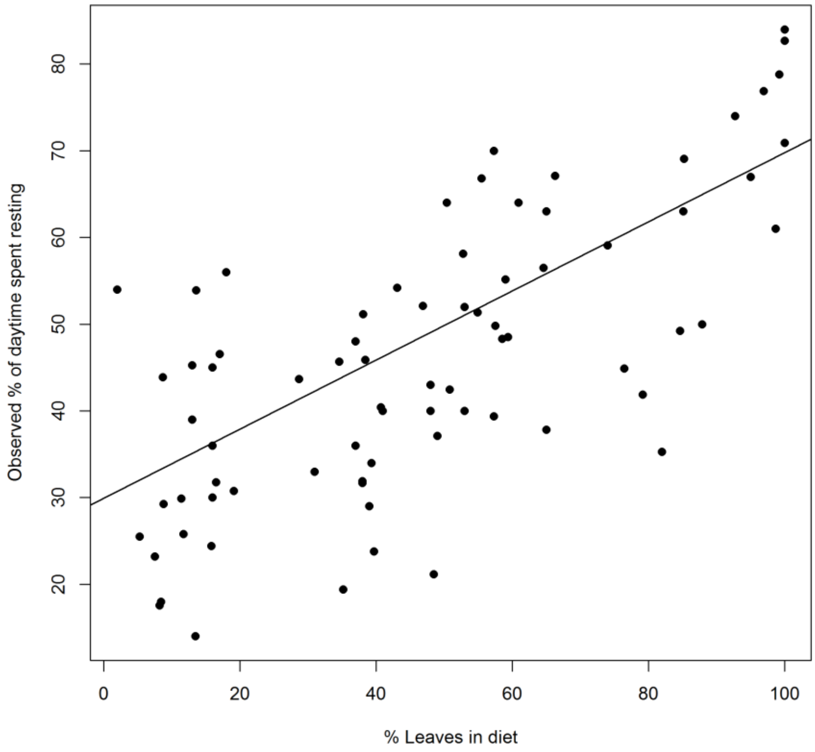

Fig. 1. Relationship between the percentage of leaves in the diet and the percentage of daily time spent in rest with base in data obtained for 77 arboreal mammalian species.

Discussion

This is the first updated review on the degree of folivory of arboreal mammals since the seminal article by Eisenberg (1978). Different from Eisenberg (1978), this review has brought species-level information, adding to its list new genera with more accurate information on the degree of folivory of the species, one of the merits of this review. It is also important to identify which species of arboreal mammals have gaps in the knowledge of their diets, because this may guide and encourage further researchs.

This review suggests that only 36.4% of the world's arboreal mammal species eat some amount of leaves. Although arising multiple times in different mammalian lineages, arboreal folivores are rare. The overall lack of diversification of this group has been attributed to the energetic constraints associated with a strategy dependent on an energetically and nutritionally poor food resource. Ideed, I confirmed that the percentage of leaves in the diet is an important factor explaining the variation of percentage of daily time that arboreal mammals spent resting. The nested linear mixed model analysis indicates that when the effect of phylogenetically relatedness is controlled, the model is better adjusted and indicated a relationship between the extent of leaves in the diet and resting time.

Nevertheless, the proportion of leaves in the diet may not to be the only factor influencing the resting time in arboreal mammals. In primates, many factors may influenced activity budgets, such group size (Teichroeb et al. 2003; Djègo-Djossou et al. 2015), different nutritional requirements between males and females (Schoener 1971), predation risk, social structure, and the availability and distribution of food resources (Kinnaird and O'Brien. 2000). This inherent plasticity of primates may explain the fact that when we used phylogeny as a random effect, our model better explained the variation of the data. Some authors have linked the impacts of habitat loss and fragmentation on the activity budget of primates (Mekonnen et al. 2017). Two distinct strategies are described as sources of variation in the activity budgets in primates. Some primates persist in forest fragments by adopting an energy maximizing strategy, spending more time feeding and less time resting (e.g., *Ateles geoffroyi*: Chaves et al. 2011) than conspecifics in continuous forest. In other way, many others primates use an energy minimizing strategy, spending less time feeding, more time resting and less time traveling, e.g., *Alouatta seniculus* (Palma et al. 2011), *Colobus vellerosus* (Wong & Sicotte, 2007), and Bale Monkey (*Chlorocebus djamdjamensis*: Mekonnen et al. 2017) than their counterparts in continuous forest. The apparent energy conservation strategy of Bale monkeys in fragments may be a response to the lower overall food availability at these sites (Mekonnen et al. 2017), similar strategy to cope with the limited abundance, density and quality of food resources in fragments adopt by other folivores, like *Colobus vellerosus* and *Alouatta seniculus* (Palma et al., 2011). The local temperature may play an important role in variation on activity budgets of primates in fragments, because ambient temperatures are often higher there than in nearby continuous forests (Korstjens et al. 2010; Silva and Ferrari, 2009).

Pavelka and Knopff (2004) suggest that diet is usually much more flexible and varied than behavior patterns in howler monkeys (*Allouata* spp.), whereas the activity levels may be more phylogenetically constrained, because the howler monkey (*Allouata pigra*) maintained an inactive lifestyle even during high fruit availability and consumption. Similarly, the ecological plasticity found in bale monkeys (*Chlorocebus* sp.) in fragments (Mekonnen et al. 2017) can be partly attributed to phylogenetic inheritance of ancestral or a recent history of hybridization with other *Chlorocebus* taxa. The ecological plasticity found in many primate lineages may influence changes in energy-savings strategies and consequently in resting activity.

The review of arboreal mammals feeding on leaves and which species depend mostly on this resource may help us to develop strategies to preserve biodiversity of this guild. I showed that resting time is associated with folivore specialization in arboreal mammals, which may influence energy budgets, daily behavior and activity, and ultimately setting biogeographical distribution constraits (Korstjens et al., 2010). Thus, the energy constraints by niche specialization on leaves, and others factors like habitat fragmentation, group size, temperature and phylogeny, may result in arboreal folivores populations being more at risk of extinction, especially in primates.

The realization of studies that clarify the impact of these factors on the conservation of arboreal mammals is firstly to identify to what degree these species depend on the foliar resource and the gaps that still exist, which enrich the update made in this review.

References

BATES, D., M. MÄCHLER, B. M. BOLKER AND S. C. WALKER. 2014. Fitting linear mixed-effects models using lme4. arXiv:1406.5823v1[stat.CO]23:1–51.

BOLKER, B. M. ET AL. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

BOONRATANA, R. 2003. Feeding Ecology of Proboscis Monkeys (Nasalis larvatus) in the Lower Kinabatangan, Sabah, Malaysia. Sabah Parks Nature Journal 6:1–26.

BRISCOE, N. J., K. A. HANDASYDE, S. R. GRIFFITHS, W. P. PORTER, A. KROCKENBERGER AND M. R. KEARNEY. 2014. Tree-hugging koalas demonstrate a novel thermoregulatory mechanism for arboreal mammals. Biology letters 10:39–45.

CASELLI, C. B. AND E. Z. F. SETZ. 2011. Feeding ecology and activity pattern of black-fronted titi monkeys (Callicebus nigrifrons) in a semideciduous tropical forest of southern Brazil. Primates 52:351–359.

CHAVES, Ó. M., K. E. STONER, V. ARROYO-RODRÍGUEZ AND A. ESTRADA. 2011. Effectiveness of Spider Monkeys (Ateles geoffroyi vellerosus) as Seed Dispersers in Continuous and Fragmented Rain Forests in Southern Mexico. International Journal of Primatology 32:177–192.

CORK, S. J. AND W. J. FOLEY. 1991. Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. Pp. 133–166inPlant defenses against mammalian herbivory(C. T. Palo, R.T. & Robbins, ed.). CRC Press, Boca Raton, Florida.

DIAS, P. A. D. AND A. RANGEL-NEGRÍN. 2015. Diets of Howler Monkeys. Pp. 383–409inHowler Monkeys: Behavior, Ecology, and Conservation.

DJÈGO-DJOSSOU, S., I. KONÉ, A. FANDOHAN, J. DJÈGO, M. HUYNEN AND B. SINSIN. 2015. Habitat use by white-thighed colobus in the Kikélé sacred forest: activity budget , feeding ecology and selection of sleeping trees. Primate Conservation 29:97–105.

DUNBAR, R. I. M. 1996. Determinants of group size in primates: a general model. Proceedings of the British Academy 88:33–57.

EISENBERG, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. P. 135 – 152. in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

FREELAND, W. J., P. H. CALCOTT AND L. R. ANDERSON. 1985. Tannins and saponin: Interaction in herbivore diets. Biochemical Systematics and Ecology 13:189–193.

FREELAND, W. J. AND D. H. JANSEN. 1974. Strategies in Herbivory by Mammals: The Role of Plant Secondary Compounds. The American Naturalist 108:269–289.

GINÉ, G. A. F., J. DUARTE, T. MOTTA AND D. FARIA. 2012. Activity, movement and secretive behavior of a threatened arboreal folivore, the thin-spined porcupine , in the Atlantic forest of southern Bahia, Brazil. Journal of Zoology 286:131–139.

GINÉ, G. A. F., C. RIGHETTO, S. S. DE ALMEIDA AND D. FARIA. 2015. Activity budget , pattern and rhythm of maned sloths (Bradypus torquatus): Responses to variations in ambient temperature. Mammalian Biology 80:459–467.

GLANDER, K. E. 1982. The impact of plant secondary compounds on primate feeding behavior. American Journal of Physical Anthropology 25:1–18.

HERBERS, J. M. . 1981. Time Resources and Laziness in Animals. Ecology 49:252–262.

IRWIN, M. T. 2008. Feeding ecology of Propithecus diadema in forest fragments and continuous forest. International Journal of Primatology 29:95–115.

JONES, K. E. ET AL. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:09–2648.

KINNAIRD, M. F. AND T. G. O'BRIEN. 2000. Comparative movement patterns of two semi- terrestrial cercopithecine primates: the Tana River crested mangabey and the Sulawesi crested black macaque. Pp. 327–350inOn the Move: How and Why Animals Travel in Groups(S. Boinski and P. A. Garber, ed.). University of Chicago Press, Chicago.

KISSLING, W. D. ET AL. 2014. Establishing macroecological trait datasets: digitalization, extrapolation, and validation of diet preferences in terrestrial mammals worldwide. Ecology and Evolution 4:2913–2930.

KORSTJENS, A. H., J. LEHMANN AND R. I. M. DUNBAR. 2010. Resting time as an ecological constraint on primate biogeography. Animal Behaviour 79:361–374.

KRONFELD-SCHOR, N. AND T. DAYAN. 2003. Partitioning of Time as an Ecológical Resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181.

MCNAB, B. K. 1986. The Influence of Food Habits on the Energetics of Eutherian Mammals. Ecological Monographs 56:1–19.

MCNAB, B. K. 1978. Ecological consequences of feeding on an ubiquitous food supply. Pp. 153–162inThe Ecology of Arboreal Folivores(G. G. Montgomery, ed.). Washington, DC.

MEKONNEN, A. ET AL. 2017. Impacts of habitat loss and fragmentation on the activity budget, ranging ecology and habitat use of Bale monkeys (Chlorocebus djamdjamensis) in the southern Ethiopian Highlands. American Journal of Primatology:22644.

MILTON, K. 1998. Physiological ecology of Howlers (Alouatta): energeic and digestive considerations and comparison with the Colobinae. Internacional Journal of Primatology 19:513–547.

NAKAGAWA, S. AND H. SCHIELZETH. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

PALMA, A. C., A. VÉLEZ, C. GÓMEZ-POSADA, H. LÓPEZ, D. A. ZÁRATE AND P. R. STEVENSON. 2011. Use of space, activity patterns, and foraging behavior of red howler monkeys (Alouatta seniculus) in an Andean forest fragment in Colombia. American Journal of Primatology 73:1062–1071.

PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pp. 205–230inThe ecology of arboreal folivores(G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

PAULI, J. N., M. Z. PEERY, E. D. FOUNTAIN AND W. H. KARASOV. 2016. Arboreal Folivores Limit Their Energetic Output , All the Way to Slothfulness. The American Naturalist 188.

PAVELKA, M. S. M. AND K. H. KNOPFF. 2004. Diet and activity in black howler monkeys (Alouatta pigra) in southern Belize: does degree of frugivory influence activity level? Primates; journal of primatology 45:105–11.

R CORE TEAM. 2015. R: a language and environment for statistical computing. Version 3.2.3. *R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.* .

RYAN, M. A., D. A. WHISSON, G. J. HOLLAND AND J. P. Y. ARNOULD. 2013. Activity patterns of free-ranging koalas (Phascolarctos cinereus) revealed by accelerometry. PLoS ONE 8:1–10.

SCHOENER, T. W. 1971. Theory of feeding strategies. Annual reviews.

SILVA, S. S. B. AND S. F. FERRARI. 2009. Behavior patterns of southern bearded sakis (Chiropotes satanas) in the fragmented landscape of eastern Brazilian Amazonia. American Journal of Primatology 71:1–7.

SORENSEN, J. S., J. D. MCLISTER AND M. D. DEARING. 2005. Plant Secondary Metabolites Compromise the Energy Budgets of Specialist and Generalist Mammalian Herbivores. Ecology 86:125–139.

TEICHROEB, J. A, T. L. SAJ, J. D. PATERSON AND P. SICOTTE. 2003. Effect of group size on activity budgets in ursine colobus (Colobus vellerosus) in Ghana. International Journal of Primatology 24:743–758.

URBANI, B. AND C. BOSQUE. 2007. Feeding ecology and postural behaviour of the three-toed sloth (Bradypus variegatus flaccidus) in northern Venezuela. Mammalian Biology - Zeitschrift für Säugetierkunde 72:321–329.

WILMAN, H., J. BELMAKER, S. JENNIFER, C. DE LA ROSA, M. M. RIVADENEIRA AND W. JETZ. 2014. EltonTraits 1 . 0: Species-level foraging attributes of the world ' s birds and mammals. Ecology 95:2027.

WILSON, D. . AND D. M. REEDER. 2005. Mammal Species of the World: A Taxonomic and Geographic Reference. P. in Baltimore, Maryland. John Hopkins University Press, Baltimore, Maryland, USA.

APPENDIX A

Table 1. List of the 386 species of arboreal mammals that are known to be folivorous. The classification is s based on a quantitative database or qualitative classification present in the current literature. Quantitative data on daily time spent resting and the percentage of leaves in the diet are shown when available in the literature.

Order	Family	Genus	Species	Rest	Leaf	Source
Dermoptera	Cynocephalidae	*Cynocephalus*	*volans*	84	100.0	Wischusen & Richmond (1998)
Dermoptera	Cynocephalidae	*Galeopterus*	*variegatus*	69.05	85.2	Byrnes et al., 2011;Dzulhelmi & Abdullah, 2009
Diprotodontia	Macropodidae	*Dendrolagus*	*lumholtzi*	61	98.7	Proctor-Gray & Ganslosser (1986); Proctor-Gray (1984)
Diprotodontia	Phalangeridae	*Ailurops*	*ursinus*	63	85.1	Dwiyahreni, et al., 1999
Diprotodontia	Phascolarctidae	*Phascolarctos*	*cinereus*	82.7	100.0	Nagy & Martin 1985; Mitchell, 1990; Moore et al. 2004
Diprotodontia	Pseudocheiridae	*Petauroides*	*volans*	40.4	40.7	Comport et al.,1996;Kavanagh and Lambert (1990)
Hyracoidea	Procaviidae	*Dendrohyrax*	*arboreus*	84	100.0	Milner and Harris 1999
Pilosa	Bradypodidae	*Bradypus*	*torquatus*	78.75	99.2	Chiarello 1998a; Chiarello 1998b; Giné et al. (2015)
Pilosa	Bradypodidae	*Bradypus*	*variegatus*	76.9	96.9	Queiroz, 1985; Urbani and Bosque 2007;Consentino 2004
Primates	Atelidae	*Alouatta*	*belzebul*	51.15	38.1	Citations in Korstjens et al. 2010 and Dias & Rangel-Negrín, 2015
Primates	Atelidae	*Alouatta*	*caraya*	56.5	64.6	Citations in Korstjens et al. 2010 and Dias & Rangel-Negrín, 2015
Primates	Atelidae	*Alouatta*	*guariba*	67.1	66.3	Citations in Dias & Rangel-Negrín, 2015; Mendes, 1989; Chiarello 1993; De Marques [1996]
Primates	Atelidae	*Alouatta*	*palliata*	66.8	55.5	Citations in Dias & Rangel-Negrín, 2015 and Mckinney, 2010
Primates	Atelidae	*Alouatta*	*pigra*	63.4	50.4	Citations in Dias & Rangel-Negrín, 2015; Silver et al. [1998]
Primates	Atelidae	*Alouatta*	*seniculus*	70	57.3	Citations in Dias & Rangel-Negrín, 2015
Primates	Atelidae	*Ateles*	*belzebuth*	43.9	8.7	Klein & Klein (1977); Nunes (1992); Nunes(1995);Castellanos (1995); Dew, 2005

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Atelidae	*Ateles*	*chamek*	45.25	10.7	Citations in Korstjens et al. 2006; Wallace, 2001; McFarland Symington (1988b)
Primates	Atelidae	*Ateles*	*geoffroyi*	46.57	17.03	Citations in Korstjens et al. 2006
Primates	Atelidae	*Ateles*	*paniscus*	45	16	Citations in Korstjens et al. 2006
Primates	Atelidae	*Brachyteles*	*arachnoides*	55.17	59.0	Citations in Korstjens et al. 2010
Primates	Atelidae	*Lagothrix*	*lagotricha*	29.9	11.4	Citations in Korstjens et al. 2010; Lemos de Sá (1988);Strier (1991); Rímoli and Ades (1997)
Primates	Atelidae	*Lagothrix*	*lugens*	36	16	Citations in Korstjens et al. 2010
Primates	Atelidae	*Lagothrix*	*poeppigii*	23.2	7.5	Citations in Korstjens et al. 2010
Primates	Cebidae	*Cebus*	*capucinus*	17.57	8.2	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercocebus*	*galeritus*	14	13.5	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercophitecus*	*ascanius*	25.8	11.7	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercophitecus*	*campbelli*	18	8.4	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercophitecus*	*diana*	24.4	15.8	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercophitecus*	*lhoesti*	19.4	35.2	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercophitecus*	*mitis*	30.76	19.1	Citations in Korstjens et al. 2010
Primates	Cercophitecidae	*Cercophitecus*	*petaurista*	23.8	39.7	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Colobus*	*angolensis*	37.81	65.0	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Colobus*	*guereza*	64	60.9	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Colobus*	*polykomos*	58.13	52.8	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Colobus*	*satanas*	54.19	43.1	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Colobus*	*vellerosus*	59.1	74.0	Citations in Korstjens & Dunbar 2007
Primates	Cercophitecidae	*Lophocebus*	*albigena*	25.5	5.3	Citations in Korstjens et al. 2010
Primates	Cercopithecidae	*Piliocolobus*	*badius*	42.45	50.8	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Piliocolobus*	*rufomitratus*	48.5	59.4	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Piliocolobus*	*temminckii*	52.1	46.9	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Piliocolobus*	*tephrosceles*	41.89	79.14	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Presbytis*	*comata*	63	65.0	Stanford 1991; Citations in Kamilar & Paciulli, 2008

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Cercopithecidae	*Presbytis*	*melalophos*	36	37.0	Citations in Korstjens & Dunbar 2010
Primates	Cercopithecidae	*Presbytis*	*potenziani*	45.7	34.6	Hadi et al., 2012; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Presbytis*	*rubicunda*	48	37.0	Ehlers et al., 2013; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Presbytis*	*thomasi*	40	48.0	Stanford 1991; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Procolobus*	*verus*	49.23	84.63	Citations in Korstjens & Dunbar 2007
Primates	Cercopithecidae	*Pygathrix*	*cinerea*	37.1	49.0	Longer et al., 2010; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Pygathrix*	*nemaeus*	35.3	82.0	Ulibarri, 2013; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Rhinopithecus*	*avunculus*	31.9	38.0	Dong Thanh Hai, 2008; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Rhinopithecus*	*bieti*	33	31.0	Ding & Zhao, 2004; Citations in Korstjens et al. 2010
Primates	Cercopithecidae	*Simias*	*concolor*	49.8	57.5	Hadi et al., 2012
Primates	Cercopithecidae	*Trachypithecus*	*auratus*	-	48.5	Palmieri et al. (1984) apud Li and Roger (2006); Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Trachypithecus*	*francoisi*	52	53.0	Zhou et al 2007; Citations in Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Trachypithecus*	*johnii*	39.36	57.3	Citations in Korstjens et al. 2010
Primates	Cercopithecidae	*Trachypithecus*	*obscurus*	43	48.0	Citations in Korstjens et al. 2010
Primates	Cercopithecidae	*Trachypithecus*	*phayrei*	21.15	48.5	Citations in Korstjens et al. 2010
Primates	Cercopithecidae	*Trachypithecus*	*pileatus*	40	53	Citations in Korstjens et al. 2010
Primates	Cercopithecidae	*Trachypithecus*	*poliocephalus*	50	87.9	Li and Roger 2006; Li et al. 2003
Primates	Hylobatidae	*Hoolock*	*hoolock*	29.27	8.8	Citations in Korstjens et al. 2010
Primates	Hylobatidae	*Hylobates*	*agilis*	29	39.0	Citations in Korstjens et al. 2010
Primates	Hylobatidae	*Hylobates*	*klossi*	54	2.0	Citations in Korstjens et al. 2010
Primates	Hylobatidae	*Hylobates*	*lar*	31.79	16.5	Citations in Korstjens et al. 2010
Primates	Hylobatidae	*Hylobates*	*pileatus*	39	13.0	Citations in Korstjens et al. 2010
Primates	Hylobatidae	*Symphalangus*	*syndactylus*	34	39.3	Citations in Korstjens et al. 2010
Primates	Indriidae	*Avahi*	*laniger*	70.88	100.0	Faulkner and Lehman 2006; Harcourt 1991; Faulkner and Lehman 2006
Primates	Indriidae	*Avahi*	*meridionalis*	67	95.0	Norscia et al., 2012
Primates	Indriidae	*Indri*	*indri*	44.9	76.5	Britt et al. (2002); Gouldberg, 1990; Powzyk and Mowry 2003

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Indriidae	*Propithecus*	*coronatus*	48.3	58.5	Pichon, 2010
Primates	Indriidae	*Propithecus*	*diadema*	43.68	28.7	Citations in Korstjens et al. 2010
Primates	Lemuridae	*Eulemur*	*fulvus*	51.36	54.9	Citations in Korstjens et al. 2010
Primates	Lemuridae	*Eulemur*	*rubriventer*	53.89	13.6	Citations in Korstjens et al. 2010
Primates	Pitheciidae	*Callicebus*	*nigrifrons*	30	16	Caseli & Setz, 2011
Primates	Pitheciidae	*Callicebus*	*personatus*	56	18	Kinzey & Beck, 1983
Rodentia	Erethizontidae	*Chaetomys*	*subspinosus*	74	92.7	Giné et al. 2012; Giné et al. 2010; Souto Lima et al. 2010
Rodentia	Erethizontidae	*Coendou*	*prehensilis*	40	41.0	Santos Júnior, 1998
Rodentia	Sciuridae	*Petaurista*	*philippensis*	45.85	38.4	Koli & Bhatnagar, 2016; Shafique et al 2006; Kuo and Lee (2003); Koli, Bhatnagar and Sharma (2013); Lee et al. (1986)
Rodentia	Sciuridae	*Ratufa*	*macroura*	31.70	38.0	Rao et al., 2015
Rodentia	Sciuridae	*Aeromys*	*tephromelas*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Ailurops*	*melanotis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cheirogaleidae	*Allocebus*	*trichotis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*nigerrima*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*sara*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*arctoidea*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*discolor*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*juara*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*puruensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*ululata*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Anomaluridae	*Anomalurus*	*beecrofti*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Anomaluridae	*Anomalurus*	*derbianus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Anomaluridae	*Anomalurus*	*pelii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Anomaluridae	*Anomalurus*	*pusillus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*azarae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*brumbacki*	-	-	Kissling et al. (2014); Wilman te al. (2014)

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Primates	Aotidae	*Aotus*	*griseimembra*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*jorgehernandezi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*lemurinus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*miconax*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*nancymaae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*nigriceps*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*trivirgatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*vociferans*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Aotidae	*Aotus*	*zonalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Ateles*	*fusciceps*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Ateles*	*hybridus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Ateles*	*marginatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*betsileo*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*cleesei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*laniger*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*meridionalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*occidentalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*peyrierasi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*ramanantsoavanai*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Avahi*	*unicolor*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Pilosa	Bradypodidae	*Bradypus*	*pygmaeus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Cacajao*	*ayresi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Cacajao*	*hosomi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Cacajao*	*melanocephalus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*aureipalatii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*baptista*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*barbarabrownae*	-	-	Kissling et al. (2014); Wilman te al. (2014)

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Primates	Pitheciidae	*Callicebus*	*bernhardi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*brunneus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*caligatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*cinerascens*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*coimbrai*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*cupreus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*discolor*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*donacophilus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*dubius*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*hoffmannsi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*lucifer*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*lugens*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*medemi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*melanochir*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*modestus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*moloch*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*ornatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*pallescens*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*purinus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Callicebus*	*regulus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*apella*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*kaapori*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*libidinosus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*macrocephalus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*nigritus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*olivaceus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cebidae	*Cebus*	*robustus*	-	-	Kissling et al. (2014); Wilman te al. (2014)

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Primates	Cebidae	*Cebus*	*xanthosternos*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercocebus*	*sanjei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*cephus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*dryas*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*erythrogaster*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*erythrotis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*hamlyni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*mona*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*neglectus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*nictitans*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*pogonias*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*preussi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*sclateri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercophitecidae	*Cercophitecus*	*solatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Chiruromys*	*forbesi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Chiruromys*	*lamia*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Chiruromys*	*vates*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Pilosa	Megalonychidae	*Choloepus*	*hoffmanni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*bicolor*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*ichillus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*insidiosus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*melanurus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*mexicanus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*roosmalenorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*spinosus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Erethizonthidae	*Coendou*	*vestitus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Conilurus*	*penicillatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)

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Rodentia	Echimyidae	*Dactylomys*	*peruanus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Petauridae	*Dactylopsila*	*megalura*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Petauridae	*Dactylopsila*	*tatei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Hyracoidea	Procaviidae	*Dendrohyrax*	*dorsalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Hyracoidea	Procaviidae	*Dendrohyrax*	*validus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*bennettianus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*dorianus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*goodfellowi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*inustus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*matschiei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*mayri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*mbaiso*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*notatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*pulcherrimus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*scottae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*spadix*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*stellarum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Macropodidae	*Dendrolagus*	*ursinus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Echimys*	*chrysurus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Echimys*	*saturnus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Echimys*	*vieirai*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Eoglaucomys*	*fimbriatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Eulemur*	*albifrons*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Eulemur*	*cinereiceps*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Eulemur*	*macaco*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Eulemur*	*mongoz*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Eulemur*	*rufifrons*	-	-	Kissling et al. (2014); Wilman te al. (2014)

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Primates	Lemuridae	*Eulemur*	*rufus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Eulemur*	*sanfordi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Hapalemur*	*alaotrensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Hapalemur*	*aureus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Hapalemur*	*griseus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Hapalemur*	*meridionalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Hapalemur*	*occidentalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Hapalomys*	*longicaudatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Hoolock*	*leuconedys*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Hylobates*	*albibarbis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Hylobates*	*muelleri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*alboniger*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*bartelsi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*lepidus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*nigripes*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*platyurus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*sipora*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*spadiceus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Hylopetes*	*winstoni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Kannabateomys*	*amblyonyx*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Lagothrix*	*cana*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*aeeclis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*ahmansonorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*ankaranensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*betsileo*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*dorsalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*fleuretae*	-	-	Kissling et al. (2014); Wilman te al. (2014)

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Lepilemuridae	*Lepilemur*	*grewcockorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*hubbardorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*jamesorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*leucopus*	50	-	Nash, 1998
Primates	Lepilemuridae	*Lepilemur*	*microdon*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*milanoii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*mittermeieri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*mustelinus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*otto*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*petteri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*randrianasoloi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*ruficaudatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*sahamalazensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*seali*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*septentrionalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*tymerlachsonorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lepilemuridae	*Lepilemur*	*wrightae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Lonchothrix*	*emiliae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Mallomys*	*rothschildi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Mesembriomys*	*macrurus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Mesomys*	*hispidus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Mesomys*	*leniceps*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Mesomys*	*occultus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Mesomys*	*stimulax*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Capromyidae	*Mysateles*	*prehensilis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Nomascus*	*concolor*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Nomascus*	*gabriellae*	-	-	Kissling et al. (2014); Wilman te al. (2014)

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Hylobatidae	*Nomascus*	*leucogenys*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Nomascus*	*nasutus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hylobatidae	*Nomascus*	*siki*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Olallamys*	*albicauda*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Echimyidae	*Olallamys*	*edax*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Oreonax*	*flavicauda*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petaurista*	*elegans*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petaurista*	*magnificus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petaurista*	*nobilis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petaurista*	*xanthotis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*crinitus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*fuscocapillus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*genibarbis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*hageni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*lugens*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*mindanensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*sagitta*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*setosus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Petinomys*	*vordermanni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Petropseudes*	*dahli*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*alexandrae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*carmelitae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*intercastellanus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*matabiru*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*matanim*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*mimicus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*orientalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)

Order	Family	Genus	Species	Rest	Leaf	Source
Diprotodontia	Phalangeridae	*Phalanger*	*ornatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*rothschildi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*sericeus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Phalanger*	*vestitus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phascolarctidae	*Phascolarctos*	*cinereus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Pithecia*	*aequatorialis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Pithecia*	*albicans*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Pithecia*	*irrorata*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Pithecia*	*monachus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Pitheciidae	*Pithecia*	*pithecia*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Pogonomys*	*championi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Pogonomys*	*fergussoniensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Pogonomys*	*loriae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Pogonomys*	*macrourus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Pogonomys*	*sylvestris*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hominidae	*Pongo*	*abelii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Hominidae	*Pongo*	*pygmaeus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*chrysomelas*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*comata*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*femoralis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*frontata*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*hosei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*natunae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Presbytis*	*siamensis*	-	36	see Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Procolobus*	*badius*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Procolobus*	*gordonorum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Procolobus*	*kirkii*	-	-	Kissling et al. (2014); Wilman te al. (2014)

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Cercopithecidae	*Procolobus*	*pennantii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Procolobus*	*preussi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Lemuridae	*Prolemur*	*simus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*candidus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*coquereli*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*deckenii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*edwardsi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*perrieri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*tattersalli*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Indriidae	*Propithecus*	*verreauxi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudocheirus*	*occidentalis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudocheirus*	*peregrinus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirops*	*albertisii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirops*	*corinnae*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirops*	*coronatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirops*	*cupreus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*canescens*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*caroli*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*cinereus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*forbesi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*larvatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*mayeri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*schlegeli*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Pygathrix*	*nigripes*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Ratufa*	*affinis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Ratufa*	*bicolor*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Rhinopithecus*	*brelichi*	-	-	Kissling et al. (2014); Wilman te al. (2014)

Order	Family	Genus	Species	Rest	Leaf	Source
Primates	Cercopithecidae	*Rhinopithecus*	*roxellana*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Callitrichidae	*Saguinus*	*imperator*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Sciurus*	*colliaei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Sciurus*	*deppei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Spilocuscus*	*kraemeri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Spilocuscus*	*maculatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Spilocuscus*	*papuensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Spilocuscus*	*rufoniger*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Spilocuscus*	*wilsoni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Syntheosciurus*	*brochus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Tamiasciurus*	*douglasii*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Thamnomys*	*kempi*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Thamnomys*	*schoutedeni*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Muridae	*Thamnomys*	*venustus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*auratus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*barbei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*cristatus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*delacouri*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*geei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*germaini*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*hatinhensis*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*laotum*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*shortridgei*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Cercopithecidae	*Trachypithecus*	*vetulus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Trichosurus*	*caninus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Trichosurus*	*cunninghami*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Rodentia	Sciuridae	*Trogopterus*	*xanthipes*	-	-	Kissling et al. (2014); Wilman te al. (2014)

Order	Family	Genus	Species	Rest	Leaf	Source
Rodentia	Platacanthomyidae	*Typhlomys*	*cinereus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Diprotodontia	Phalangeridae	*Wyulda*	*squamicaudata*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Pilosa	Megalonychidae	*Choloepus*	*didactylus*	-	-	Kissling et al. (2014); Wilman te al. (2014)
Primates	Atelidae	*Alouatta*	*macconnelli*	-	50.2	Citations in Dias & Rangel-Negrín, 2015
Primates	Indriidae	*Avahi*	*occidentalis*	-	77	Thalman 2001
Primates	Atelidae	*Brachyteles*	*hypoxanthus*	-	54	Lemos de Sá (1988);Strier (1991);Rímoli and Ades (1997)
Pilosa	Bradypodidae	*Bradypus*	*tridactylus*	-	97.2	Carmo, 2002 (Dissertation)
Rodentia	Sciuridae	*Eoglaucomys*	*fimbriatus*	-	2.3	Shafique et al 2006
Diprotodontia	Pseudocheiridae	*Hemibelideus*	*lemuroides*	-	94	Gouldberg, 1990
Primates	Lepilemuridae	*Lepilemur*	*edwardsi*	-	74.4	Thalman 2001
Rodentia	Sciuridae	*Petaurista*	*alborufus*	-	71	Lee et al., 1986
Rodentia	Sciuridae	*Petaurista*	*leucogenys*	-	38	Ando and Imaizumi (1982); Kawamichi 1997
Rodentia	Sciuridae	*Petaurista*	*petaurista*	-	20.6	Shafique et al 2006
Primates	Cercopithecidae	*Presbytis*	*femoralis*	-	29	see Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Presbytis*	*hosei*	-	69	see Kamilar & Paciulli, 2008
Primates	Cercopithecidae	*Piliocolobus*	*kirkii*	-	65	Bonvicino et al., 2008
Primates	Cercopithecidae	*Piliocolobus*	*pennantii*	-	66	Bonvicino et al., 2008
Primates	Cercopithecidae	*Piliocolobus*	*preussi*	-	89	Bonvicino et al., 2008
Diprotodontia	Pseudocheiridae	*Pseudochirops*	*archeri*	-	90.9	Gouldberg, 1990; Jones, Maclagan, Krockenberger, 2007
Diprotodontia	Pseudocheiridae	*Pseudochirulus*	*herbertensis*	-	87.7	Gouldberg, 1990
Primates	Cercopithecidae	*Rhinopithecus*	*brelichi*	-	71	see Kamilar & Paciulli, 2008
Diprotodontia	Phalangeridae	*Trichosurus*	*vulpecula*	-	66	Fitzgerald, 1978

Capítulo 2: Factors influencing dietary diversity and composition of an arboreal mammalian folivore: the thin-spined porcupine in the fragmented Brazilian Atlantic forest.

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Abstract

Diet selection in browsing mammals involves a delicate balance between the energetic and nutritional intake and the negative effects triggered by plant secondary metabolites – PSMs. Despite the potential implications of this trade-off on food selection of wild animals, and thus its ecology, this information is still scarce for most species. This is the case for the thin-spined porcupine (*Chaetomys subspinosus*), arboreal mammal rodent strictly folivorous and highly selective in its diet, wich concentrates its feeding on a small subset of the total species available within its home range in Atlantic Forest. The feeding ecology of this species is not fully known since few animals (< 8 animals) were studied, always in small forest fragments. Herein we assessed the diet composition of 19 individuals of this target species and compared the richness, diversity, and similarity of diet of the animals living in small (< 200 ha) and large (> 500 ha) forest fragments. We also tested whether the levels of phenolics compounds, protein, and fiber content of the leaves affected the frequency of consumption of leaves by this porcupine. Our result indicates that a richer diet in radio-tracked porcupines from large forest fragments compared with those individuals located in small forest fragments. The few plant species that are present in the diet of the animals living in both fragment size categories were also some of the most frequently consumed species in both situations. (*A. pedicellaris*, *P. glabrata*, *H. balsamifera* and *I. affinis*), confirming the high selectivity of the target specie. The condensed tannins (0.10 ± 0.007, $p = 0.004$), total phenolics (-0.04 ± 0.009, $p = 0.045$), and acid detergent fiber (0.05 ± 0.004, $p = 0.007$) were good predictors of frequency of consumption of plant species.

Keywords: Folivory; Feeding ecology; Diet, Porcupine; Plant secondary metabolites; Nutrients; Fragmentation; Tropical rainforest.

Introduction

The energy intake for mammalian arboreal folivores is limited mainly by the low content of the non-structured carbohydrates on the leaves consumed as well as the low protein content, physical plant defenses (e.g. cellulose and thorns), and plant secondary metabolites, these latter traits acting as digestibility or intake reducers (Dearing et al., 2005; Laca et al. 2001; Dziba and Provenza 2008). All folivores to some degree must be able to cope physiologically and behaviorally with such toxic or feeding deterrents that reduce the palatability of plants, or as digestibility-reducers that decrease nutrient intake (Iason 2005). Therefore, diet selection in browsing mammals involves a delicate balance between the energy and nutrients intake and the negative effects of plant secondary metabolites - PSMs (Guglielmo et al., 1996; Sorensen et al., 2005; Villalba and Provenza, 2005; Iason and Villalba, 2006; Mote et al., 2007; Ulappa et al., 2014). Nevertheless, for most folivorous species we have no quantitative data demonstrating the existence of this trade-off between the acquisition of nutrients and the avoidance of toxin as an important driver on food selection in the wild (Jensen et al. 2015).

The thin-spined porcupine (*Chaetomys subspinosus* Olfers 1818) is a small and threatened arboreal rodent (Erethizontidae; Vilela et al., 2009) endemic to the Atlantic forest biome, currently highly fragmented (Ribeiro et al. 2009). This species is currently recognized as vulnerable to extinction (Catzeflis et al. 2008) and a great effort has been made for gather basic information of its ecology, including home range and habitat selection (Giné et al., 2015; Oliveira et al., 2012), activity patterns (Giné et al. 2012), and feeding ecology (Giné et al., 2010; Souto Lima et al., 2010), as well as genetic and sanitary aspects of the their populations (Oliveira et al., 2011; Bezerra et al., 2015a, 2015b).

This small arboreal mammal (1.25-1.75 kg - Oliver and Santos, 1991) has a highly selective folivorous diet, concentrating its feeding on a small subset of the total species available within its home range, showing preference for species from the Fabaceae family (Giné et al., 2010). However, until nowadays few animals were studied, and all of them were monitored in small and disturbed forest fragments (4 individuals in 0.7 - 18 ha south BA – Giné et al. 2010; and other 3 within the limits of the Paulo César Vinha State Park, ES – de Souto Lima et al., 2010). The small samples obtained so far do not allow us to answer two important questions regarding diet selection. First, it is unclear whether the species selective diet reported is a result of an acclimation to relatively poor floristic composition of the assessed small forest patches. In addition, despite the high protein content of leaves consumed, nutritional traits alone were unable to explain the preference for the most-consumed species. It is possible that other features not addressed by Giné et al. (2010) may drive food selection of this species, such as the presence, composition, and feeding constraints (i.e., PSMs).

To provide data in this direction herein we monitored a larger number of individuals in the wild, aiming to compare the richness, diversity, and similarity of diet for animals living in two categories of forest patches sizes: small (< 200 ha) and large (> 500) forest fragments. We predicted that the diet richness and diversity will be lower in smaller forests patches, because it is expected the establishment of edge-affected habitats in small ones that leads to tree species impoverishment and homogenization via the dominance and proliferation of shade-intolerant tree species (Tabarelli et al., 2004; Laurance et al., 2006; Michalski et al., 2007; Santos et al., 2008; Lôbo et al., 2011; Thier and Wesenberg, 2016) as well as by species-area relation (Benchimol and Peres 2015). At food item level, we check whether the animals remain strictly folivore in large fragments, assuming that in these areas the availability of other items (such as fruit) is greater.

In addition, we also investigated whether levels of phenolics compounds, protein, and fiber content of the leaves affect food consumption of the target species, since the previous study found no relation between food selection and primary nutritional compounds (Giné et al. 2010). Our hypothesis is that in response to phytochemical challenges, the thin-spined porcupine may selectively forage on plants with higher crude protein content and lower PSMs concentrations relative to other plants. Finally, considering that this species prefer Fabaceae species (Giné et al. 2010), we also investigate whether the consumed leaves from Fabaceae species have higher concentrations of secondary metabolites and total protein content relative to other plants consumed by these animals. Due to its ability to fix nitrogen, it increases its availability, being able to be allocated for the production of secondary defense metabolites, also reflecting high levels of protein in the leaves (Roggy and Prévost 1999), their growth rates substitution, and leaf biomasses (Kursar and Coley 2003), factors that may be influencing the frequency of leaf´s species consumed by the thin-spined porcupine.

Methods

Study Area

We conducted the study in the Atlantic Forest of southern Bahia (38°90′–39°32′W and 14°29′–15°23′S), eastern Brazil. The local annual average temperature is 24–25°C, and the annual rainfall averages 2.000 mm/year (Mori et al, 1983). The landscape is variegated, still retaining a relatively large amount of rainforest composed of a mosaic that includes mature vegetation, secondary and shaded cocoa plantations. The bulk of the remaining forest is located along the poor sandy coastal soils, where are evergreen forests classified as a Tropical Lowland Rainforest (Thomas et al. 1998). The region still maintains large fragments with high forest cover in protected areas such as Una Biological Reserve (REBio-Una) and Serra do Conduru State Park (CFSP), but as it moves away north or south from these regions the fragments become smaller and with lower forest cover (Fig. 1).

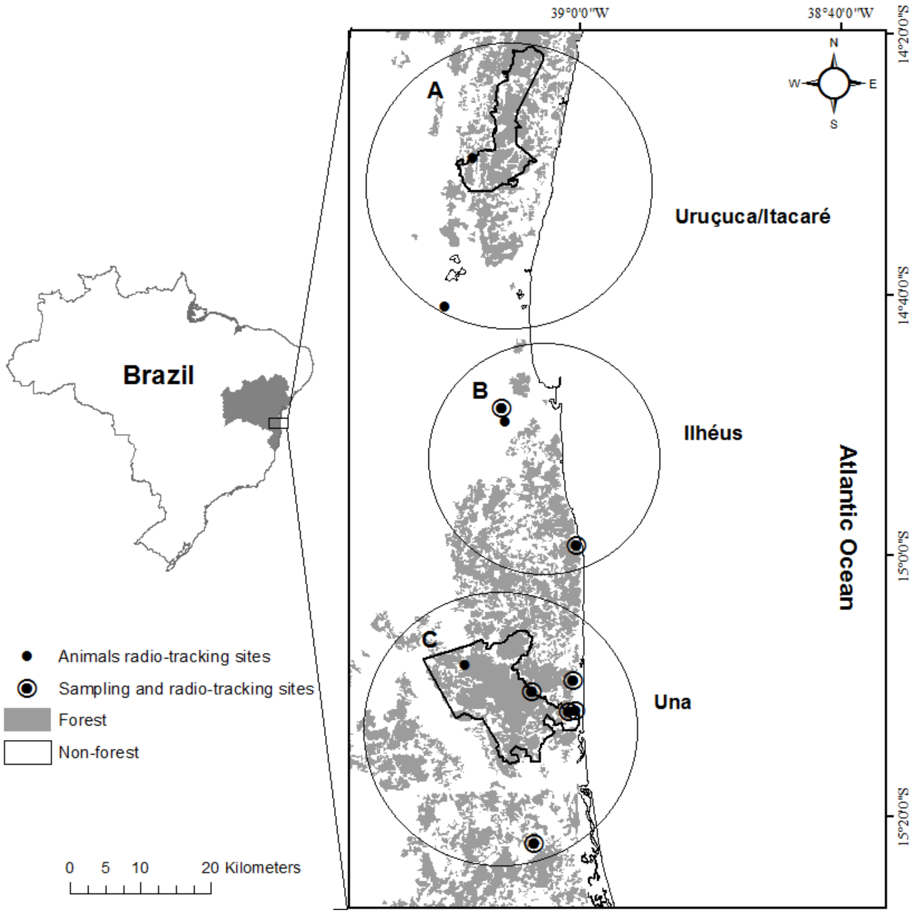

Fig. 1. Map of the study area in southern Bahia, northeastern Brazil showing forest remnants, localities for exclusively radio-tracking thin-spined porcupines (black dots) and localities both for leaves sampling and radio-tracking animals (circles with black dots). The study area can be divided into three distinct regions: the north portion (A) is represented by the conservation unit Serra do Conduru State Park – PESC, at

municipalities of Uruçuca and Itacaré), the region (B) in the middle (municipality of Ilhéus), and south region (C), represent by Una Biological Reserve (REBIO-Una, municipality of Una).

The remnants located in more deforested landscapes retain early successional forest attributes, with tree assemblages that are less dense, shorter, thinner, with an overall basal area loss, and with increasing canopy openness (Rocha-Santos et al. 2016).

Capture, radio-tracking and behavioral observations

We located and captured 19 free-living thin-spined porcupines (5 males and 14 females) with the help of local residents next protected areas or by our own capture team, along trails through the forest remnants of cocoa farms and conservation units, totalizing 11 different sites (Fig. 1).

Immediately after of each capture, we immobilized the thin-spined porcupine and fitted 40-g radio-collar with VHF telemetry system (Model LB81/MS6A; 3.9 × 2.0 × 1.9 cm; Telonics Inc., Mesa, Arizona), which was attached reflector adhesives for better nocturnal detection by halogen flashlights. Then, they were released in its origin local. Details of the capture methods, handling, immobilization and tagging were described by Giné et al (2010), and followed the recommendations of the American Society of Mammalogists (Sikes et al. 2011). We radio-tracked the tagged individuals during 238 crepuscular-nocturnal sessions (time series) from 17h00 to 05h00, totalizing 2.385 hours of the behavioral observation, between 2005 and 2013 (Table 1).

Table 1. Sex of individuals monitored, forest fragments size (FFS), fragment size category (FSC); sampling effort (monitoring period, number of crepuscular-nocturnal sessions and hours of observation), and behavior and feeding records of the thin-spined porcupines in Brazilian Atlantic Forest, south Bahia, Brazil. [a] Giné et al (2010). F: female and M: male.

			Sampling effort			Records	
Individual	FFS (ha)	FSC (ha)	Period	N.º sessions	Hours	Behavior	Feeding
F1	2686	>500	Jan 12 - May 13	7	88	332	38
F2	941	>500	May 11 - Dec 11	3	27	97	12
F3	585	>500	Oct 11 - Oct 13	7	86	260	19
F4	585	>500	Sep 12 - Mar 13	6	77	299	39
F5	585	>500	Apr 13 - Oct 13	4	50	265	51
F6	585	>500	May 13 - Nov 13	4	50	132	12
F7	585	>500	Aug 13 - Nov 13	5	56	264	42
M8	585	>500	Jan 13 - Nov 13	7	72	259	31
M9	585	>500	Nov.13 - Nov. 13	2	24	122	9
F10	146	<200	Mar. 05 - Apr. 05	3	39	182	17
F11	146	<200	Nov 11 - Mar 13	10	97	478	88
F12	52	<200	Apr 13 - Nov 13	7	88	211	33
F13	22	<200	Jan. 05 - Jun. 05	4	41	109	15
F14[a]	18	<200	Oct 05 - Sep 06	36	334	1872	319
M15[a]	18	<200	Aug 05 - Sep 06	39	349	1850	339
M16	18	<200	Nov.10 - Dec. 10	3	39	179	29
M17	11.7	<200	Sep 13 - Oct. 13	1	12	44	3
F18[a]	2.1	<200	Mar 05 - Mar 06	40	383	2027	413
F19[a]	0.7	<200	Jun 05 - Jul 06	50	473	2604	507
Total				238	2385	11586	2016

In every crepuscular-nocturnal session, we recorded the individual behavior by an instantaneous focal-sampling method (Altmann et al. 1974) to each 10-min interval, recording the 1st behavior visible (resting, moving, feeding, and others). We described feeding behavior as all activities related to the search, exploitation, handling and consumption of food. We considered the search as the displacement between a consumer event and another within the canopy of the same tree, and the exploration, handling and consumption, the whole repertoire that involves feeding, from the olfactory investigation until the swallowing. When the animal was feeding, we recorded the type of plant in which it was foraging (tree, shrub, liana and epiphyte), the part of the plant consumed (leaves, fruit, flowers or other) and the maturity of consumed leaves (young or undefined). Because leaves appear monochromatic at night, we adopted the criteria defined by Giné et al. (2010), considering young leaves (including buds) those that were located up to the 3rd node from outer part of the tree branch. However, when precise location of the animal was not possible or when they feed in other tree crown parts, we considered that leaves were undefined regarding maturity state. Later, feeding trees were sampled and identified in UESC/Herbarium.

Forest fragment size, diet diversity and richness

Based on individuals' location data and habitat mapping provided by Giné et al. (2015), we classified sampling sites into small (<200 ha) and large forest fragments (>500 ha). We tracked and observed 9 individuals in small (range: 0.7-146.0 ha) and 10 animals in large forest fragments (range: 585-2886 ha). For each fragment size category we estimated richness and diversity of diet. We considered each crepuscular-nocturnal session as the sampling unit. Based on presence/absence of plant species in the diet of each individual in each sampling unit, we performed an rarefaction curve (Magurran 2004), with 1000 bootstrap randomizations, using the software EstimateS 9.1.0 (Colwell 2013), that estimates diet richness (S) by 'Mao Tau' method (Colwell et al. 2012). As we could not get the same number the samples for two fragment size categories, we compared S in each fragment size category for a weighted sampling effort, i.e. based in the lower effort performed among the categories. In addition, we performed Monte Carlo analysis to evaluate differences in diet richness and diet diversity, here estimated by Shannon-Wiener index (H'), between two fragment size categories. We randomized the sampling units for each fragment size category (Small or Large) using 5000 permutations in R environment (version 3.2.3; R Core Team 2015).

We performed a hierarchical cluster analysis to produce a dendrogram to verify if similarity (Jaccard index) within groups is greater than between fragment size groups and which species are shared by two treatments. We used unweight pair-group average (UPGMA) algorithm in PAST software (Hammer et al. 2001) . Clusters are joined based on the average distance between all members in the two groups.

Diet composition and main food species

To determine the relative importance of each plant species used in the diet of thin-spined porcupines, we ranked species by consumption frequency (CF), followed by the number of animals (NA) fed on each species. The CF corresponds to the proportion of records that each tree species was consumed in relation to total feeding records obtained. We selected seven most consumed plant species (including one liana) based on this ranking to access the leaf chemical content.

Leaf chemical content assessment

Between February and October 2014, we collected five to ten samples with 200 grams each approximately of young leaves from seven plant species most consumed by free-living thin-spined porcupines. We collected leaves primarily on plants that were consumed by the most recently monitored porcupines (between the years 2011 and 2013) and complemented with trees randomly sampled within of the home range from others tagged individuals, totalized seven sampling sites in our study area (Fig. 1).

We sampled only adult trees (diameter at breast height [DBH] >10cm), and whenever possible, each sample was composed by subsamples randomly collected from different parts and heights of each tree. Soon after the sample collection, fresh leaves were weighted, dried at 40ºC in an air forced circulation stove and milled to 0.25mm. Posteriorly chemical analysis were performed to determine the content of crude protein (CP), acid detergent fiber (ADF), total phenolic (TP) and condensed tannins (CT). First, we estimated dry matter (DM), defined as a weight percentage of the each sample after complete drying. To determine CP (g kg^{-1} dry weight) we first access nitrogen (N) content with micro-Kjeldahl method (AOAC 1995). The nitrogen value was multiplied by the factor 6.25 to obtain crude protein from leaves samples. The acid fiber content - ADF (g kg^{-1} of dry weight), mainly the fraction of cellulose and lignin, were accessed using Van Soest et al. (1991) assay. Thus, we obtained the CP:ADF ratio, an important factor in food selection for folivores primates (Milton and McBee 1983).

We accessed total phenolic (TP) and condensed tannins (CT) content using Folin-Ciocalteu (according to Makkar et al., 1993), and Butanol-HCl (Porter et al. 1986) assays, respectively. The TP were expressed in tannic acid equivalents (g kg^{-1} dry weight), and CT in leucocianidin equivalents (g kg^{-1} dry weight).

Leaf quality and consumption ranking

We performed linear models on data sets analysis to investigate the influence of leaf quality variables (DM, CP, TP, CT, ADF, and CP:ADF) on the of consumption frequency (CF) for each plant species. We used behavior data only for the 15 most recently monitored thin-spined porcupines (only radio-tracked individuals from 2011 to 2013). We excluded four animals monitored by Giné et al. (2010), due to the disproportional greater sampling effort. We used the mean value of the chemical variables from samples of each of the seven plant species to represent a single value for linear regression models (Table 3). Before model fitting, we built a Pearson (r) correlation matrix to avoid using highly autocorrelated variables in the same model ($r > 0.8$), thus avoiding data colinearity. We found high colinearity ($r > 0.70$) of dry matter and protein: fiber ratio with crude protein variable (see appendix Table A1). We selected crude protein, because its content is expected to be critical for this species (Giné et al., 2010). We tested normality of residuals and homoscedasticity with visual residual plots. We used the "lmer" function from the "lme4" package to run those analyses. All analyses were performed in R environment (R Core Team 2015).

Fabaceae and non-Fabaceae plant species

To investigate why Fabaceae species are the most consumed, we established a binary classification — Fabaceae (*Inga thibaudiana*, *I. affinis*, *Albizia pedicellaris*, and *Mimosa seratonia*) and non-Fabaceae (*Pera glabrata*, *Thyrsodium spruceanum*, and *Humiria balsamifera*). We conducted a student´s *t*-test to compare the means of each leaves variables (DM, CP, TP, and CT) between the two categories created, and when the normality assumption is not met, we used a permutation test ($n = 5000$) to verify statistical significance. Log transformation was performed for TP values to attend normality and variance homoscedasticity assumptions.

Results

Diet composition and main food species

We recorded a total of 2016 feeding events for the 19 thin-spined porcupines observed (Table 1), with a positive identification of plant parts consumed for 1940 (96.3%) of these records. The porcupines feed exclusively on leaves, and at least 54.07% (n = 1090) of the diet was based on young leaves, once the animals fed on leaves at the tips of the branches. We could not identify leaf maturity for 45.3% of records (n = 913) due to visual difficulties during the nocturnal sampling.

Table 2. The seven species investigated in the study and their ranking based on consumption frequency (CF) and number of animals that eat each plant species (NA) of 19 free-living thin-spined porcupines in southern Bahia, Brazil.

Rank	Family	Plant species	CF	NA
1	Fabaceae	*Albizia pedicellaris* (DC.) L.Rico	36.65	10
2	Fabaceae	*Inga thibaudiana* DC.	26.92	7
3	Euphorbiaceae	*Pera glabrata* (Schott) Poepp. ex Baill.	11.48	13
5	Fabaceae	*Inga affinis* Benth	1.90	4
6	Humiriaceae	*Humiria balsamifera* (Aubl.) J. St.-Hil.	1.64	7
12	Fabaceae	*Mimosa ceratonia* L.	0.74	1
13	Anacardiaceae	*Thyrsodium spruceanum* Benth.	0.69	5

We identified the plant species consumed for 1891 feeding records (93.8%). Porcupines consumed leaves from 219 individual trees, belonging to 64 species and 31 families (full list of species at Appendix A; Table A2). The most consumed family was Fabaceae (69.06%), followed by Euphorbiaceae (12.22%), and Anacardiaceae (4.49%). The Fabaceae family also comprised most of species consumed (n = 14). Despite the high number of species consumed, the seven species considered in the analyzes comprised 80.01% of the thin-spined porcupines diet (Table 2).

Forest fragment size, diet diversity, richness, and similarity

The rarefaction curve plot for plant species richness shows that the diet richness of the radio-tracked porcupines from large forest fragments was greater than those estimated for individuals inhabiting small forest fragments ($p < 0.001$), when considering the same number of night sampling sessions (n = 39; Fig. 2). Diet diversity was significantly higher for those individuals living in large fragments (H'= 2.99) than those inhabiting small ones (H'= 1.81; Shannon diversity index using 5000 permutations ($p < 0.001$).

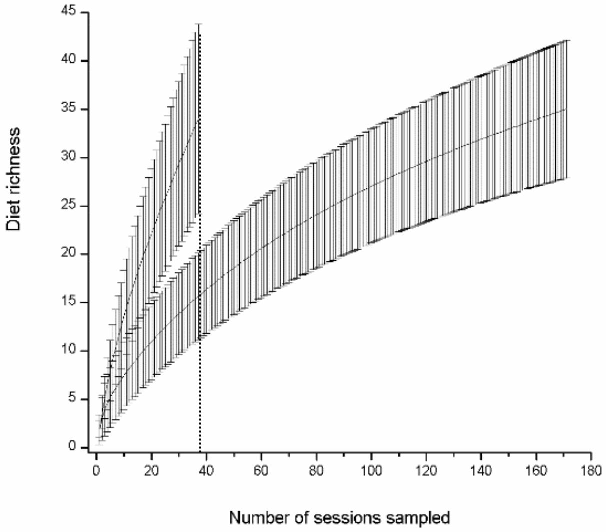

Fig. 2. Rarefaction curves of diet richness (S) in function of number of crepuscular-night sessions sampled in small forest fragments (with more night sessions) and larger forest fragments (less night sessions) for thin-spined porcupines in Atlantic Forest of South Bahia, northeast Brazil. Bar describes the confidence intervals.

The similarity between the diet of the animals living in small and larger fragments was low (Jaccard similarity coefficient = 0.07), indicating that the diet composition of the animals was distinct when living in such situations. In fact, few plant species were present in the diet of the animals living in both fragment size categories (*Humiria balsamifera, Albizia pedicellaris*, *Inga affinis*, *Parkia pendula, and Pera glabrata*; Fig. 3), while only two species of shared plant were the most frequently consumed in both situations (*A. pedicellaris* and *P. glabrata*; Appendix A: Tables A3 and A4).

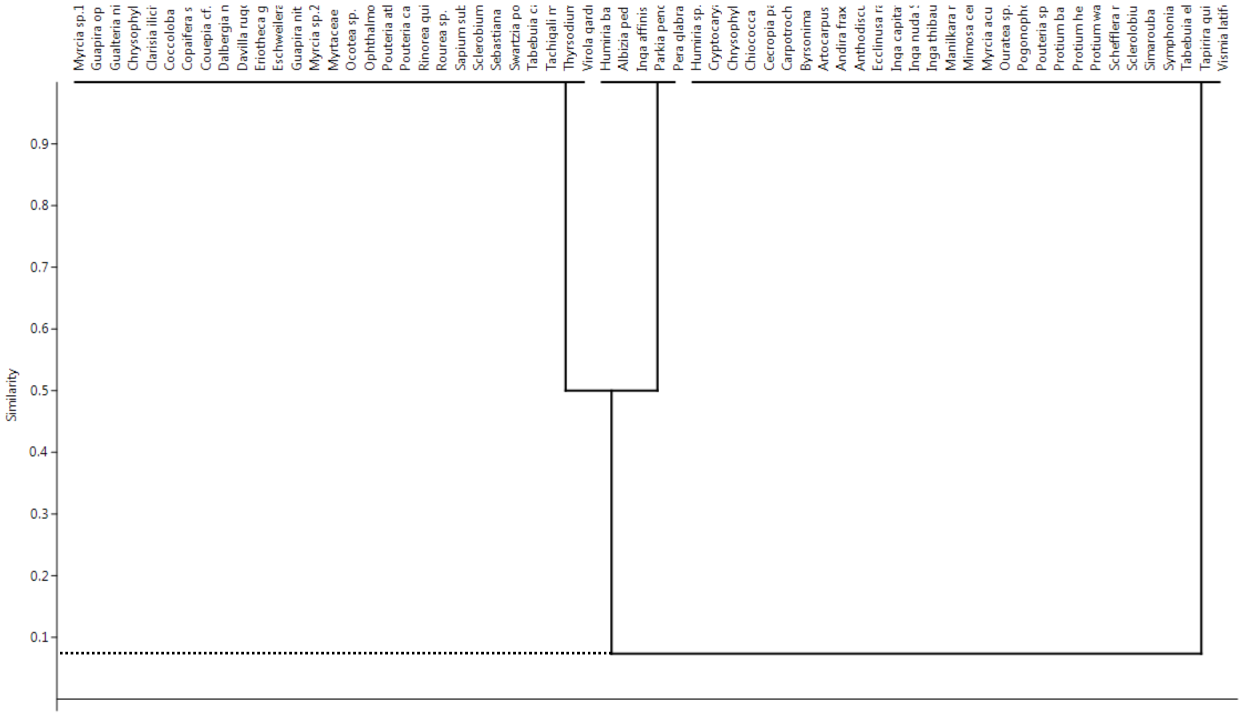

Fig. 3. Dendrogram of 64 plant species consumed by 19 thin-spined porcupines showing Jaccard distance index value (n = 0.07; dashed line) for hierarchical clustering between two fragment sizes categories (small and large) in southern Bahia, Brazil. Species from small forest fragments (right side of dendrogram); species from larger forest fragments (left side of dendrogram), and in the middle of the dendrogram, the plant species shared by two size forest fragments categories.

Leaf quality and consumption ranking

We calculated a multiple linear regression to predict consumption frequency (CF) based on nutritional variables ($F_{4, 2} = 71.46$; $R^2_{adj} = 97.9$; $p = 0.013$). The condensed tannins (0.10 ± 0.007, $p = 0.004$), total phenolics (-0.04 ± 0.009, $p = 0.045$), and acid detergent fiber (0.05 ± 0.004, $p = 0.007$) were good predictors of CF. Only protein content (0.01 ± 0.01, $p = 0.31$) did not serve to this purpose (Fig. 4).

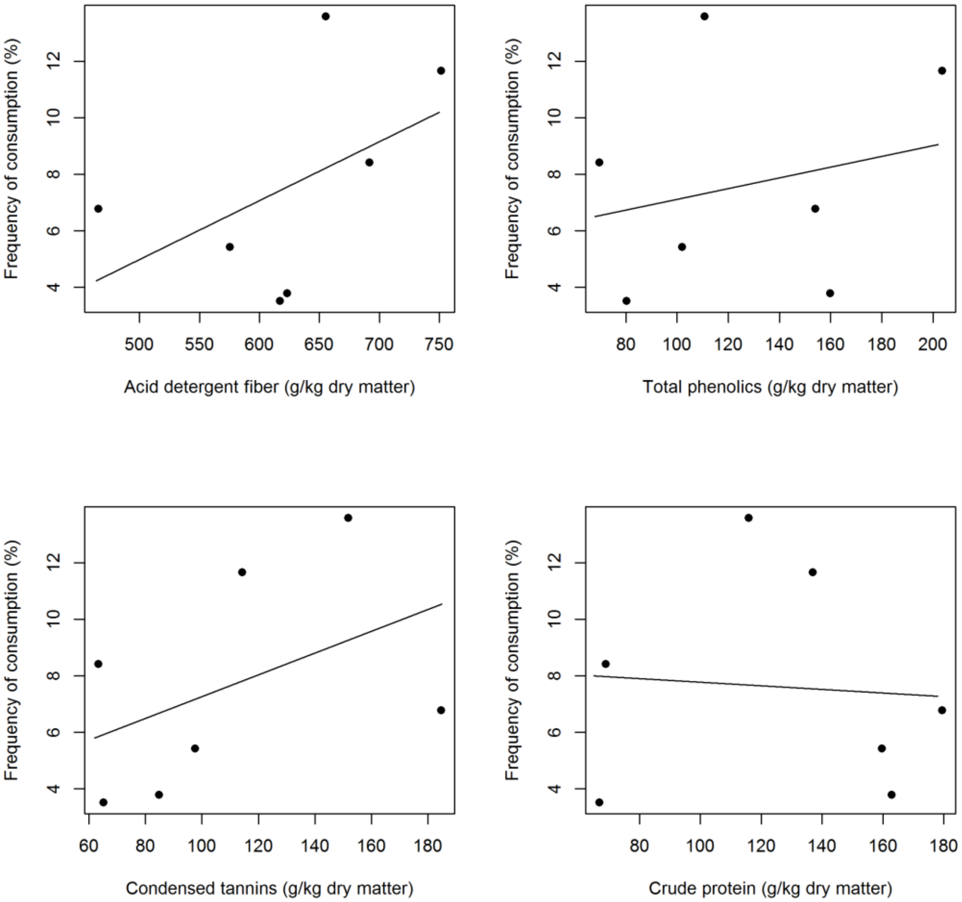

Fig. 4. Plots for the predicted probability for each predictor separately (nutritional variables) on frequency of consumption of seven plant species consumed by thin-spined porcupines at southern Bahia, northeast Brazil.

Fabaceae and non-Fabaceae plant species

Total protein content (df = 50; p <0.001) and total phenolics (df = 50; p <0.001) were greater for Fabaceae species when compared to non-Fabaceae. Condensed tannin content (df = 50; p = 0.257) and dry matter (df = 50; p = 0.868) did not differ between groups (Fig. 5).

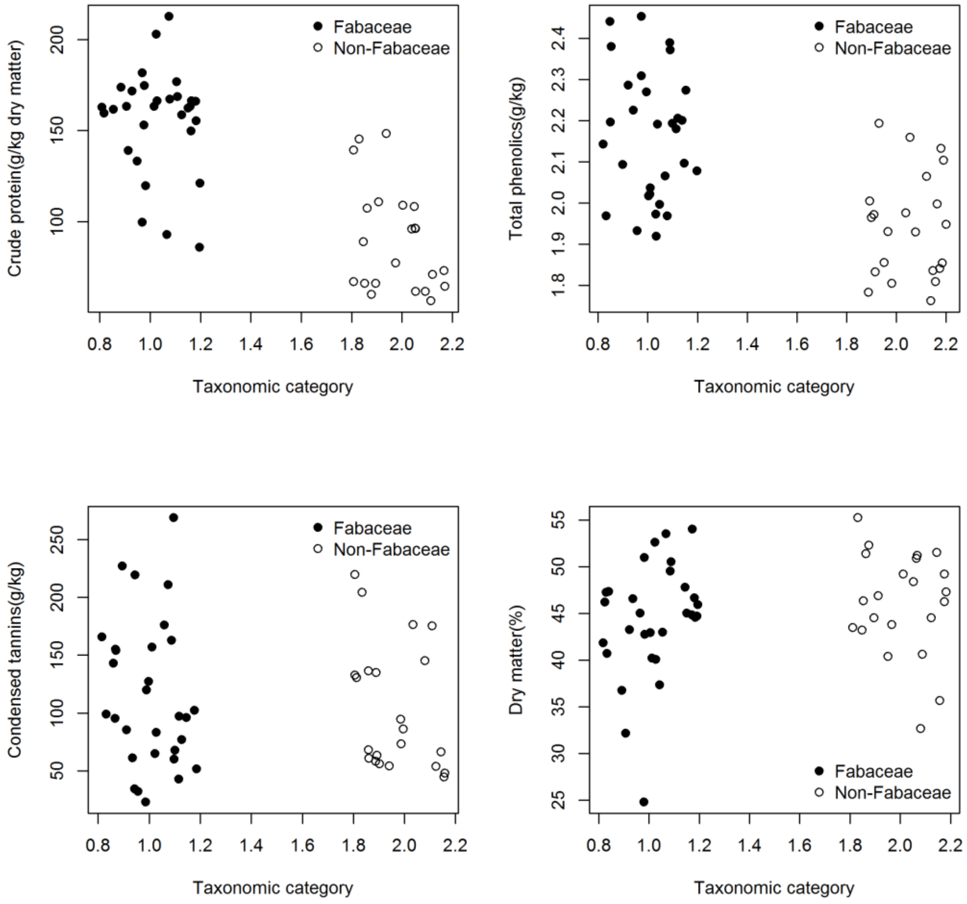

Fig. 5. Plots for difference on nutritional variables between Fabaceae and non-Fabaceae plant taxonomic categories in southern Bahia, Brazil. Only total phenolics and crude protein variables were statiscal significant.

Discussion

We confirmed that the thin-spined porcupine have a diet strictly based on leaves of trees mainly from the Fabaceae family (including Mimosaceae) as indicated by Giné et al. (2010), and we show consume of leaves of lianas from this plant family also. Leaves were the unique item consumed during visual sampling and the tree species *A. pedicellaris* and *P. glabrata* are present and predominate in the diets of the animals, regardless of fragment size. It reinforces that this is a highly selective rodent folivore species with a highly specialized diet, corroborating with previous evaluations (Giné et al. 2010). We recommended that the species should be considered a "strictly folivorous" arboreal mammal species, following the criterion defined by Eisenberg (1978). It is definitely not a frugivorous species, as ancient anecdotal observations may suggested. In addition, we have shown the diversity of animals' diet decreased in smaller forest fragments, although little change in dietary basis has been observed. The most consumed species of their diet may be found easily in small and large forest remains, since are shade-intolerant, abundant and widespread species (Giné et al. 2010). Thus, the main feeding resource is not limitant for the species persistence in such forests fragment sizes, corroboring hypothesis suggested by Giné et al. (2010), although poorer diets occur in smaller forest fragments.

Diet impoverishment in small fragments may be primarily caused by the loss of plant diversity relationed to area size for plant species establish and persistence (species-area ratio), or by the direct loss of species unable to tolerate the small fragments' conditions, as it is known to happen with shade tolerant species. It is still unknown whether this poor diet may cause changes in the performance or fitness of these animals. Recent studies suggests that females of common brushtail possum (*Trichosurus vulpecula* Kerr), with better quality trees in their home range, reproduced more often and had faster-growing offspring (DeGabriel et al. 2009).

According to our results suggest, the preference for Fabaceae species should be associated with a greater amount of protein found in its leaves, if we compare with other species with high consumption frequency (*Pera glabrata*, *Thyrsodium spruceanum*, and *Humiria balsamifera*). Although these non-Fabaceae species do not have relative high levels of protein, they may be selected by other factors, such as high availability and replacement rate of new leaves, as in the case of *Pera glabrata*, but especially if these characteristics are associated with lower levels of total phenolics found for these species in our study, when we compared to species of Fabaceae. Other species intrinsic and untested characteristics may be favoring the consumption of less protein species by porcupines, as in the case of *H. balsamifera*, which contains chemical elements with antimalarial properties (Silva et al. 2004).

The thin-spined porcupines prefer young leaves, probably due to the smaller fiber content (more easier to digest than mature leaves; Hladik 1978), containing fewer toxins (McKey 1981), higher proportional levels of protein and energy (Milton 1982), and may also be an important source of minerals and nutrients such as potassium, magnesium, phosphorus and nitrogen (Waterman et al. 1984).

The low fiber content may be important at food item level selection (new leaves versus mature), but was not an important factor in the consumption of plant species by thin-spined porcupines, since it was positively correlated with consumption. A plausible explanation may come from digestive tract of this species. The analysis of a *Chaetomys* stomach (Giné et al. 2010) showed a simple and small stomach, a large intestine longer than the small intestine, and an enlarged and sacculated cecum, suggesting that this porcupine is a cecal fermenter with typical adaptations for high-fiber diets and conservation of water like others porcupines species (Johnson and Mcbee 1967; Parra 1978; Felicetti et al. 2000). The positive relationship between the consumption frequency of and the fiber content of plant species suggests that they does not choice plant species by fiber contend, although these animals seem to make choices regarding the maturity of the leaves (young leaves). Their morphological adaptations may allow the selection only for feeding item-scale, while may not always prefer it at species-scale.

Although our study suggests that this species tolerates different levels of condensed tannins, increasing concentration of total phenolics has a negative impact on leaves consuming by thin-spined porcupines. It is possible that they do not completely avoid total phenolics, but there is evidence that they restrict their ingestion to within limits that they are physiologically able to tolerate, and balance this toxicity consuming others food resources with less defense compounds, such as non-Fabaceae species in this study. Other important factor here is that the monophyletic clade of Fabaceae (Mimosaceae) tend to share chemical defense strategies (Wink and Mohamed 2003), whence it is possible that thin-spined porcupines are selecting related species due to the presence of specific types or levels, or both, of phenolics compounds which they might be more tolerant. The association with nitrogen-fixing bacteria supplies more nitrogen for legumes plants, which in turn can increase their growth rates (foliar expansion and substitution), leaf biomasses (Kursar and Coley, 2003; Roggy and Prévost, 1999), and nitrogen easily available for secondary metabolism (quinolizidine alkaloids, non-protein amino acids, cyanogens, protease inhibitors, lectins) (Wink and Mohamed, 2003; Wink, 2003).

We were unable to identify why some species of plants are more consumed than others, although we have identified that they are not clear nutritional advantages that are linked to consumption maximization of protein in relation to fiber, nor in avoiding high levels of total tannins.

We believe that physiological mechanisms, acting concomitantly or not, may be allowing the consumption of high levels of condensed tannins by *C. subspinosus*. It is known that some herbivorous mammals may counter the negative effects of tannins through tannin-binding salivary proteins (TBSPs), that inactivate tannins by forming insoluble complexes and prevent them from interacting with other more valuable proteins (Mehansho et al., 1987; Shimada, 2006). The presence of TBSPs in six neotropical wild mantled howlers (*Alouatta palliata mexicana*), suggests that the continuous expression of these salivary proteins is part of a dietary strategy that enables howlers to consume diets with variable tannin contents, thus partly explaining their dietary flexibility (Espinosa Gómez et al. 2015). Other possible mechanism to mitigate negative effects of tannins would be the presence of tannin-degrading microorganisms in the gastrointestinal tract of animals. This was proven by the presence of gut tannin-degrading bacteria in the plateau zokor (*Myospalax baileyi*), which consumes tannin-rich herbaceous plants (Dai et al. 2015), root voles (*Microtus oeconomus*), and plateau pikas (*Ochotona curzoniae*) (Dai et al. 2014).

High consumption of PSMs was already described for other herbivores. For example, one of the most preferred trees (*Prunus africana*) by red colobus monkeys

(*Procolobus badius*) was the species with the highest levels of cyanogenic glycosides, and a species of the same genus that one of our most consumed species (*Albizia*), had the highest concentrations of saponins (Chapman and Chapman 2002). The thin-spined porcupine should therefore balance the intake of PSMs by selecting young leaves with high crude protein levels. This is possible when we look to consumed Fabaceae species in this study, with protein levels above or near 16%, which is high in comparison to values observed for neotropical tree species (Sambuichi 2002; Barreto 2007).

Total protein content was not a reliable predictor of consumption frequency, and it may be partly explained by tannins presence, making part of the protein content indigestible. Thus, total nitrogen concentration may not reflect total protein availability for herbivores. Still, it may be correlated as shown in the study of the greater gliders (*Petauroides volans*), where the available nitrogen (total nitrogen, dry matter digestibility and tannins), with a particular combination of phenolic compounds (formylated phloroglucinol compounds), significantly influenced positively leaves consumption (Jensen et al. 2015).

Our study helps to reveal patterns of food selection still not understood for the thin-spined porcupines, and in more general lines, help to elucidated the factors that influence diet of arboreal herbivory mammals face to high tree diversity tropical rainforest diversity and fragmented landscapes. Our data showed that certain plant species of the thin-spined porcupine´s diet were consumed in both small and large fragments and had at the same time a high frequency of consumption by all the individuals studied (eg *A. pedicellaris*, *P. glabrata*, and *I. thibaudiana*). These tree species can assist in the free-living management of thin-spined porcupine. This is because they are easily recognizable in the field, allowing guiding the identification of areas that have these plants as a priority for the maintenance of this mammal. These thin-spined porcupine´s diet trees can also be of extreme importance if they are used in restoration programs in the natural environments of southern Bahia, providing key food species for this endangered species.

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References

ALTMANN, J., J. LOY AND S. WAGNER. 1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

AOAC. 1995. Official methods of analysis of AOAC. P. in. AOAC international.

BARRETO, R. M. F. 2007. Uso de Hábitat pela Preguiça-de-Coleira Bradypus torquatus Illiger 1811 , no Sul da Bahia.

BENCHIMOL, M. AND C. A. PERES. 2015. Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation.

Journal of Ecology 103:408–420.

BEZERRA, R. A., G. ANDRÉS, F. GINÉ, B. M. MACIEL AND F. A. GAIOTTO. 2015a. Identification and genetic characterization of Toxoplasma gondii in free-ranging bristle-spined porcupine (Chaetomys subspinosus), a threatened arboreal mammal from the Brazilian Atlantic Forest. Parasites & Vectors 8:6–11.

BEZERRA, R. A., E. L. S. MARQUES AND R. P. REZENDE. 2015b. Elucidation of bacterial community structure on thin-spined porcupine (Chaetomys subspinosus) spines by denaturing gradient gel electrophoresis (DGGE) and sequencing. Genetics and molecular research : GMR 14:11867–11875.

CATZEFLIS, F., J. PATTON, A. PERCEQUILLO, C. BONVICINO AND M. WEKSLER. 2008. Chaetomys subspinosus. *The IUCN Red List of Threatened Species*. .

CHAPMAN, C. A. AND L. J. CHAPMAN. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Comparative Biochemistry and Physiology 133:861–875.

COLWELL, R. K. ET AL. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21.

COLWELL, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates. http://purl.oclc.org/estimates.

DAI, X. ET AL. 2014. Identification of tannin–degrading microorganisms in the gut of plateau pikas (Ochotona curzoniae) and root voles (Microtus oeconomus). Symbiosis

63:1–9.

DAI, X., L. JIANG, A. WANG, W. WEI AND S. YANG. 2015. Tannin-degrading bacteria with cellulase activity isolated from the cecum of the Qinghai-Tibet plateau zokor (Myospalax baileyi). Israel Journal of Ecology & Evolution 61:21–27.

DEARING, M. D., W. J. FOLEY, S. MCLEAN AND M. D. DEARING. 2005. The Influence of Plant Secondary Metabolites on the Nutritional Ecology of Herbivorous Terrestrial Vertebrates. Annual Review of Ecology, Evolution, and Systematics 36:169–189.

DEGABRIEL, J. L., B. D. MOORE, W. J. FOLEY AND C. N. JOHNSON. 2009. The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. Ecology 90:711–719.

EISENBERG, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. Pp. 135 – 152inThe ecology of arboreal folivores(G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

ESPINOSA GÓMEZ, F. ET AL. 2015. Howler Monkeys (Alouatta palliata mexicana) Produce Tannin-Binding Salivary Proteins. International Journal of Primatology 36:1086–1100.

FELICETTI, L. A, L. A SHIPLEY, G. W. WITMER AND C. T. ROBBINS. 2000. Digestibility, nitrogen excretion, and mean retention time by North American porcupines (Erethizon dorsatum) consuming natural forages. Physiological and biochemical zoology : PBZ 73:772–80.

GINÉ, G. A. F., E. H. DE BARROS, J. M. B. DUARTE AND D. FARIA. 2015. Home Range and Multiscale Habitat Selection of Threatened Thin-Spined Porcupine in the Brazilian

Atlantic Forest. Journal of Mammalogy 96:1095–1105.

GINÉ, G. A. F., J. M. B. DUARTE AND D. FARIA. 2010. Feeding ecology of a selective folivore, the thin-spined porcupine (Chaetomys subspinosus) in the Atlantic forest. Journal of Mammalogy 91:931–941.

GINÉ, G. A. F., J. DUARTE, T. MOTTA AND D. FARIA. 2012. Activity, movement and secretive behavior of a threatened arboreal folivore, the thin-spined porcupine , in the Atlantic forest of southern Bahia, Brazil. Journal of Zoology 286:131–139.

GUGLIELMO, C. G., W. H. KARASOV AND W. J. JAKUBAS. 1996. Nutritional Costs of a Plant Secondary Metabolite Explain Selective Foraging by Ruffed Grouse. Ecology 77:1103–1115.

HAMMER, Ø., D. A. T. A. T. HARPER AND P. D. RYAN. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1):1–9.

HLADIK, A. 1978. Phenology of leaf production in rain forest of Gabon: Distribution and composition of food for folivores. Pp. 51 – 71inThe Ecology of Arboreal Folivores(G. G. Montgomery, ed.). Smithsonian Institu- tion Press, Washington, DC.

IASON, G. 2005. The role of plant secondary metabolites in mammalian herbivory: ecological perspectives. Proceedings of the Nutrition Society 64:123–131.

IASON, G. R. AND J. J. VILLALBA. 2006. Behavioral strategies of mammal herbivores against plant secondary metabolites: the avoidance-tolerance continuum. Journal of chemical ecology 32:1115–1132.

JENSEN, L. M., I. R. WALLIS AND W. J. FOLEY. 2015. The relative concentrations of nutrients and toxins dictate feeding by a vertebrate browser, the greater glider Petauroides volans. PLoS ONE 10:1–12.

JOHNSON, J. L. AND R. H. MCBEE. 1967. The Porcupine Cecal Fermentation. The Journal of Nutrition.

KURSAR, T. . AND P. . COLEY. 2003. Convergence in defense syndromes of young leaves in tropical rainforests. Biochemical Systematics and Ecology 31:929–949.

MAGURRAN, A. E. 2004. Measuring Biological Diversity. P. in. Blackwell Publishing.

MAKKAR, H. P. S., M. BLÜMMEL, N. K. BOROWY AND K. BECKER. 1993. Gravimetric determination of tannins and their correlations with chemical and protein precipitation methods. Journal of the Science of Food and Agriculture 61:161–165.

MCKEY, D. B. 1981. Food selection by colobus monkeys (Colobus satanas) in relation to plant chemistry. Biological Journal of the Linnean Society 16:115–146.

MEHANSHO, H., L. G. BUTLER AND D. M. CARLSON. 1987. Dietary tannins and salivary proline-rich proteins: interactions, induction, and defense mechanisms. Annual Review of Nutrition 7:423–440.

MILTON, K. 1982. Dietary quality and demographic regulation in a howler monkey population. Pp. 273–289inThe Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes(E. G. Leigh, A. S. R. And & D. M. Windsor, eds.). Smithsonian Institution Press, Washington, DC.

MILTON, K. AND R. H. MCBEE. 1983. Rates of fermentative digestion in the howler monkey, Alouatta palliata (Primates: Ceboidea). Comparative biochemistry and physiology. A, Comparative physiology 74:29–31.

MORI, S. A., B. M. BOOM, A. M. DE CARVALHO AND T. S. DOS SANTOS. 1983. Southern Bahian moist forests. The Botanical Review 49:155–232.

MOTE, T. E., J. J. VILLALBA AND F. D. PROVENZA. 2007. Relative availability of tannin- and terpene-containing foods affects food intake and preference by lambs. Journal of chemical ecology 33:1197–206.

OLIVEIRA, C. G., R. A MARTINEZ, G. A F. GINÉ, D. M. FARIA AND F. A GAIOTTO. 2011. Genetic assessment of the Atlantic Forest bristle porcupine, Chaetomys subspinosus (Rodentia: Erethizontidae), an endemic species threatened with extinction. Genetics and molecular research : GMR 10:923–31.

OLIVEIRA, P. A., R. B. S. LIMA AND A. G. CHIARELLO. 2012. Home range, movements and diurnal roosts of the endangered thin-spined porcupine, Chaetomys subspinosus (Rodentia: Erethizontidae), in the Brazilian Atlantic Forest. Mammalian Biology - Zeitschrift für Säugetierkunde 77:97–107.

OLIVER, W. L. R. AND I. B. SANTOS. 1991. Threatened endemic mammals of the Atlantic forest region of south-east Brazil. Special Scientific Report 4. Jersey, Channel Islands.

PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pp. 205–230inThe ecology of arboreal folivores(G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

PORTER, L. J., L. N. HRSTICH AND B. G. CHAN. 1986. The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. Phytochemistry 25:223–230.

R CORE TEAM. 2015. R: a language and environment for statistical computing. Version 3.2.3. *R Foundation for Statistical Computing, Vienna, Austria. http://www.R-*

project.org. .

RIBEIRO, M. C., J. P. METZGER, A. C. MARTENSEN, F. J. PONZONI AND M. M. HIROTA. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153.

ROCHA-SANTOS, L. ET AL. 2016. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biological Conservation 196:1–9.

ROGGY, J. AND M. PRÉVOST. 1999. Nitrogen-fixing legumes and silvigenesis in a rain forest in French Guiana: a taxonomic and ecological approach. New Phytologist 144:283–294.

SAMBUICHI, R. H. R. 2002. Fitossociologia e diversidade de espécies arbóreas em cabruca (mata atlântica raleada sobre plantação de cacau) na Região Sul da Bahia, Brasil. Acta Botanica Brasilica 16:89–101.

SHIMADA, T. 2006. Salivary proteins as a defense against dietary tannins. Journal of chemical ecology 32:1149–63.

SIKES, R. S., W. L. GANNON, MAMMALOGISTS AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SILVA, T. B. C. ET AL. 2004. Chemical Constituents and Preliminary Antimalarial Activity of Humiria balsamifera. Pharmaceutical Biology 42:94–97.

VAN SOEST, P. J., J. B. ROBERTSON AND B. A. LEWIS. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition.

Journal of dairy science 74:3583–3597.

SORENSEN, J. S., J. D. MCLISTER AND M. D. DEARING. 2005. Novel plant secondary metabolites impact dietary specialists more than generalists (Neotoma spp.). Ecology 86:140–154.

SOUTO LIMA, R. B. DE, P. A. OLIVEIRA AND A. G. CHIARELLO. 2010. Diet of the thin-spined porcupine (Chaetomys subspinosus), an Atlantic forest endemic threatened with extinction in southeastern Brazil. Mammalian Biology 75:538–546.

THIER, O. AND J. WESENBERG. 2016. Floristic composition and edge-induced homogenization in tree communities in the fragmented Atlantic rainforest of Rio de Janeiro , Brazil . Tropical Conservation Science 9:852–876.

THOMAS, W., A. CARVALHO, A. AMORIM, J. GARRISON AND A. ARBELÁEZ. 1998. Plant endemism in two forests in southern Bahia, Brazil. Biodiversity and Conservation 7:311–322.

ULAPPA, A. C. ET AL. 2014. Plant protein and secondary metabolites influence diet selection in a mammalian specialist herbivore. Journal of mammalogy 95:834–842.

VILELA, R. V, T. MACHADO, K. VENTURA, V. FAGUNDES, M. J. DE J SILVA AND Y. YONENAGA-YASSUDA. 2009. The taxonomic status of the endangered thin-spined porcupine, Chaetomys subspinosus (Olfers, 1818), based on molecular and karyologic data. BMC evolutionary biology 9:29.

VILLALBA, J. J. AND F. D. PROVENZA. 2005. Foraging in Chemically Diverse Environments: Energy, Protein, and Alternative Foods Influence Ingestion of Plant Secondary Metabolites By Lambs. Journal of Chemical Ecology 31:123–138.

WATERMAN, P. G., J. A. M. ROSS AND D. B. MCKEY. 1984. Factors affecting levels of some phenolic compounds, digestibility, and nitrogen content of the mature leaves of Barteria fistulosa (Passifloraceae). Journal of Chemical Ecology 10:387–401.

WINK, M. 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. Phytochemistry 64:3–19.

WINK, M. AND G. I. A. MOHAMED. 2003. Evolution of chemical defense traits in the Leguminosae: mapping of distribution patterns of secondary metabolites on a molecular phylogeny inferred from nucleotide sequences of the rbcL gene. Biochemical Systematics and Ecology 31:897–917.

APPENDIX A

Table A1.Correlation matrix between nutritional variables (explanatory variables) and frequency of consumption (response variable) used in diet selection analysis. We considered high correlate with index Pearson (r) ≥ 0.70.

	CF	DM	CP	TP	CT	ADF	CPADF
CF	1.00	0.30	-0.07	0.24	0.45	0.49	-0.20
DM	0.30	1.00	-0.70	-0.18	-0.29	0.53	-0.69
CP	-0.10	-0.70	1.00	0.67	0.62	-0.51	0.93
TP	0.24	-0.18	0.67	1.00	0.45	0.10	0.48
CT	0.45	-0.29	0.62	0.45	1.00	-0.50	0.69
ADF	0.49	0.53	-0.51	0.10	-0.50	1.00	-0.77
CPADF	-0.20	-0.69	0.93	0.48	0.69	-0.77	1.00

CF: consumption frequency; DM: dry matter; CP: crude protein; TP: total phenolics; CT; condensed tannins; ADF: acid detergent fiber; CPADF: crude protein and acid detergent fiber ratio.

Table A2. List of 64 species with leaves consumed by 19 thin-spined porcupine in southern Bahia, northeast Brazil.

Family	Plant species
Euphorbiaceae	*Pera glabrata (Schott) Poepp. ex Baill.*
Fabaceae	*Albizia pedicellaris (DC.) L.Rico*
Fabaceae	*Inga thibaudiana DC.*
Humiriaceae	*Humiria balsamifera (Aubl.) J. St.-Hil.*
Anacardiaceae	*Thyrsodium spruceanum Benth.*
Anacardiaceae	*Tapirira guianensis Aubl.*
Fabaceae	*Inga affinis Benth*
Fabaceae	*Swartzia polita (R. S. Cowan) Torke*
Polygonaceae	*Coccoloba alnifolia Casar.*
Araliaceae	*Schefflera morototoni (Aubl.) Maguire, Steyrm. & Frodin*
Moraceae	*Artocarpus heterophyllus Lamarck.*
Lecythidaceae	*Eschweilera ovata (Cambess.) Miers*
Clusiaceae	*Vismia latifolia (Aubl.) Choisy*
Burseraceae	*Protium heptaphyllum (Aubl.) March.*
Fabaceae	*Parkia pendula (Willd.) Benth.*
Fabaceae	*Inga capitata Desv.*
Myrtaceae	*Myrcia sp.1*
Burseraceae	*Protium warmingianum March*
Fabaceae	*Mimosa ceratonia L.*

Dilleniaceae	*Davilla rugosa Poir*
Myrtaceae	*Myrcia acuminatissima O. Berg*
Sapotaceae	*Ecclinusa ramiflora Mart.*
Chrysobalanaceae	*Couepia cf. monteclarensis*
Simaroubaceae	*Simarouba amara Aubl.*
Caryocaraceae	*Anthodiscus amazonicus Gleason & A. C. Smith*
Malpighiaceae	*Byrsonima sericea DC.*
Rubiaceae	*Chiococca alba (L.) Hitch*
Sapotaceae	*Chrysophyllum sp.*
Fabaceae	*Copaifera sp.*
Fabaceae	*Dalbergia miscolobium Benth.*
Malvaceae	*Eriotheca globosa (Aubl.) A. Robyns*
Nyctaginaceae	*Guapira opposita (Vell.) Reitz*
Humiriaceae	*Humiria sp.*
Euphorbiaceae	*Ophthalmoblapton sp.*
Violaceae	*Rinorea guianensis Aubl.*
Connaraceae	*Rourea sp.*
Euphorbiaceae	*Sapium sublanceolatum (Mull. Arg.) Huber*
Fabaceae	*Sclerolobium chrysophyllum Poepp. & Endl.*
Clusiaceae	*Symphonia globulifera L.f.*
Fabaceae	*Andira fraxinifolia Benth.*
Flacourtiaceae	*Carpotroche brasiliensis (Raddi) A. Gray*
Annonaceae	*Gualteria nigrensis W. A. Rodrigues.*
Fabaceae	*Inga nuda Salzm. Ex Benth.*
Sapotaceae	*Manilkara maxima T. D. Penn.*
Lauraceae	*Ocotea sp.*
Ochnaceae	*Ouratea sp.*
Sapotaceae	*Pouteria caimito (Ruiz & Pavon) Radlk.*
Urticaceae	*Cecropia pachystachya Tréc.*
Myrtaceae	*Myrcia sp.2*
Sapotaceae	*Chrysophyllum cainito L.*
Fabaceae	*Sclerolobium densifolium Benth.*
Fabaceae	*Tachigali multijuga Benth.*
Myristicaceae	*Virola gardneri (A. DC.) Warb.*
Moraceae	*Clarisia ilicifolia (Spreng) Hanj. & Rossb.*
Burseraceae	*Protium bahianum D.C. Daly*
Sapotaceae	*Pouteria atlantica*
Bignoniaceae	*Tabebuia cassinoides (Lam.) DC.*
Euphorbiaceae	*Sebastiana gaudichaudii (Muell. Arg.) M Arg.*
Euphorbiaceae	*Pogonophora schomburgkiana Miers ex Benth.*
Lauraceae	*Cryptocarya mandioccana meissn. In. Dc.*
Myrtaceae	*Myrtaceae sp.1*
Bignoniaceae	*Tabebuia elliptica (A. DC.) Sandw.*
Nyctaginaceae	*Guapira nitida (Mart.) Lundell*
Sapotaceae	*Pouteria sp.*

Table A3. List of plant species, feeding records, and consumption frequency (CF) for thin-spined porcupine located in large forest fragments (> 500 ha) of southern Bahia, northeast Brazil.

Plant species	Feeding records	CF (%)
Pera glabrata (Schott) Poepp. ex Baill.	30	14.49
Humiria balsamifera (Aubl.) J. St.-Hil.	29	14.01
Albizia pedicellaris (DC.) L.Rico	21	10.14
Myrcia sp.1	14	6.76
Thyrsodium spruceanum Benth.	13	6.28
Couepia cf. monteclarensis	10	4.83
Coccoloba alnifolia Casar.	8	3.86
Guapira nitida (Mart.) Lundell	8	3.86
Swartzia polita (R. S. Cowan) Torke	8	3.86
Myrtaceae sp.1	7	3.38
Sebastiana gaudichaudii (Muell. Arg.) M Arg.	6	2.90
Eschweilera ovata (Cambess.) Miers	5	2.42
Pouteria atlantica	5	2.42
Tabebuia cassinoides (Lam.) DC.	5	2.42
Clarisia ilicifolia (Spreng) Hanj. & Rossb.	4	1.93
Tachigali multijuga Benth.	4	1.93
Virola gardneri (A. DC.) Warb.	4	1.93
Davilla rugosa Poir	3	1.45
Myrcia sp.2	3	1.45
Gualteria nigrensis W. A. Rodrigues.	2	0.97
Inga affinis Benth	2	0.97
Ocotea sp.	2	0.97
Parkia pendula (Willd.) Benth.	2	0.97
Pouteria caimito (Ruiz & Pavon) Radlk.	2	0.97
Chrysophyllum sp.	1	0.48
Copaifera sp.	1	0.48
Dalbergia miscolobium Benth.	1	0.48
Eriotheca globosa (Aubl.) A. Robyns	1	0.48
Guapira opposita (Vell.) Reitz	1	0.48
Ophthalmoblapton sp.	1	0.48
Rinorea guianensis Aubl.	1	0.48
Rourea sp.	1	0.48
Sapium sublanceolatum (mull. Arg.) Huber	1	0.48
Sclerobium chrysophyllum	1	0.48

Table A4. List of plant species, feeding records, and consumption frequency (CF) for thin-spined porcupine located in large forest fragments (< 200 ha) of southern Bahia, northeast Brazil.

Plant species	Feeding records	CF (%)
Albizia pedicellaris (DC.) L.Rico	672	39.90
Inga thibaudiana DC.	509	30.23
Pera glabrata (Schott) Poepp. ex Baill.	187	11.10
Tapirira guianensis Aubl.	72	4.28
Inga affinis Benth	34	2.02
Simarouba amara Aubl.	29	1.72
Artocarpus heterophyllus Lamarck.	25	1.48
Inga capitata Desv.	22	1.31
Schefflera morototoni (Aubl.) Maguire, Steyrm. & Frodin	18	1.07
Mimosa ceratonia L.	14	0.83
Protium warmingianum March	13	0.77
Pouteria sp.	9	0.53
Parkia pendula (Willd.) Benth.	7	0.42
Protium heptaphyllum (Aubl.) March.	7	0.42
Tabebuia elliptica (A. DC.)Sandw.	7	0.42
Cryptocarya mandioccana meissn. In. Dc.	6	0.36
Ecclinusa ramiflora Mart.	6	0.36
Pogonophora schomburgkiana Miers ex Benth.	6	0.36
Vismia latifolia (Aubl.) Choisy	6	0.36
Chrysophyllum cainito L.	4	0.24
Protium bahianum D.C. Daly	4	0.24
Sclerolobium densifolium Benth.	4	0.24
Cecropia pachystachyaTréc.	3	0.18
Myrcia acuminatissima O. Berg	3	0.18
Andira fraxinifolia Benth.	2	0.12
Carpotroche brasiliensis (Raddi) A. Gray	2	0.12
Humiria balsamifera (Aubl.) J. St.-Hil.	2	0.12
Inga nuda Salzm. Ex Benth.	2	0.12
Manilkara maxima T. D. Penn.	2	0.12
Ouratea sp.	2	0.12
Anthodiscus amazonicus Gleason & A. C. Smith	1	0.06
Byrsonima sericea DC.	1	0.06
Chiococca alba (L.) Hitch	1	0.06
Humiria sp.	1	0.06
Symphonia globulifera L.f.	1	0.06

Script R: Comparison diet richness for thin-spined porcupines (*Chaetomys subspinosus*) between large and small forest patches in southern Bahia, Brazil by permutation tests.

```
#Permutation R script#
#Author: Pavel Dodonov (pdodonov@gmail.com)
#User: Kena F. M. da Silva (kenaferrari@gmail.com)

myData
group <- myData$group
sps <- myData[,-c(1:3)]
sps <- as.matrix(sps)

sps.larger <- subset(sps, group=="larger")
sps.small <- subset(sps, group=="small")
divers.larger <- Shannon(sps.larger)
divers.small <- Shannon(sps.small)
divers.dif <- divers.grande - divers.pequeno
Nrand <- 5000
divers.dif.rand <- numeric(Nrand)
divers.dif.rand[1] <- divers.dif
for (i in 2:Nrand) {
group.rand <- sample(group)
 sps.larger.rand <- subset(sps, group.rand=="larger")
 sps.small.rand <- subset(sps, group.rand=="small")
 divers.larger.rand <- Shannon(sps.larger.rand)
 divers.small.rand <- Shannon(sps.small.rand)
 divers.dif.rand[i] <- divers.larger.rand - divers.small.rand
 if(i %% 100 == 0) print(i)
```

```
}
hist(divers.dif.rand, breaks=40)
abline(v=divers.dif, col="red")
signif <- sum(divers.dif.rand >= divers.dif)/Nrand
signif
richness.larger <- Richness(sps.larger)
richness.small <- Richness(sps.small)
richness.dif <- richness.larger - richness.small
Nrand <- 5000
richness.dif.rand <- numeric(Nrand)
richness.dif.rand[1] <- richness.dif
for (i in 2:Nrand) {
 group.rand <- sample(group)
 sps.larger.rand <- subset(sps, group.rand=="larger")
 sps.small.rand <- subset(sps, group.rand=="small")
  richness.larger.rand <- Richness(sps.larger.rand)
  richness.small.rand <- Richness(sps.small.rand)
  richness.dif.rand[i] <- richness.larger.rand - richness.small.rand
  if(i %% 100 == 0) print(i)
}
hist(richness.dif.rand, breaks=40)
abline(v=richness.dif, col="red")
signif <- sum(richness.dif.rand >= richness.dif)/Nrand
signif
##
```

Capítulo 3: Local features driving patterns of habitat use by thin-spined porcupine (*Chaetomys subspinosus*) at home range scale: the influence of edge proximity, forest structure and the abundance and nutritional traits of food resources.

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Abstract

We studied the effects of features linked with habitat quality, such as distance to the forest edge, local forest structure, and the abundance and nutritional traits of food resources, on patterns of habitat use of a small arboreal folivore, the thin-spined porcupine (*Chaetomys subspinosus*) living in a fragmented landscape, the Brazilian Atlantic forest. We also evaluated whether the quality and abundance of selected food plant species differed depending on theirs location (edge x interior) within forest fragments, and if such differences could explain the spatial bias in habitat use. We estimated the utilization distribution (UD) (representing the relative intensity that animal uses the various sites of its home range) by biased random bridge kernel estimator for four adult animals monitored by radio-telemetry in small fragments of the cacao region from southern Bahia state. We identified that total tree basal area, density of lianas, abundance of food tree species, distance to the home range centroid and the distance to forest edge are altogether important variables driving the intensity of habitat use. Although we found no marked differences in the nutritional characteristics of the food items between forest edge and interior, local food abundance was higher in edge, suggesting that its distribution in these locals were important features determining the UDs of the animals. The results suggest that multiple environmental factors here studied, probably in complex ways, are acting together to determine the movement of these animals and consequently influencing the use of space by the target species within of Atlantic forest fragments.

Keywords: home range, edge effect, movement, arboreal folivore, utilization distribution; biased random bridge, plant secondary metabolites.

Introduction

Patterns of space use have been an important issue in animal ecology, and such information has increasingly become essential to understand the impacts of fragmentation and degradation of natural habitats. The decision to move, including the extension and direction of movements, is a an individual response to changes in the environmental space (Van Moorter et al. 2016), but is also a combined result of the species requirements and its abilities to explore and choose available resources (Nathan et al., 2008). In this sense, the evaluation of space-use patterns can provide key information of specie's requirements, allowing the comprehension on how it deals with environmental heterogeneity and anthropogenic-caused changes (Diffendorfer et al. 1995; Ganzhorn 1995; Morales and Ellner 2002; Anderson et al. 2003; Morales et al. 2005; Lehman et al. 2006; Coulon et al. 2008; Moore et al. 2010; Campera et al. 2014).

To access to the full range of foliage, fruits and seeds produced by trees, the arboreal plant-eating mammals apparently must weigh less than 15 kg (Eisenberg 1978). This upper limit of body-weigh severely constrains the ability of these mammals to meet their nutritional requirements from a diet of tree foliage. Such limitations are particularly severe for those species foraging on the foliage of woody plants, dealing with a low nutrient concentration diet (especially protein), high concentrations of components that negatively interfere with digestion (especially lignin and tannins) and a range of potentially toxic allelochemicals (Cork and Foley 1991; Cork 1996). The arboreal folivores tend to strongly respond at individual and population levels to the spatial variations present in tropical forests, which includes the local aspects of vegetation structure, as well as the quantity and quality of food resource available (Ganzhorn 1995; Moore et al. 2010).

The habitat loss and fragmentation are major drivers triggering changes in such local aspects of the forest. In particular, the opening of clearings or edge formation characteristic of disturbed fragments and landscapes, may lead to changes in the structure of the vegetation (Tabarelli et al., 2004; Laurance et al., 2006; Michalski et al., 2007; Santos et al., 2008; Lôbo et al., 2011; Thier and Wesenberg, 2016; Rocha-Santos et al. 2016). Forest remnants in more deforested landscapes retain early successional forest attributes, with overall basal area loss than those more preserved and continuous forest fragments (Rocha-Santos et al. 2016). The edge and gap formations within disturbed forests are likely to trigger major changes in the quality and quantity of leaves (Johns and Skorupa 1987). Although most forest-dependent species are negatively affected by edge-disturbed habitats (Laurance et al. 2000), some particular environmental changes make such disturbed habitats more attractive to some folivorous mammals (Ganzhorn 1995; Lehman et al., 2006). It is expected that the overall structural changes related to edge-formation increase light penetration within a rainforest, thus increasing leaf production, particularly of pioneer or shade-intolerant species that are known to proliferate (Laurance et al. 2006; Tabarelli et al. 2008). In addition, these fast growing species usually show a lower investment in chemical defense compared with those from late successional stage (Coley 1983). Therefore, it is expected that the increased leaf production dominated by species with lower levels of chemical defenses, increases the density of this mammals in edges patches (Ganzhorn 1995; Harding and Gomez 2006).

In addition, it is known that biotic conditions such as light and temperature, influence the concentration of plant secondary metabolites and nutritional traits (Moore et al. 2004; Ballaré 2014, Coley 1983). For instance, some studies of lemurs showed that the exposure to light, due to creation of the edges and forest clearings, leads to an increase in phenolics compounds and tannins (Mole et al. 1988), proteins, sugar, and tannins in leaves available for this strict folivorous mammals (Ganzhorn, 1995). The defensive and nutritional chemistry of most plant populations may be spatially structured (Covelo and Gallardo 2009; DeGabriel et al. 2010; Moore et al. 2014). Therefore, quantitative and qualitative variations in resources availability for arboreal folivore mammals in tropical forests may to occur as a response to edge and gap formations, thus influencing their decisions on how to use the space within their home ranges. This is an issue scarcely investigated, particularly for non-primates folivores mammals from South America, such as sloths and rodents.

The thin-spined porcupine (*Chaetomys subspinosus* Olfers 1818) is a good model to address this question. It is a medium-sized rodent (body weight = 1.6 kg), strictly arboreal and folivore, endemic to the Atlantic Forest biome. Previous studies indicated that individuals have a dietary preference for some pioneer trees species, concentrating its feeding activities on forest edges (Giné et al. 2015), also selecting forest habitats and trees with high structural complexity (i.e., tall trees with high amount of lianas; Giné et al. 2015). At home range and landscape scale, Giné et al. (2010) and Giné et al. (2015) investigated feeding ecology and habitat selection by *Chaetomys* using physical and quantitative attributes of trees, such as diameter, number of lianas and proximity to forest limits, using the frequency of the visits to trees as response variable. Here, we re-evaluated this information within a different spatial scale, using a different approach, aiming to evaluate which habitat features influenced the intensity of use of forest patches within their home range. We used movement-based kernel estimator to characterize the intensity of use (response variable) and aspects of the vegetation structure (tree basal area, density of lianas), proximity (distance to forest edge), cognitive fidelity (distance to center of the home range) and resource abundance (density of foraging trees) as explanatory variables. In addition, we seek to investigate why the thin-spined porcupines prefer edge areas for their feeding activities, particularly addressing the potential role played by its dietary components. We specifically asked: are the plant species comprising its diet more abundant on forest edges than interiors? Are the leaves consumed more nutritious and less chemically defended in the forest edges than interiors? We expected that the increased light incidence on edge provides a more suitable environment for the establishment and growth of seedlings of the pioneer trees that make up the bulk of the diet of this species, such *Albizia pedicellaris, Inga thibaudiana* and *Pera glabrata,* which consequently become more abundant at forest edges. Finally, due to both afore mentioned reasons, we expect that smaller distances to forest limits positively correlates with the intensity to which the thin-spined porcupine use the areas within their home range.

Methods

Study Area

The study was carried out in forest fragments of Southern Bahia, eastern Brazil. The region was originally covered by lowland wet forest (Oliveira-Filho and Fontes 2000), but nowadays is characterized by a variegated landscape composed of a mosaic that includes mature vegetation, secondary, and cocoa shaded plantations. The forest vegetation usually has a tall canopy (20-30 m), abundant epiphytes, ferns, bromeliads, and lianas, highlighting the great diversity and high level of endemism of tree species (Thomas et al., 1998). Average annual temperature is 24 ºC and mean annual precipitation is 2000 mm, with no marked seasonality (Mori et al. 1983). The study area comprises three forest remnants of cocoa farms with 0.7, 2.1 and 18 ha in municipality of Ilhéus (14º25’-15º07’S; 39º32’-38º59’W). These are areas where four individuals of *C. subspinosus* were previously captured and monitored by radio telemetry (Giné et al. 2010; 2015) (Fig. 1). In addition, we included areas located within the limits of the Una

Biological Reserve (Rebio-Una) and neighboring farms located in the municipality of Una (39°18’-39°00’W, 15°23’-15°03’S; Fig. 1) for the collection of leaf samples, necessary to investigate the influence of the edge effect on the levels of the secondary metabolites and nutritional traits from leaves of the diet of thin-spined porcupines.

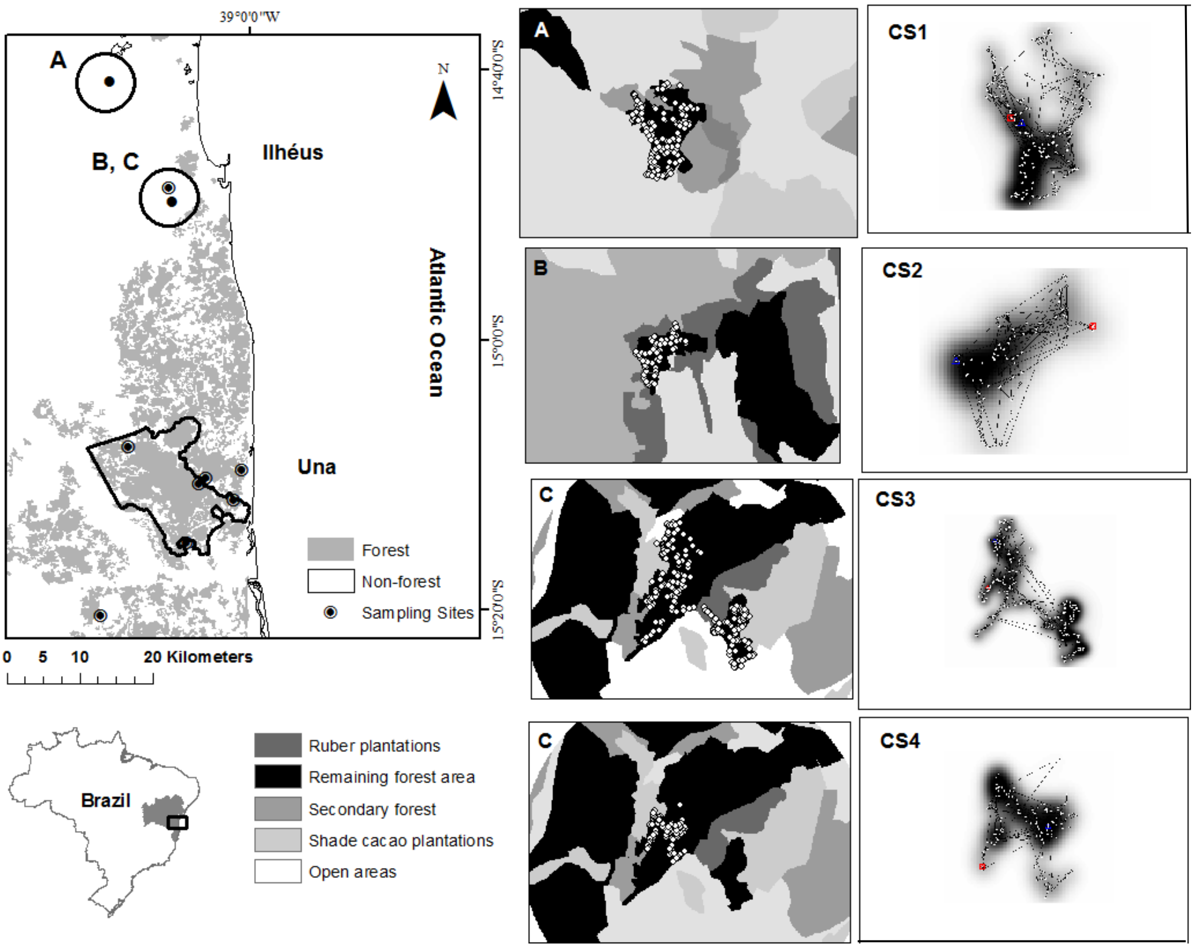

Fig. 1. Study area showing utilization distribution (UD) of four thin-spined porcupines studied (CS1, CS2, CS3, and CS4) inside three forest fragments (A, B, C), and 8 sampling sites (black circles) at southern Bahia, southeastern Brazil.

Capture and tracking

We captured 4 free-ranging adult thin-spined porcupines (3 females and 1 male) that were detected on the canopy of the forest remnants (see Giné et al., 2010; Table 1). After manually captured, we immobilized each animal with an intramuscular injection of ketamine (5 mg/kg) and xylazine hydrochloride (2 mg/kg). While sedated, we weighed each individual and fitted on its neck a ball-chain collar with an attached radio-transmitter weighing 50 g (model 080; Telonics Inc., Mesa, Arizona). We attached a reflective tape to each transmitter to improve the visual detection of each animal during the observation sessions when using flashlights. Once tagged, the animal was released in same place of its capture.

Table 1. Tracking period, number of sampled trajectories (burst), number of relocations (fixes), and number of trees used (trees) by 4 porcupines studied in Atlantic Forest, Brazil. FS = forest fragment size; BM = body mass (adapted from Giné et al. 2010).

Individual	BM	FS	Tracking Period	Bursts	Fixes	Trees
CS01	1650	2.1	Apr 2005–Mar 2006	35	2300	171
CS02	1650	0.7	Jun 2005-Jul 2006	42	2838	89
CS03	1500	18	Oct 2005-Sep 2006	35	2088	238
CS04	2000	18	Oct 2005-Sep 2006	34	2003	135
Total				146	9229	633

We monitored each animal for 2 to 4 nights each month, during 34–42 nocturnal periods of 6 h (1800–0000 h or 0000–0600 h), totalizing 146 half-night periods (944 h) from March 2005 to September 2006. Details are described in Giné et al. (2010). In each session, we recorded the animal location every 10 min, marking the tree used with plastic tag and then obtained the geographical position of the tree used by mapping all tree as described by Giné et al. (2012). The set of the successive relocations obtained for each half-night period was considered as one trajectory distinct in subsequent analysis, named as “burst” (Calenge, 2006).

Utilization distribution (UD)

Based on the movement descriptors, (i.e. trajectories recorded of the each thin-spined porcupine) we evaluated how intensely animals used different areas of the forest remnants, estimating the distribution of utilization performed by animal within its home range applying the Biased Random Bridge kernel method (BRB; Benhamou 2011). This procedure generates a particular movement-based kernel density estimator (MKDE). For this, we used the "BRB" function of the adehabitatHR package (Calenge, 2006) from R software (R Core Team, 2015). We defined the smoothing parameters (hmin) as equal to 10 (GPS-error), tau equal to 1.0*60, Lmin equal to 0.5, Tmax equal to 8*60*60, and the diffusive coefficient D was estimated by maximum likelihood. This analysis generates a utilization distribution raster map with 2.5 m cell size, representing the relative time spent in different areas or, in other words, how intensely each animal used each area (cell) within its home range. We used this raster layer to extract the UD value for each animal location. We chose the BRB method because, contrary to the traditional Brownian bridge method (Benhamou and Cornélis 2010), it assumes an advection–diffusion process (i.e. a biased random walk) between locations instead of a purely and constantly diffusive (random) movement between relocations (Benhamou, 2011). At this spatial scale, it is more realistic and reliable, as trajectories are sets of sequential movements directly subjected to habitat selection (Giné et al. 2015). In addition, this approach also allows us to consider the dependency on the time between locations using Brownian motion variance to describe the animal's mobility (Benhamou 2011).

Habitat descriptors

In order to sample the potential habitat traits explaining the intensity of use of the areas within home ranges, we estimated for each animal location the distance to forest limits (EDGED) and distance to the center of the home range (CENTER). To do it, we firstly mapped the forest limits of every vegetation types within and around of each individual’s home range using 1:5,000-scale aerial photographs taken in 2001 and 2002 (Giné et al. 2015). We also used the same maps to estimate the center of each animal home range defined by the minimum convex polygon method (MCP100%). We then created a raster map with the distance to forest limits and the distance to the center of the home range using the “Euclidean distance” function of the Spatial Analyst Tools extension from ArcGIS software version 10.1 (ESRI 2012) and the same resolution used for previous UD’s raster (cell size = 2.5 m). For each animal location we extracted the values of EDGED and CENTER using the “extract multi values to points” function.

For assessing the remaining variables, we allocated 100 m^2 plots (10 x10 m) regularly distributed in each home range (determined by MCP100% method; see details in Giné et al. 2010). In each plot, we identified and measured all the trees with ≥ 10 cm diameter at breast height (DBH), also recording the number of lianas. This information allowed us to estimate, for each plot, ABASAL (i.e., sum the basal area of each individual tree within plot); PIONEER (i.e., density of pioneers species); NLIANAS (i.e., sum of the number of lianas climbing each individual tree within plot), FORAGE (i.e., density of the trees whose species was consumed by animals); PREFER (i.e., density of three most preferred species by porcupines: *Albizia pedicellaris*, *Pera glabrata*, *Inga thibaudiana*, including *Inga capitata*, and *Inga affinis*). Then, in order to generate environmental raster that represent the variation of each habitat measure in home range, we performed for each variable of the plots an interpolation by kriging method using the default of the “kriging” function from Spatial Analyst Tools extension. Finally, we extracted for each animal location the values of each environmental raster created using “extract multi values to point” function (ESRI 2012).

Leaf secondary metabolites and nutritional traits

To evaluate whether leaf chemical and nutritional traits of the foraging species consumed by thin-spined porcupine differed between edge and interior forest fragments, we sampled leaves of individual trees located within the forest edge (0 - 10 m of the forest limits) and forest interior (at least 50 of forest limits) and accessed their nutritional and chemical content. We selected the two plant species most consumed by porcupines, *Pera glabrata (Schott)* Poepp. ex Baill. (Euphorbiaceae) and *Albizia pedicellaris* DC. (Fabaceae) (see "Capítulo 2" from this thesis). We first established plots of 1000 m^2 (10 x 100 m) in the forest edge and interior of the 8 forest fragments (Fig. 1). In each plot we collected at least two samples of ~ 200 g of young leaves of each plant species. When the species was absent from the plot, we actively searched for trees outside the plot respecting the pre-established distance of edge and interior categories. In total, 34 samples were collected from leaves of each species. We averaged the values of the trees sampled in each environmental category (edge and interior) to get a single value for data analysis.

After sampling, fresh leaves were weighted, dried in an air forced circulation stove (40ºC) and posteriorly, milled to a fine powder (0.25mm). We accessed the foliar contend of the dry matter (DM; expressed in percentage), crude protein (CP; expressed in g/kg dry weight and then by percentage), total phenolic content (TP; expressed in tannic acid equivalents - g/kg dry weight) and condensed tannins (CT; expressed in leucocyanidin equivalents - g/kg dry weight). The dry matter (DM %), defined as the fraction of the food excluded its natural moisture, was determined as the percentage of the weight of the dry matter (weight after complete drying) in relation to fresh matter (weight immediately after field collection) (Wilson et al. 1999). We assumed that the leaf when collected was in perfect state of water balance and that it did not vary significantly between the collection campaigns. The content of mineral nitrogen were accessed with micro-Kjeldahl method (AOAC 1995) and the crude protein (CP) was estimated by multiplying the value of mineral nitrogen by 6.25, based on the assumption that proteins of typical animal feeds contain 16% nitrogen in average, a common approach (McDonald et al. 2010). We accessed the total phenolic content (TP) and condensed tannins (CT) contents using Folin-Ciocalteu (according to Makkar et al., (1993) and Butanol-HCl (following Porter et al. 1986) assays, respectively.

Abundance of the main foraged plant species

To evaluate if forest edge (0 - 10 m of the forest limits) and interior (> 50m of the forest limits) differ regarding the abundance of the main foraged plant species, we counted all adult individuals (DBH> 10cm) of such plants in each sampling plot. We could not find sufficient number of *Inga thibaudiana* to include this species on the bromatologically analysis.

Statistical analysis

Habitat variables and utilization distribution (UD)

Generalized additive models (GAM) with “Beta” distribution (link logit) were performed on data sets to examine which habitat variables influenced the intensity of use (or utilization distribution - UD) of porcupines on their home ranges. GAM enabled us to analyze highly non-linear and non-monotonic relationships, and also allows us to know the relation of each variable separately. Previously, we performed Spearman correlations between all pairs of explanatory variables and, since low correlations ($r < 0.6$) were observed, all habitat variables sampled were considered in the models. In addition, we performed Mantel test for UD values of the animal location and we found spatial autocorrelation of this variable (Pearson’s product moment correlation: $r=0.63$; $p=0.001$). Then, the coordinates for each tree utilized were included as smoothed terms in GAM models. In this class of models, the residuals are assumed as independent.

We ran the model using "gam" function from the "mgcv" package (Wood 2011). We then performed a model selection (Burnham and Anderson, 2002) based on Akaike's Information Criterion corrected for small sample size (AICc), testing all possible combinations among explanatory variables and null model using "dredge" function from the "MuMIn" package (Barton 2013). The candidate models were ranked and considered equally plausible to explain the observed pattern, when AICc differences (Δi) were lower than 2. Then, we determined the best model choosing the most parsimonious model among those with lower AICc and corresponding higher Akaike weights (ωi). We performed all statistical analyses in R version 3.2.3 (R Core Team 2015).

The role of edge effects on chemical leaf traits

To determine whether chemical leaf traits differed between plants located in forest edges and interiors, we performed a linear mix models (LMM), assuming fulfillment of data linearity, residuals normality, and variance homoscedasticity premises. When the responses variable had non-normal distribution (CP, TP, and CT) we used a generalized linear mixed model (GLMM), with Gamma distribution and identity link function. We added the environment (edge and interior) as fixed effect, and the study sites as random effects. We compared the fixed effect with the null model for each response variable (DM, CP, TP, and CT) using the likelihood ratio test approach, which compares the odds of two models to consider a fixed effect if the difference between the likelihood of these two models is significant ($p<0.05$). Models were run for GLMM and LMM, using "glmer" or "lmer" functions, respectively, both from the "lme4" package from R software (R Core Team 2015). Finally, we determined whether abundance of most consumed plants species differed between interior and edge plants by applying paired-samples *t*-tests.

Results

The influence of the habitat descriptors on utilization distribution (UD)

The four thin-spined porcupines assessed used 633 trees during the 146 trajectories and 9,229 relocations sampled (Table 1). The GAM analyses showed that the best model ($R^2_{adj} = 0.992$, $n = 633$) predicting the utilization distribution (UD) included all explanatory variables assessed, except the density of pioneer species (PIONEER; Table 2).

Table 2. Model selection based on Akaike´s criterion correct for small samples (AICc), to evaluated which habitat features best explain the utilization distribution (UD) made by thin-spined porcupines (*Chaetomys subspinosus*) within their home range. Generalized additive models used the following explanatory variables: total basal area (ABASAL); number of lianas (NLIANAS); density of top-ranked forage species (PREFER); density of total forage species (FORAGE); density of pioneer species (PIONEER); edge distance (EDGE), center home range distance (CENTER).We also show the number of degrees of freedom (K), AICc differences (Δi), and Akaike weights (ωi).

Model rank	Candidate models[a]	K	Δi	ωi
1	ABASAL+NLIANAS+PREFER+FORAGE+EDGE+CENTER	76	0.0	0.484
2	ABASAL+NLIANAS+PREFER+FORAGE+EDGE+CENTER+PIONEER	77	1.08	0.283
3	ABASAL+NLIANAS+ FORAGE+EDGE+CENTER	69	2.06	0.173
4	ABASAL+NLIANAS+FORAGE+EDGE+CENTER+PIONEER	70	4.18	0.060

[a] Only models with Akaike weights(ωi) greater than 0 are show.

The model including all possible variables (full model) was equally plausible, but with lower Akaike weight (ωi) and less parsimonious, suggesting that PIONEER variable has low relevance to the model. The best model showed significant *p*-values for all explanatory variables (ABASAL [$p < 0.001$, edf = 8.21]; NLIANAS [$p < 0.001$, edf = 7.58]; PREFER [$p < 0.05$, edf = 5.29]; FORAGE [$p < 0.001$, edf = 7.72]; EDGE [$p < 0.001$, edf = 4.75], CENTER [$p < 0.001$, edf = 7.87]), except for the PIONEER variable ($p = 0.51$; edf = 1). The Pearson's product moment correlation (r) between UD and explanatory variables was significant for EDGE (r = - 0.19, p < 0.001), CENTER (r = - 0.26, $p < 0.001$; t = - 6.95), ABASAL (r = 0.22, $p < 0.001$), and NLIANAS (r = 0.17, $p < 0.001$). The utilization distribution (UD) was positively correlated with total basal area (ABASAL), especially in the range between 1500 and 3000 m^2 (Fig. 2a). The UD was also positively influenced by edge distance (EDGE), being noticed the upturn of the UD close to 20 m from the edge.

When we looked at distance to home range center (CENTER) smooth curve through the residuals, we observed that thin-spined porcupines preferred to use areas far 50 to 100 meters from the center of their home range. We also observed a clear downturn in the trend of UD after about 100m to center and again a smoother increase between 150-200m, showing a clear multi-modal response to this single variable. Although there is also a positive relationship between liana and UD, animals did not use sites with high infestation of lianas (NLIANAS) (Fig. 2a).

We observed that both the density of all foraged (FORAGE) and preferred species (PREFER) for consumption are important to predict the increase of UD, but for FORAGE, the number of species is between 3 - 4, whereas for the preferred, one species is enough for increase UD. The density of pioneer species within animals' home range plots is the only variable not influencing habitat use by these animals (Fig. 2b).

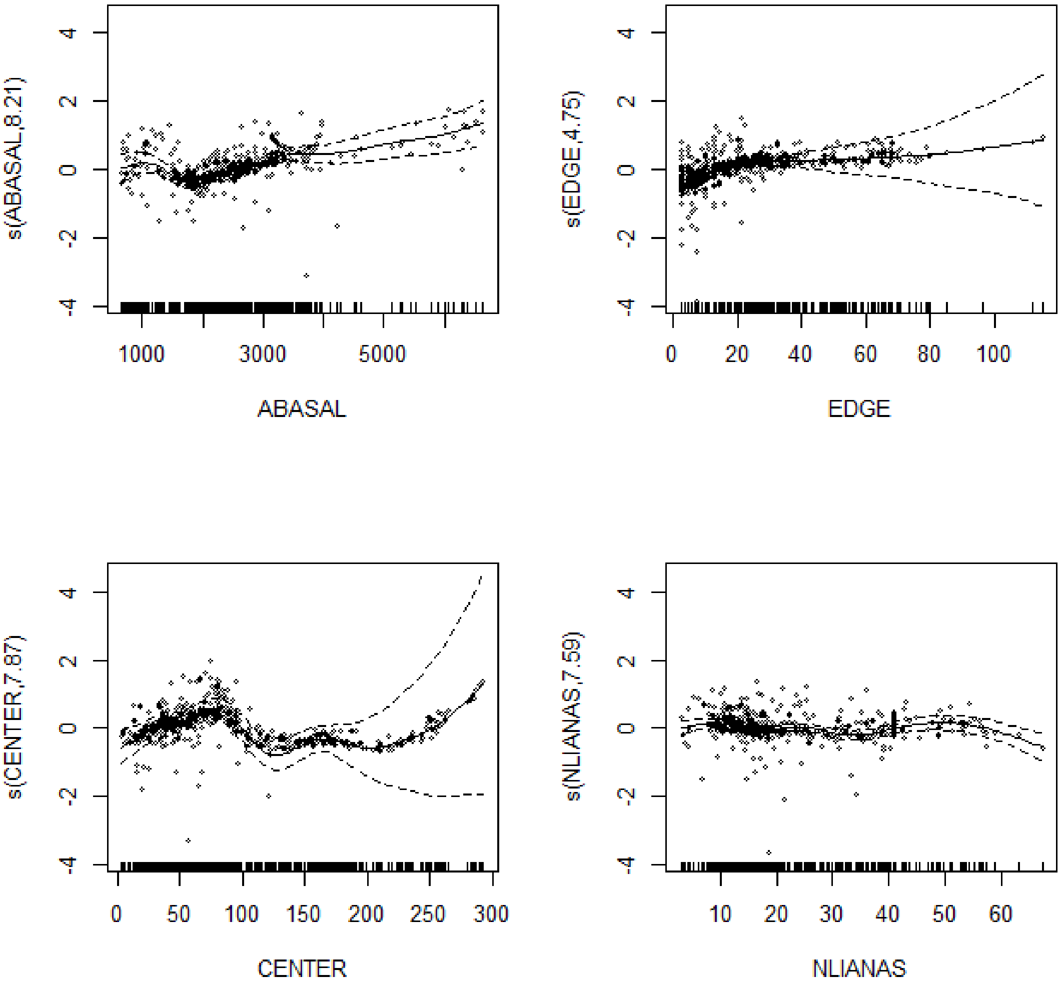

Fig. 2a. Contributions of the model terms (ABASAL, EDGE, CENTER, and NLIANAS) to utilization distribution (UD) for thin-spined porcupines at south Bahia, Brazil. Residuals from the regression of UD on model terms, with smooth curve fit. The solid line is the predicted value of the dependent variable (UD) as a function of the x axis. Dotted lines represent standard errors.

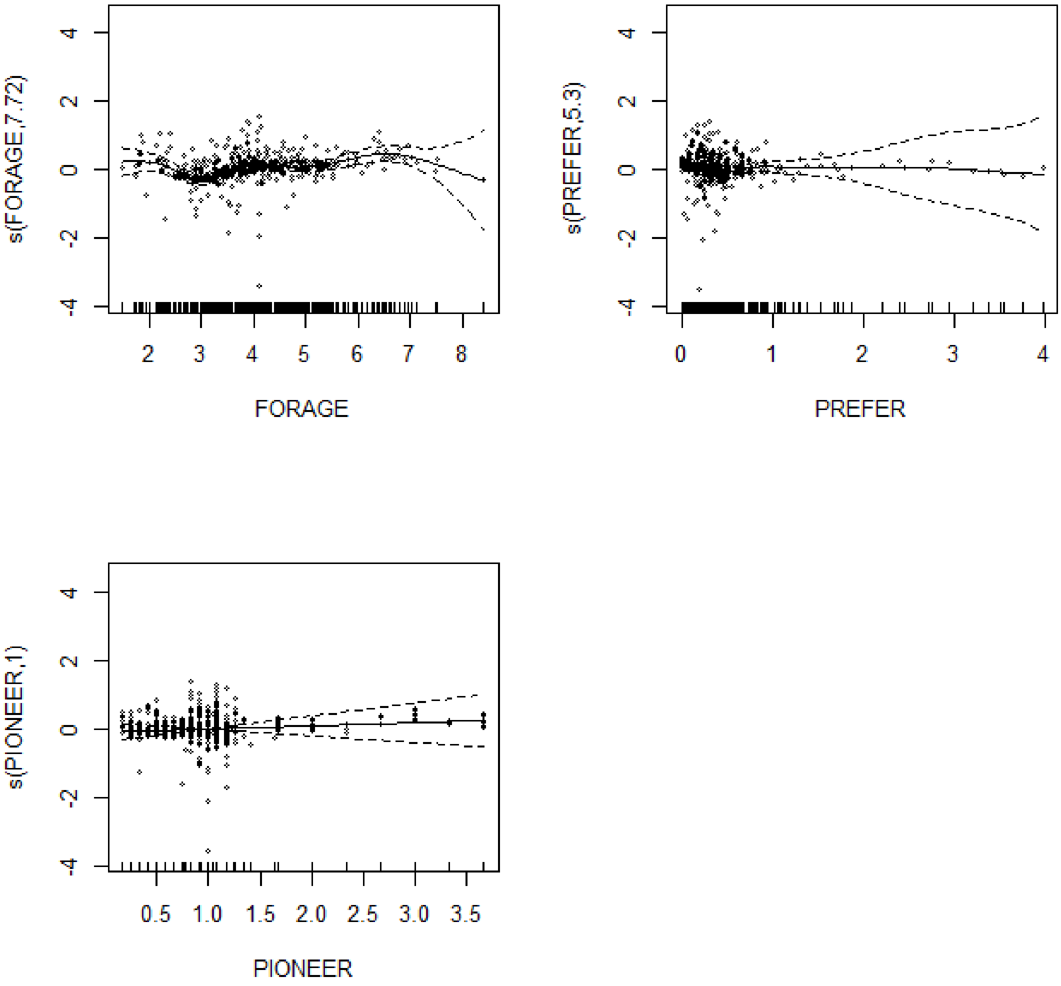

Fig. 2b. Contributions of the model terms (FORAGE, PREFER, and PIONEER) to utilization distribution (UD) for thin-spined porcupines at southern Bahia, Brazil. Residuals from the regression of UD on model terms, with smooth curve fitting. The solid line is the predicted value of the dependent variable (UD) as a function of the x axis. Dotted lines represent standard errors.

Edge effects

Dry matter content (DM%) from *A. pedicellaris* leaves was lower in the forest edge than interior (49.45 ± 3.64% vs 51.0 ± 4.42%, respectively; p =0.031; χ^2 = 4.60; df = 1), indicating that leaves of this species have a greater amount of moisture when located in forest edge. We found no evidence of difference in the content of the crude protein - CP (*p* = 0.209, χ^2 = 1.57, df = 1), TP (*p* = 0.772, χ2 = 12.08, df = 1), and condensed tannins - CT (*p* = 0.915; χ^2 = 0.01, df = 1) in the leaves of this species between these categories. In leaves of *P. glabrata*, we found lower concentrations of the CP (p = 0.042, χ^2 = 4.1, df = 1) in the forest edge (9.29 ± 2.21 %) than interior (10.55 ± 1.81 %; Table 3), but no significant differences in mean concentrations of DM (*p* = 0.49., χ^2 = 0.45, df = 1), TP (*p* = 0.95, χ^2 = 0.003, df = 1) and CT (*p* = 0.54, χ^2 = 0.35, df = 1). We observed a greater abundance of *Albizia pedicellaris* (Fabaceae) in the forest edges than interior (3.25 ± 1.98 *vs* 0.63 ± 1.56, respectively, *p* = 0.02, n = 31, df = 7) for all eight studied areas. It was not seen for *Pera glabrata* (4.25 ± 5.65 *vs* 3.25 ± 7.30, respectively, *p* = 0.65, n = 60, df = 7) (Table 3). *Inga thibaudiana* trees were only found at forest edges (0.5 ± 1 *vs* 0, respectively, n = 4), and just in two sampling areas.

Table 3. P-values (*p*) and estimates (standard error SE) for comparisons between edge and interior trees in leaves content of dry matter (%), crude protein (%), total phenolics (g.kg^{-1} dry weight), and condensed tannins (g.kg−1 dry weight), for tree species *Albizia pedicellaris* and *Pera glabrata*. Generalized linear mixed models (GLMM) and linear mix models (LMM)* and were computed with sampling sites and environment category (interior or edge) as random and fixed effects, respectively. * *p* < 0.05.

Response variables	*Albizia pedicellaris*		*Pera glabrata*	
	Estimate (SE) $^{a.}$	*p*	Estimate (SE) $^{a.}$	*p*
DM	2.49 (1.10)	0.031*	0.58 (0.86)	0.498
CP	-9.41 (7.40)	0.203	10.5 (5.09)	0.043*
TP	4.14 (14.33)	0.915	0.81 (13.77)	0.953
CT	-1.40 (13.22)	0.772	-13.17 (21.90)	0.547

[a.]Values for estimates (SE = standard error) are the differences between means from edge plants and interior plants (positive estimate values show high means for interior plants).

Discussion

Our results reveal that an array of local features linked to the complexity of the forest structure (basal area, density of lianas), the abundance of resources (density of the consumed and preferred foraging species), site fidelity (distance to home range center) and edge distance, contributed to porcupine's habitat choice during their movements. In other words, these features are important determinants of the utilization distribution patterns, thus affecting how intensively the individuals use the different areas within their home range. Of particular importance, although our results corroborates that edges are attractive areas to thin-spined porcupine, but this pattern is not driven by differences in the chemical or nutritional contents of leaves at these sites (< 10 m of the forest limits), but it rather occurs as a function of a higher abundance of the two most consumed plant species on forest edges.

The studied species distribute their activities within their home range in a complex way, influenced by a multitude of variables. For an animal with such metabolic restrictions to meet it daily needs to obtain and save energy, feeding and resting are probably the most important activities of its routine, being selective and spending more time where the abundance of the feeding resources is high. We also observed that the intensity of space use is highly influenced by the distance to center of the home range. However, in this case some studies have shown that this behavior may also be associated with cognition abilities, safety conditions, and resource use efficiency (Forrester et al. 2015; Bartlett et al. 2016). When an individual concentrates its movement in specific patch habitat close to the center of its home range, the animal relies on its previous experience to increase the frequency of visiting more suitable areas, thus directing its movements towards these more rewarding areas. Therefore, decisions involving departure from the previous location are based on observed or anticipated local environmental conditions (e.g., resource depletion, bad experience with predators), whereas decisions regarding visiting a new location are based on expected environmental conditions, that are obtained through perception or memory (Van Moorter et al. 2016).

Giné et al. (2015) showed that the thin-spined porcupine is highly selective regarding trees attributes related to resting and moving, choosing those large trees with high presence of lianas, while preferably feeding on large trees located on forest edges. Our results indicate that habitat use by this species is also influenced by the structure of the forest around the used trees, with the species selecting areas (forest patches) with high density of the lianas and woody density. The choice of areas with higher woody density, or carbon storage, and lianas infestation probably brings advantages for routine displacement and resource acquisition as well as escape routes and hiding places from predators, as already discussed by Giné et al. (2015). In addition, Giné et al. (2015) showed that the species usually selected tangles of lianas to rest during the day, mainly located near forest edges (20 m). This is very similar to our findings, with the increasing of the utilization distribution (UD) from this distance to the limit of the fragment. Altogether, the afore mentioned preferences are compatible to an energy-conserving lifestyle, as resting near the food likely reduces movement costs thus increasing the efficiency of the resource allocation.

Based on the results regarding vegetation structure we suggest that this species is likely to be affected by anthropogenic actions. The most evident is the illegal conversion of the native forest habitats to open areas or some structurally more simplified habitats, including those resulting from the formation of agroforest systems (e.g. shade cacao plantations) and due to the advance of residential areas on forests. In addition, forest remnants are further explored by selective logging and lianas extraction, processes that are likely to decrease the quality of the habitat for focal species. On other hand, anthropogenic effects linked to habitat fragmentation such edge formation may actually increase the amount of lianas and pioneer species in forest remnants, two resources largely used by thin-spined porcupine. Although the density of pioneer species did not influence animals UD´s, possibly due to a uniform distribution in studied forest area, the most consumed plant species are pioneers and our results suggested that these plants are favored in forest edges.

The content of secondary metabolites and nutritional of the leaves between the two environments (edge and interior of the fragments) did not allow us to answer the question of which drives the preference of *Chaetomys* for feeding on the forest edges. We addressed this issue focusing on potential differences in the quality and quantity of food resource between forest edge and interior, assessing these differences in three species most consumed by the species. The content of phenolic compounds, which included condensed tannins, did not vary at patch-scale regarding edge and interior. The *A. pedicellaris* is an emergent species from forest canopy, which means that even the leaves of those trees located in the interior of fragment are still highly exposed to intense sunlight, implying that the species can keep the concentrations of tannins (CT), total phenolics (TP) and crude protein (CP) to levels similar to those individuals located within forest edges. We found that the new leaves of *A. pedicellaris* have more water and less dry matter at the edge, which may be an indication that the leaf is more palatable at the edge (less lignified).

Analyzing the leaf content of the *P. glabrata*, we found that the total protein content is significantly higher at forest interior, oppositely to what we predicted (Woodward 1990; Ganzhorn 1995). This may have occurred for multiple reasons likely due to a higher availability of nutrients, possibly as a response to a deeper litter and richer soil commonly found in the forest interior or be due to protein denaturation and inhibition of the protein synthesis at higher temperatures in the edge, since the injury from high temperature has often been attributed to the denaturation of proteins (Gulen and Eris 2004).

Therefore, our results suggest that the preference for foraging in edges areas was influenced by a greater local abundance of the *A. pedicellaris* and *Inga thibaudiana*, which are the two species most consumed by the target species in this region (Giné et al. 2010; Chapter 02) and over which the studied animals spent 77.8% of their feeding time (Giné et al. 2010). It has been shown that the abundance of *I. thibaudiana* decreases from the edge to the interior in the areas studied by (Charles-Dominique et al. 1981). Therefore, it is possible that *I. thibaudiana* is not absent from the interior of the fragments, but probably its abundance is so low that it was not captured by our sampling. In addition, the higher humidity was obtained in leaves of the *A. pedicellaris* from forest edges, a feature that can be linked to a higher productivity of young leaves. As we did not control for such variable, probably both are affecting the selection since that allow greater access to resource and water by porcupines.

The results of this study reinforce the findings of Giné et al. (2015) on the factors that influence the frequency of visits to trees, home range and habitat selection, but mostly importantly, it is occurring in a different spatial scale. We detected that edge formation may have a positive effect on the focal species by allowing for the proliferation of important food items and increasing the complexity of specific features of the forest structure with a key role on the species movement, the lianas. However, fragmentation also triggers further degradations of remnants, such as fire and selective logging, that are likely to alter other aspects of the vegetation structure that are likely to be detrimental for this species. Although the species is well adapted to these small fragments of secondary vegetation, the concentration on the use of space in certain patches within its home range may increase the vulnerability of the focal species to local disturbances in the fragment boundaries.

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References

AOAC. 1995. Official methods of analysis of AOAC. P. in. AOAC international.

BALLARÉ, C. L. 2014. Light regulation of plant defense. Annual review of plant biology 65:335–63.

BARTLETT, T. Q., L. E. O. LIGHT AND W. Y. BROCKELMAN. 2016. Long-term home range use in white-handed gibbons (Hylobates lar) in Khao Yai National Park, Thailand. American Journal of Primatology 78:192–203.

BARTON, K. 2013. MuMIn: Multi-model inference. R package version 1.9.13. <http://cran.r-project.org/package=MuMIn>.

BENHAMOU, S. 2011. Dynamic approach to space and habitat use based on biased random bridges. PLoS ONE 6.

BENHAMOU, S. AND D. CORNÉLIS. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. Journal of Wildlife Management 74:1353–1360.

CALENGE, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

CAMPERA, M. ET AL. 2014. Effects of Habitat Quality and Seasonality on Ranging Patterns of Collared Brown Lemur (Eulemur collaris) in Littoral Forest Fragments. International Journal of Primatology 35:957–975.

CHARLES-DOMINIQUE, P. ET AL. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt Guyanaise: interrelations plantes-animaux. La Terre et la Vie, Revue d'Ecologie 35:341–435.

CORK, S. J. 1996. Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: Why Koalas and Colobines are different. Australian Journal of Ecology 21:10–20.

CORK, S. J. AND W. J. FOLEY. 1991. Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. Pp. 133–166inPlant defenses against mammalian herbivory(C. T. Palo, R.T. & Robbins, ed.). CRC Press, Boca Raton, Florida.

COULON, A., N. MORELLETT, M. GOULARD, B. CARGNELUTTI, J. M. ANGIBAULT AND A. J. M. HEWISON. 2008. Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. Landscape Ecology 23:603–614.

COVELO, F. AND A. GALLARDO. 2009. Changes in the spatial structure of oak carbon-based secondary compounds after pine harvesting. Forest Ecology and Management 258:2511–2518.

DEGABRIEL, J. L., B. D. MOORE, K. J. MARSH AND W. J. FOLEY. 2010. The effect of plant secondary metabolites on the interplay between the internal and external environments of marsupial folivores. Chemoecology 20:97–108.

DIFFENDORFER, J. E., M. S. GAINES AND R. D. HOLT. 1995. Habitat fragmentation and movements of three small mammals. Ecology 76:827–839.

EISENBERG, J. F. 1978. The evolution of arboreal herbivores in the class Mammalia. P. 135 – 152. in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

ESRI. 2012. ArcGIS Desktop: Release 10.1. Redlands, CA: Environmental Systems Research Institute.

GANZHORN, J. U. 1995. Low-Level Forest Disturbance Effects on Primary Production, Leaf Chemistry, and Lemur Populations. Ecology 76:2084–2096.

GULEN, H. AND A. ERIS. 2004. Effect of heat stress on peroxidase activity and total protein content in strawberry plants. Plant Science 166:739–744.

HARDING, E. K. AND S. GOMEZ. 2006. Positive edge effects for ar boreal marsupials : an assessment of potential mechanisms. Wildlife Research 33:121–129.

LAURANCE, W. F. ET AL. 2006. Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy of Sciences of the United States of America 103:19010–4.

LAURANCE, W. F., H. L. VASCONCELOS AND T. E. LOVEJOY. 2000. Forest loss and fragmentation in the Amazon. Oryx 34:39–45.

LEHMAN, S. M., A. RAJAONSON AND S. DAY. 2006. Edge effects and their influence on lemur density and distribution in southeast Madagascar. American Journal of Physical Anthropology 129:232–241.

MAKKAR, H. P. S., M. BLÜMMEL, N. K. BOROWY AND K. BECKER. 1993. Gravimetric determination of tannins and their correlations with chemical and protein precipitation methods. Journal of the Science of Food and Agriculture 61:161–165.

MCDONALD, P., R. A. EDWARDS, J. F. D. GREENHALGH, C. A. MORGAN, L. A. S. HARPER AND R. G. WILKINSON. 2010. Animal Nutrition. P. in. 7th Editio.

MOLE, S., J. A M. ROSS AND P. G. WATERMAN. 1988. Light-induced variation in phenolic levels in foliage of rain-forest plants - I. Chemical changes. Journal of Chemical Ecology 14:1–21.

MOORE, B. D., R. L. ANDREW, C. KÜLHEIM AND W. J. FOLEY. 2014. Explaining intraspecific diversity in plant secondary metabolites in an ecological context. The New phytologist 201:733–50.

MOORE, B. D., I. R. LAWLER, I. R. WALLIS, C. M. BEALE AND W. J. FOLEY. 2010. Palatability mapping: A koala's eye view of spatial variation in habitat quality.

Ecology 91:3165–3176.

MOORE, B. D., I. R. WALLIS, J. T. WOOD AND W. J. FOLEY. 2004. Foliar nutrition, site quality, and temperature influence foliar chemistry of tallowwood (Eucalyptus microcorys). Ecological Monographs 74:553–568.

VAN MOORTER, B., C. M. ROLANDSEN, M. BASILLE AND J. GAILLARD. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology 85:21–31.

MORALES, J. M. AND S. P. ELLNER. 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. Ecology 83:2240–2247.

MORALES, J. M., D. FORTIN, J. L. FRAIR AND E. H. MERRILL. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. Landscape Ecology 20:301–316.

MORI, S. A., B. M. BOOM, A. M. DE CARVALHO AND T. S. DOS SANTOS. 1983. Southern Bahian moist forests. The Botanical Review 49:155–232.

NATHAN, R. ET AL. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105:19052–19059.

OLIVEIRA-FILHO, A. . AND M. A. A. FONTES. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern brazil and the influence of climate. Biotropica 32:793–810.

PORTER, L. J., L. N. HRSTICH AND B. G. CHAN. 1986. The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. Phytochemistry 25:223–230.

R CORE TEAM. 2015. R: a language and environment for statistical computing. Version 3.2.3. *R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.* .

ROCHA-SANTOS, L. ET AL. 2016. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biological Conservation 196:1–9.

TABARELLI, M., A. V. LOPES AND C. A. PERES. 2008. Edge-effects Drive Tropical Forest Fragments Towards an Early-Successional System. Biotropica 40:657–661.

THIER, O. AND J. WESENBERG. 2016. Floristic composition and edge-induced homogenization in tree communities in the fragmented Atlantic rainforest of Rio de Janeiro , Brazil . Tropical Conservation Science 9:852–876.

WILSON, P. J., K. A. THOMPSON AND J. G. HODGSON. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytologist 143:155–162.

WOOD, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73:3–36.

WOODWARD, F. I. 1990. From ecosystems to genes. The importance of shade tolerance. Trends in Ecology & Evolution 5:111–115.