

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

**INFLUÊNCIA DA DISPONIBILIDADE DE ALIMENTO NA ÁREA DE
VIDA DE BRADYPUS VARIEGATUS (XERNARTHRA:
BRADYPODIDAE) EM FLORESTA ALAGADA DE IGAPÓ**

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Manaus, Amazonas

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BRADYPODIDAE) EM FLORESTA ALAGADA DE IGAPÓ**

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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

ATA DA DEFESA PÚBLICA DA
DISSERTAÇÃO DE MESTRADO DO
PROGRAMA DE PÓS-GRADUAÇÃO EM
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Sinopse

O trabalho investiga a área de vida, deslocamento e uso do espaço por *Bradypus variegatus* e os efeitos da sazonalidade da produção vegetal do *igapó*. Também são levantados as estratégias adotadas pela espécie para perpetuar em um ambiente sazonal.

Palavras-chave: Área de vida, *Bradypus*, produção foliar, sazonalidade.

Ao amor de uma vida

Daniele

RESUMO

O uso do espaço por animais é influenciado por fatores bióticos e abióticos. Para animais herbívoros a sazonalidade na produção vegetal é considerada o principal preditor da movimentação, migração, área de vida e conseqüentemente, uso do espaço. Enquanto os efeitos da sazonalidade da produção vegetal são bem descritos para regiões temperadas e para os Paleotrópicos, pouco é conhecido sobre o efeito *bottom-up* em mamíferos herbívoros do Neotrópico. Um dos mais abundantes herbívoros das Américas são as preguiças-comum, *Bradypus variegatus*. A vasta distribuição da espécie inclui populações com grande variedade no padrão de atividade e tipos de habitat. Na bacia Amazônica a espécie pode ser encontrada em um ambiente fortemente sazonal, o *igapó* – uma floresta alagada sazonal com fenologia demarcada por pulsos de produção foliar. Utilizando uma combinação de telemetria e análises fenológicas, este estudo apresenta padrões na movimentação das preguiças relacionando com conseqüentes estações e diferenças na disponibilidade de alimento. As preguiças ocuparam em média 1.29ha da floresta alagada como área de vida e se deslocaram em média 32m por dia. A dieta foi integralmente constituída de folhas e *Hevea spruceana* demonstrou ser um recurso importante e consumida em todas as estações.

ABSTRACT

Use of space by animals is influenced by both biotic and abiotic factors. For herbivorous mammals seasonality in forage production is considered to be the main driver of movement patterns, home range size and consequently, the use of space. While such effects are well-researched in temperate regions and the Palearctic, little is known about the bottom up effect of productivity on herbivorous mammals in the neotropics. One of the most abundant herbivores in the Americas is Brown-throated sloth, *Bradypus variagatus*. The species' wide distribution includes populations with a great variety of activity patterns and habitat types. In the Amazon basin the species can be found in a strongly seasonal environment, the *igapó* – a seasonally-flooded riverine forests with strongly-pulsed leaf-production phenology. Using a combination of telemetry and phenological analysis, this study recorded patterns in sloth movement, and relate these to seasonal and within-forest differences in food availability. Mean home range size was 1.29ha mean daily movement was 32m, and did not vary seasonally.

Diet was entirely of leaves and *Hevea spruceana* was a important resource and used in all seasons.

LISTA DE FIGURAS

Figure 1. Açutuba Igapo a) State of Amazonas, Brazil. b) Iranduba, AM. Açutuba represented by the black square. c) Açutuba Protect Forest. Area of study represented by the white square.

Figure 2. *Bradypus variegatus* on Igapó.

Figure 3. *hevea spruceana* with new leaves in Igapó.

Figure 4. Home Range use of sloths in Açutuba.

Figure 5. Forage production along the time.

Figure 6. Forage production in *Igapó* assemblage and *hevea spruceana* population.

Figure 7. Sloth daily displacement and forage production.

INDICE GERAL

| | |
|--|---|
| INTRODUÇÃO GERAL | 10 |
| OBJETIVO GERAL | 103 |
| Capítulo I..... | 144 |
| ABSTRACT..... | Erro! Indicador não definido. 5 |
| INTRODUCTION..... | Erro! Indicador não definido. 6 |
| METHODS | 19 |
| STUDY AREA | 19 |
| DATA COLLECTION | 20 |
| CAPTURE AND MARKING THREE-TOED SLOTHS..... | 21 |
| MOVEMENTS AND RANGE ESTIMATES..... | 21 |
| FORAGE AVAILABILITY | 22 |
| STATISTICAL ANALYSIS AND HYPOTHESIS TESTING..... | 23 |
| RESULTS | Erro! Indicador não definido. 4 |
| DISCUSSION | Erro! Indicador não definido. 5 |
| ACKNOWLEDGMENTS..... | Erro! Indicador não definido. 27 |
| LITERATURE CITED | 28 |
| CONCLUSÃO GERAL | 151 |
| REFERENCIAS BIBLIOGRAFICAS..... | 44 |

INTRODUÇÃO GERAL

A movimentação animal é um comportamento que expressa busca por alimento, abrigo e busca por novos territórios (Boinski & Paul, 2000). Tais ações são influenciadas por fatores bióticos e condições abióticas que proporcionam mudanças no uso do espaço, incluindo variações no padrão de movimentação e tamanho da área de vida (Seaman & Powell, 1990). Mudanças no uso do espaço também são consideradas uma resposta a alterações em recursos chave, e mais frequentemente a qualidade ou volume dos itens alimentares (van Beest *et al.*, 2011). Enquanto é comum para um sub-adulto dispersar de sua área natal (Lidicker & Stenseth, 1992), uma vez estabelecido em uma área, o animal residente tende a ajustar seu comportamento de acordo com períodos de abundância e escassez de alimento (Silvius & Fragoso, 2003; Herfindal *et al.*, 2005; Rigamonti, 1993; Singleton & Schaik, 2001). Consequentemente, dentro de uma cadeia ecológica, o efeito bottom-up sob o comportamento animal é primeiramente aplicado em herbívoros com dieta limitada (Vucetich & Peterson, 2004; Tufto, Andersen & Linnell, 1996; McLoughlin & Ferguson, 2000). Apesar de os diferentes efeitos da sazonalidade de recursos sob herbívoros de regiões temperadas serem bem documentados, globalmente, a natureza e extensão das mudanças sazonais varia entre regiões (Mueller *et al.*, 2011), e pouco se sabe sobre a influência da sazonalidade de recursos sob a movimentação de herbívoros nos neotrópicos. Estudos com padrões destas variações, e os consequentes impactos na utilização do espaço por vertebrados é essencial para efetivos manejo de espécies, assim como são intimamente ligados a densidade e tamanho populacional (Palminteri & Peres, 2012; Powell, 2000).

A sazonalidade de recursos é uma característica que define um habitat Amazônico pouco conhecido, as florestas alagadas por rios de água preta. Localmente conhecida

como *igapó* (Prance, 1979), essas florestas cobrem uma área de 119,000 km² (Melack & Hess, 2010). O anual pulso de inundação de até 10m com duração de até 9 meses, e seu impacto na flora e na fauna foram comparadas aos invernos em regiões temperadas pois são os principais condutores de processos ecológicos, incluindo a sazonalidade na produção de folhas e frutos (Wittman *et al.*, 2006). Conseqüentemente, variações sazonais na disponibilidade de recursos alteram padrões do uso do espaço por animais que habitam o *igapó*, uma vez que em florestas alagadas o uso do espaço não é unicamente associado com a disponibilidade ou qualidade do alimento, mas também com acessibilidade (Antunes *et al.*, 2017; Barnett *et al.*, 2012; Bodmer, 1990; Haugassen & Perres, 2007; Renton, 2002). Logicamente, mamíferos terrestres podem visitar o *igapó* apenas quando ele não está alagado. Outras espécies, como as preguiças (*Bradypus variegatus*), macacos guaribas (*Alouatta*) e uacari (*Cacajao*) podem permanecer no *igapó* como residentes permanentes e assim ajustar seu comportamento em resposta a gama de mudanças anuais na disponibilidade de recursos guiada pelo pulso de inundação (Barnett *et al.*, 2013; Bezerra *et al.*, 2010).

Enquanto que uma série de estudos ecológicos tem sido realizado com primatas no *igapó* (Barnett *et al.*, 2017 in press), não há estudos prévios com preguiças nesse habitat. A preguiça-comum (*Bradypus variegatus*) é um folívoro especialista com o mais lento metabolismo dentre os mamíferos (Pauliniet *al.*, 2016; Nagy & Montgomery, 1980). Entre as singelas adaptações associadas com o baixo metabolismo está o tempo de digestão que pode durar até 50 dias da ingestão até a excreção (Foley *et al.*, 1995, Montgomery & Sunquist, 1978). Em comparação, outros mamíferos herbívoros com o mesmo tamanho (6 Kg) tem um tempo de digestão com cerca de 20 horas (e.g. *Alouatta*- Milton, 1998). Adicionalmente, e diferente de outros mamíferos, as preguiças

não são endotérmicas, pois sua temperatura corporal varia com o ambiente (Paulini *et al.*, 2016). *Bradypus variegatus* possui uma distribuição de Nicaguara ao oeste do Peru e o sudoeste do Brasil. Dentro desta extensiva área há uma variedade de florestas tropicais, incluindo florestas ombrófilas, florestas densas e florestas montanhosas (Moraes-Barros, 2011). Nos locais onde foi estudada, *B. variegatus* demonstrou grandes diferenças no uso do espaço, padrão de atividade e extensão das suas variações anuais (Queiroz, 1995; Sunquist & Montgomery, 1973; Vaughan *et al.*, 2000).

A principal variável que determina a natureza e extensão da movimentação em animais é a disponibilidade e qualidade de alimento (McLoughlin & Ferguson, 2000). Consequentemente isso ocorre em organismos que tem uma dieta restritiva, nos quais não são hábeis para usar recursos alternativos (van Beest *et al.*, 2011). Preguiças, que possuem uma dieta que compreende 99% de folhas, sendo 70% exclusivamente de folhas jovens (Castro-Sa *et al.*, submitted), seguem este critério. Consequentemente, para demonstrar como as preguiças são abeis a permanecer em uma área restrita mesmo quando sua dieta preferencial é escassa, nós quantificamos a movimentação das preguiças e a produtividade florestal. Assim nós hipotetizamos que as preguiças residentes do *igapó* podem [i] não deixar esse tipo de habitat; [ii] pode aumentar a movimentação durante períodos de baixa disponibilidade de alimento, e assim suprir sua necessidade metabólica e, contrariamente, apresentar movimentação reduzida em períodos com picos de produção de folhas, devido a abundância de alimento em sua área de vida. Em suma, nós predizemos que, em uma floresta tropical sazonal, a movimentação de um estrito folívoro arborícola é negativamente correlacionada com a produção de folhas.

OBJETIVO GERAL

Analisar a área de vida, movimentação e uso do espaço pela preguiça-comum *Bradypus variegatus* em relação a produção vegetal de uma floresta alagada de *igapó*, juntamente com as estratégias comportamentais que lhe permite ser um residente permanente das florestas alagadas.

a)

Capítulo I.

Castro-Sa, M.J.*¹, Gordo, M., Barnett, A.A. **Home range use of sloths in central Amazonian flooded forests.** Manuscrito submetido ao periódico *Journal of Animal Ecology*

Home range use of sloths in central Amazonian flooded forests

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ABSTRACT:

Use of space by animals is influenced by both biotic and abiotic factors. For herbivorous mammals seasonality in forage production is considered to be the main driver of movement patterns, home range size and consequently, the use of space. While such effects are well-researched in temperate regions and the Palearctic, little is known about the bottom up effect of productivity on herbivorous mammals in the neotropics. One of the most abundant herbivores in the Americas is Brown-throated sloth, *Bradypus variagatus*. The species' wide distribution includes populations with a great variety of activity patterns and habitat types. In the Amazon basin the species can be found in a strongly seasonal environment, the *igapó*'' – a seasonally-flooded riverine forests with strongly-pulsed leaf-production phenology. Using a combination of telemetry and phenological analysis, this study recorded patterns in sloth movement, and relate these to seasonal and within-forest differences in food availability. Mean home range size was 1.29ha mean daily displacement was 32m, and did not vary seasonally. Diet was entirely of leaves, but the sloths balance out the variation in leaf-availability between seasons. *Hevea spruceana* was an important resource and used in all seasons. This is the first study of sloth ecology in *igapó* forests.

KEY WORDS: Home Range, Bradypus, Forage Production, Seasonality

INTRODUCTION

An animal may move as a result of the search for food, a mate, shelter, new territories, and during the care of young, among others (Boinski & Paul, 2000). Both biotic and abiotic environmental conditions influence these movements (Seaman & Powell, 1990). Changes in used space are often considerable, a response to alterations in availability of key resources (van Beest *et al.*, 2011). While it is common for sub-adult mammals to disperse from the natal area (Lidicker & Stenseth, 1992), once established in an area, a resident animal tends to adjust ranging behavior according periods of abundance and scarcity of food (Silvius & Fragoso, 2003; Herfindal *et al.*, 2005; Rigamonti, 1993; Singleton & Schaik, 2001). Consequently, specialist herbivores with diets of limited breadth are the first to be impacted by bottom-up effects on animal behavior (Vucetich & Peterson, 2004; Tufto, Andersen & Linnell, 1996; McLoughlin & Ferguson, 2000). The effects of resource seasonality on grazing (*Rangifer tarandus* - Ferguson, 2004; *Procapra gutturosa* - Imai *et al.*, 2016; *Capreolus capreolus* - Mysterud, 1999; *Cervus elaphus* - Frair *et al.*, 2005) and browsing (*Lama guanicoe* - Cavieres & Fajardo, 2005; *Alces alces* - van Beest *et al.*, 2011; *Axis axis* - Raman, 1997) herbivores are well documented in temperate regions. However, globally, the nature and extent of seasonal change vary between regions and scale (Mueller *et al.*, 2011; van Beest *et al.*, 2011), and little is known about the influence of resources seasonality underpinning the movement of herbivores in the neotropics. Studies of the patterns of such variation, and the consequent impacts on vertebrate spatial utilization, are essential for effective species management, as these are intimately linked to density and hence population size (Palmeri & Peres, 2012; Powell, 2000).

Resource seasonality is a defining characteristic of one of the Amazon's least-known environments - the black water seasonally-flooded forests. Locally known as *igapó*

(Prance, 1979), these forests cover an area of some 119,000 km² (Melack & Hess, 2010). An annual flood-pulse up to 10m lasts for up to 9 months, impacting the flora and fauna. This season has been compared to the winter of temperate regions because the abiotic factors of flooding cycle and ambient temperature are major drivers of near-synchronous fruit and seasonal leaf production (Wittman *et al.*, 2006). Consequently, seasonal variation in resource availability is likely to change the patterns of space use by *igapó*-inhabiting animals. However, responses will be based not only on the availability and quality of food, but also with accessibility (Antunes *et al.*, 2017; Barnett *et al.*, 2012; Bodmer, 1990; Haugassen & Perres, 2007; Renton, 2002). This means that terrestrial and arboreal mammals may respond differently to the seasonal flooding cycles of *igapó* so that, terrestrial mammals may visit *igapó* only when it is unflooded, either to feed directly on germinating seeds or on those species feeding on them (Antunes *et al.*, 2017), while during flooded periods, many arboreal mammals, such as howler (*Alouatta*), capuchin (*Sapajus*) and squirrel (*Saimiri*) monkeys, move (at least temporarily) into the *igapó* to exploit seasonal peaks in leaf and insect availability (Barnett *et al.* submitted). Other species, such as the sloths (*Bradypus variegatus*) and uacari (*Cacajao ouakary*) monkeys, may be full-time *igapó* residents and so their ranging behavior will respond to the gamut of annual changes in flood-pulse driven resource availability (Barnett *et al.*, 2013; Bezerra *et al.*, 2010).

While a series of ecological studies have been undertaken on *igapó* primates (Barnett *et al.*, 2017 in press), there are no previous studies on sloths in this habitat. The brown throated three-toed sloth (*Bradypus variegatus*), is a specialist folivore which has the slowest metabolism of any known mammal (Paulini *et al.*, 2016; Nagy & Montgomery, 1980). Amongst the suite of adaptations associated with this, these sloths have a digesta

passage time which can take up to 50 days from ingestion to excretion (Foley *et al.*, 1995, Montgomery & Sunquist, 1978). In comparison, another highly folivorous mammal of similar body weight (*Alouatta*, 6 kg) has passage times of around 20 hours (Milton, 1998). Additionally, and unlike almost all other mammals, sloths not endothermic, but have a body temperature that varies with the environment (Paulini *et al.*, 2016). *Bradypus variegatus* has a broad distribution, ranging from Nicaragua to western Peru and south-eastern Brazil, where it inhabits a variety of tropical forest types, including rainforest, dense forest and mountain forest (Moraes-Barros *et al.*, 2011). In the few locations where they have been studied, *B. variegatus* have shown great differences in use of space, activity pattern and the extent of their annual variation (Queiroz, 1995; Sunquist & Montgomery, 1973; Vaughan *et al.*, 2000). Throughout Amazonia *B. variegatus* is often one of the most abundant arboreal mammals (Taube *et al.*, 1999), and is not only an important folivore, but is a key prey item for a variety of predators, such as tayra (*Eira barba*: Bezerra *et al.*, 2009; Sozobra *et al.*, 2016), jaguar (*Panthera onca*: Ramalho & Magnusson, 2008), harpy eagle (*Harpia harpyja*: Miranda, 2015); and even spectacled-owl (*Pulsatrix perspicillata*: Voirin *et al.*, 2009). Despite this, *B. variegatus* has been little studied within the Amazon Basin.

The availability and quality of food is a key factor in determining the nature and extent of movement patterns by individual animals (McLoughlin & Ferguson, 2000). This most commonly occurs in organisms that have a diet limited in breadth, and which are unable to switch easily to alternative resources (van Beest *et al.*, 2011). Sloths, whose diet generally comprises 99% leaves, with 70% being exclusively new leaves (Castro-Sa *et al.*, submitted), meet this criterion. Consequently, to study how sloths are able to remain in a restricted area even when their preferred diet resources are scarce, we

quantified both the movement of three-toed sloths in *igapó* forest and the productivity of this forest. We did this to test whether variation in seasonal availability of resources is sufficient to predict the movement of a tropical arboreal folivorous mammal with a low metabolic rate.

Accordingly, we hypothesized that *igapó*-living three-toed sloths would (i) not leave this habitat type; (ii) would increase their extent of displacement in periods of low food availability (low leaf production during the *igapó* flood pulse), thus meeting their energetic needs; and, in contrast, show reduced displacement during periods of peak young leaf production (the ebb, the period of non-inundation), due to the abundance of food present in their home ranges. In sum, we predict that, in a strongly seasonal tropical forest environment, the rate of movement of this strictly folivorous arboreal mammal will be negatively correlated with leaf production.

MATERIALS AND METHODS

Study area

This is part of a larger integrative research project on *igapó* ecology and conservation (the *Igapó* Study Project), and the first-ever study of sloth biology in *igapó* flooded forests. The study was conducted in Açutuba (ca. 1,840 ha; 3°05'S, 60°18'W), an *igapó* conservation area at Iranduba, a municipality 25 km from Manaus, the capital of Amazonas State, in central Amazonian Brazil, which integrates the permanent preservation area (APA) of the right bank of the Negro River, Sector Paduari / Solimões. (Fig. 1). Vegetation is composed of *igapó* and *buritizais* (palm swamps dominated by the buriti palm, *Mauritia flexuosa*).

Because of its position at the very eastern-most end of the lower Rio Negro, the precise extent and duration of the flood pulse at Açutuba is a collective consequence of rainy periods throughout the 100,000 km² of the Rio Negro Basin (Junk, 1989). This can vary

substantially between years but, in general, inundation lasts for some 9 months during which flood waters may reach 7 m (Junk *et al.*, 1989). In consequence, *igapó* trees have developed a suite of strategies for survival in a flooded environment, from rapid growth and tolerance of low oxygen levels in seedlings (da Silva *et al.*, 2009; de Simone, 2003; Parolin, 2001; Parolin, 2002; Parolin *et al.*, 2001), to the presence of aerenchyma, lenticels and aerial roots in adult trees (Armbrüster *et al.*, 2004; Parolin, 2009; Piedade *et al.*, 2010). In addition, new leaf production in the *igapó* occurs largely during an non-inundation season, when highest solar incidence occurs. Because all are subject to similar environmental conditions, approximately 86% of the *igapó* tree species have a synchronized phenology (Ferreira & Parolin, 2007; Parolin *et al.*, 2002; Wittman & Parolin, 1999; Schongart *et al.*, 2002).

Data Collection

Forest forage production was monitored monthly during the ebb period (September and October 2016) and the inundation period (November 2016 and January 2017), where the intensity of phenophases - production of new leaves - was recorded from 570 individual trees in *igapó* flooded forest. Movements of five radio-collared adult sloths were tracked with Very High Frequency Technology (VHF) in dry (July to October) and rainy (November to January) seasons. The animals were on average, spaced some 500 m apart, and were captured between July and November (Table 1). Monitoring data was collected daily in sessions of 10 h duration, during which all study animals were visited sequentially and their geographical position registered with a Garmin V GPS unit. The monitoring data were gradually entered to the analyses as the number of monitored animals increased. If individuals were feeding when observed, we marked the feeding tree with plastic flagging with a unique number for subsequent identification of the

plant species, and recorded the GPS position. The spatial data obtained gave 115 geographical points of sloth locations and 450 hours of monitoring with radio tracking.

Capture and marking three-toed sloths

The animals were encountered after active searches in a paddled wooden canoe. Animals were captured in the canopy by an experienced local guide using rope climbing safety equipment. Encountered animals were placed in individual cloth bags and passed to the canoe with the aid of a rope. The animals were then fitted with Tigrinus VHF 150 MHz radio transmitters attached to a nylon collar. To track them we used a Telonics TR-4 radio receptor and a Yagi 3 antenna. Once collared, animals were returned to the same tree in which they had been found (Fig. 2). Due to the generally phlegmatic and slow behavior of the study animals, and the brevity of the period required to fit each collar, collaring occurred without the animals being sedated. However, to avoid unintentional harm, the animal's limbs were loosely tied with broad strips of soft cloth during the operation. To retrieve the collars radios, study animals were recaptured in May 2017. Field research was carried out under license nº 51267-1 do SISBIO - Sistema de Autorização e Informação em Biodiversidade (Biodiversity Information and Authorization System).

Movements and Range Estimates

We determined the daily displacement traveled (m) and home range size (ha) using the package *adhabitatHR* (Calenge, 2006) for R software (R Development Core Team, 2011). Home-range size estimation used 100% Minimum Convex Polygon - MPC (for sloths *vide* Chiarello 1998), and for the 95% Kernel Method (for sloths *vide* Vaughan *et al.*, 2007). The MCP method computes the size of home range, delineating a convex

polygon around the most extreme points registered (Hayne, 1949), while the Kernel Method uses the density of the internal points, and produces a buffer with the probability of finding the animal in each sector of home range (Powell, 2000).

Forage availability

Leaf production was estimated in nine 100 x 4m permanent transects in the flooded forest *igapó* at Açutuba. Transects were separated by a minimum of 500 m of flooded forest. Flood duration influences *igapó* composition strongly (Ferreira, 1997), and many plant species have, as a result, spatially-restricted distributions (Barnett *et al.*, 2015). In consequence, transects were established at three levels of flood intensity: (1) Long duration (>200-days inundation), (2) Medium duration (100-200-days inundation), and (3) Short duration (<100 days inundation).

The effect of forage production may differ depending on the scale under investigation (van Beest *et al.*, 2011). Then the leaf production was estimated in both assemblage and on a population scale. At the assemblage level, the phenophase intensity was recorded for all trees within the transects with DBH>10cm, including those with trunks 50% or more inside the boundary markers. To record phenophase intensity, the crown of each tree was divided into four equal quadrants, and in each the presence or absence of leaf flushing was recorded. Thus, each individual tree received an intensity index ranging from 0 to 4. According to the formula, the total value of monthly phenophase, was obtained from the sum of the obtained phenophase intensity values, divided by the total number of individuals and multiplied by the maximum value of the intensity index:

$$\left(\sum x \mid n.4 \right) = fm$$

where x is values of phenophase intensity, n is the number of individuals trees, 4 is maximum intensity value of each individual tree, and fm is monthly phenophase value.

At the population level, we monitored five individuals of *Hevea spruceana* (Euphorbiaceae) (Fig. 3), a common *igapó* tree species, and a member of a genus known to be used by sloths (Carvalho 1960). Monitoring was conducted for three consecutive months in the non-inundation season, during which time branches were collected monthly from individual *Hevea* trees, and (following Camargo *et al.*, 2008) the number of total leaves and the proportion of new leaves were quantified for each branch.

Statistical analysis and hypothesis testing

We used a Kruskal-Wallis Test to test the hypothesis that forage production influences the movement of the study sloths, and a mixed generalized linear model (GLMM) to analyze the influences on each individual sloth. For a GLMM, the predictor variable is inserted into the model, while the explanatory variable and the individual identification of the animals act as a random variable. Consequently, the analysis treats the data for each individual as dependent on each other, but independent of individuals. For the relation between daily displacement and leaf production, we selected only the periods for which there were simultaneous samples of monthly phenology and sloth displacement data (as a result, sloth data from July was excluded as extreme floods meant phenology data collection was not possible). In addition, we considered that three-toed sloths, being slow-moving animals, might well remain in the same tree for several days and so, might not show apparent movement over short time periods (Sunquist & Montgomery, 1973). Consequently, we selected for analysis only

monitoring data that had points for five consecutive days, so excluding 6.95% of the instantaneous scans in our database.

A monthly comparison of forage production was used to determine seasonal changes in food availability for *B. variegatus*. Between-season variation was evaluated with a Wilcoxon nonparametric test. Finally, we used a parametric test-t to verify differences in forage production between the assemblage and population level.

RESULTS

To elucidate the home range of sloths is presented a map, in Fig 4. A summary of the extent of the movements and measurements in MPC and Kernel Home Range estimates is given in Table 1.

At the assemblage level, leaf production in *igapó* showed variation between seasons ($W = 0$, p-value = 0.0001213), with peak production corresponding to the beginning of the ebb period (September and October 2016), which corresponds to the river flood level being between 18 and 22 meters. In contrast, minimum forage production occurred in January, a period that corresponded to the end of the dry season and start of progressive flooding of the habitat (Fig. 5). At the population level, no evidence was found in the sampled time of significant variations in forage production of *Hevea spruceana*. However, a decrease in forage production during the dry season as a whole was found.

There is a significant difference in the values of forage production at the assemblage level and at the population level ($df = 2$, p-value = 0.04508). It is worthy of note that the production of leaves by *Hevea spruceana* can be twice that of average tree assemblage production (Fig. 6).

Mean daily displacement remained constant throughout the seasons, indicating that variation in leaf production had no effect on the extent of displacement of the sloths

studied ($\chi^2 = 0.21807$, $df = 3$, $p\text{-value} = 0.9746$) (Fig. 7). In addition, the animals did not present individual differences in daily displacement (GLMM $df = 48.0$, $t = 0.359$, $p\text{-value} > 0.05$).

Table 1. Extent of movements and MPC and Kernel estimates.

| ID | Capture date | Home Range size (ha) | | Daily Movimentation (m) | |
|-----|--------------|----------------------|------------|-------------------------|----------------------|
| | | MPC 100% | Kernel 95% | Range | Mean (\pm SD) |
| A ♂ | 07/07/2016 | 0.64 | 1.01 | 4 – 88 | 32.12 (\pm 23.94) |
| B ♂ | 08/07/2016 | 1.1 | 1.5 | 8 – 71 | 28.45 (\pm 19.01) |
| C ♂ | 31/10/2016 | 0.53 | 1.38 | 6 – 65 | 29 (\pm 21.25) |
| D ♀ | 15/09/2016 | 2.88 | 7.88 | 27 – 64 | 43(\pm 16.25) |
| E ♀ | 02/11/2016 | 1.32 | 3.15 | 11 – 76 | 31.17 (\pm 24.03) |

DISCUSSION

Radio tracking monitoring showed that the sloths did not leave the *igapó*, and that they were able to remain in the flooded forest to occupy a niche ecologically inaccessible to other mammals. So, along with a small number of other mammals (including the porcupine *Countou prehensilis*, several species of smaller rodent, and the primates *Aotus vociferans*, *Cacajao ouakary* and *Saimiri sciureus*: Antunes *et al.*, submitted; Barnett, in press), the species *Bradypus variegatus* can be considered as a species where whole populations are specialized for life in flooded forests. The constant presence of the three-toed sloth in flooded forests, together with its high abundance (Eisenberg & Thorington, 1973), may even explain the purely arboreal behavior of jaguar in the eastern amazon, for whom sloths are a major diet item (Ramalho & Magnusson, 2008).

The home range size recorded in the current study corresponds to those recorded for other three-toed sloths populations in other habitats (Table 2), while, within the *igapó*, the extent of daily displacement was similar for all individuals. However, it appears that females may cover areas larger than males, a behavior that may well reflect the

polygenic social organization of the species, with females visiting home ranges of several males during their reproductive cycles (Pauli & Perry, 2012).

Table2. Home Range size for *Bradypus* sloths in other studies

| Specie | Home Range (ha) | Method | Author |
|---------------|-----------------|--------|------------------------------|
| B. torquatus | 4.7-16.2 | Grids | Pinder, 1997 |
| B. torquatus | 2.8-5.9 | MPC | Chiarello, 1998 |
| B. variegatus | 0.5-3.7 | MPC | Montgomery & Sunquist, 1975 |
| B. variegatus | 0.15-1.4 | MPC | Queiroz, 1995 |
| B. variegatus | 5.2 | Kernel | Vaughan <i>et al.</i> , 2007 |
| B. variegatus | 0.19-19.9 | Kernel | Pauli & Perry, 2012 |
| B. pygmaeus | 0.08-0.49 | MPC | Viorin, 2015 |

Unlike herbivores from temperate regions, the bottom-up effect of plant production did not alter the ranging extent of sloths in *igapó*. This may well be because tropical forests, even the forests of *igapó*, are extremely diverse when compared to temperate regions (Pianka, 1966; Klaus, 1992). A non-flooded forest (*terra firme*) in the Açutuba region may have 200-300 arboreal species *per* ha, in turn *igapó* flooded forest shelter only 60 species *per* ha, which is low by tropical standards, but still greater than temperate regions, where a preserved forest might have 30 species at the very most (Bernadzki *et al.*, 1998; Ferreira & Prance, 1998; Ferreira, 1997). Thus the tropical forests may be able to provide a sufficiently broad diet for herbivores of the neotropics. To exploit the breadth of resources, arboreal mammals that reside permanently (or near-permanently) in the *igapó*, such as the flood-forest specialists uacari monkeys, use alternative foods and change their diet in periods of preferential resource are scarce (Barnett *et al.*, 2013). However, populations of three-toed sloths have a diet limited in breadth, maintain a stable diet throughout the year (Castro-Sa *et al.*, unpublished data), and are known for using leaves of only a small number of food trees species at any location. As we recorded a significant between-season variation in forage production in the landscape, and as this can involve up to 80% of the tree species of the *igapó* (Parolin *et al.*, 2002;

Parolin & Wittmann, 2010), we believe that sloths of forest with flood pulse-linked seasonality will select food trees that produce new leaves all year round (see Chiarello, 1998 for a similar situation in Atlantic Forest, Brazil). In our study area sloths constantly and consistently use new leaves of *Hevea spruceana* an arboreal species widely distributed by the *igapó* and able to produce new leaves, even when the great majority of species in the *igapó* tree assemblage have old, dry and fibrous leaves (Piedade *et al.*, 2006; Maia & Piedade, 2002). Therefore, the sloths' feeding strategy, which involves the selection of productive and fast-growing species (Castro-Sa *et al.*, unpublished data, for diet lists; Parolin *et al.*, 2004; Parolin & Ferreira, 1998 for tree species growth strategies), and extensive movement between them, to reduce the impact of bottom-up effects of strong seasonal pulsing in plant resource availability. Similar strategies have been recorded for another, strictly folivorous, mammal with a low metabolism, the kolas (Cork *et al.*, 1990), where the use of space is not closely linked with phenological patterns but with nutritional and metabolic needs (Briscoe *et al.*, 2014; Moore & Foley, 2000). We believe, then, that the lack of seasonal variation in the extent of between-day movements by the sloths studied at Açutuba indicates that the forage production, even within a highly seasonal environment such as *igapó*, is not the main determinant of the use space for strictly folivorous mammals of low metabolism. It also shows the highly specialized adaptations required to meet survival demands under the strongly seasonal leaf phenologies in Amazonian *igapó* forests.

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Figures legends

Figure 1. Açutuba *igapó* a) State of Amazonas, Brazil. b) Iranduba, AM. Açutuba represented by the black square. c) Açutuba *igapó*. Area of study represented by the white square.

Figure 2. *Bradypus variegatus* on *Igapó*.

Figure 3. *Hevea spruceana* with new leaves in *Igapó*.

Figure 4. Home Range use of sloths in Açutuba *igapó*.

Figure 5. Forage production along the time.

Figure 6. Forage production in *Igapó* assemblage and *Hevea spruceana* population.

Figure 7. Sloth daily displacement and forage production.

Fig. 1

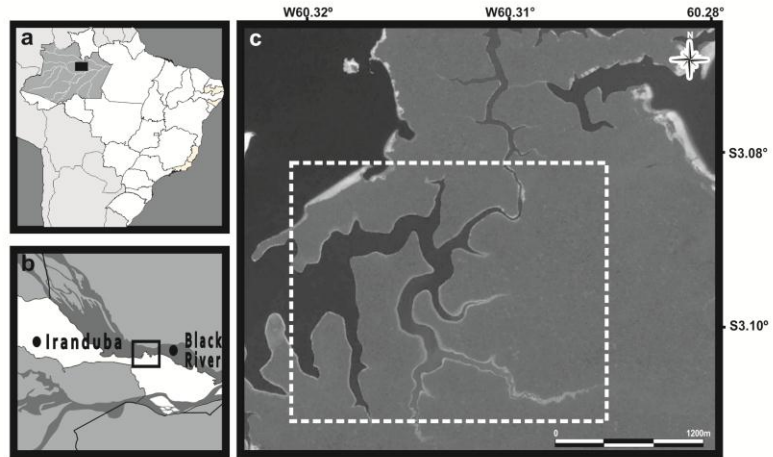


Fig. 4

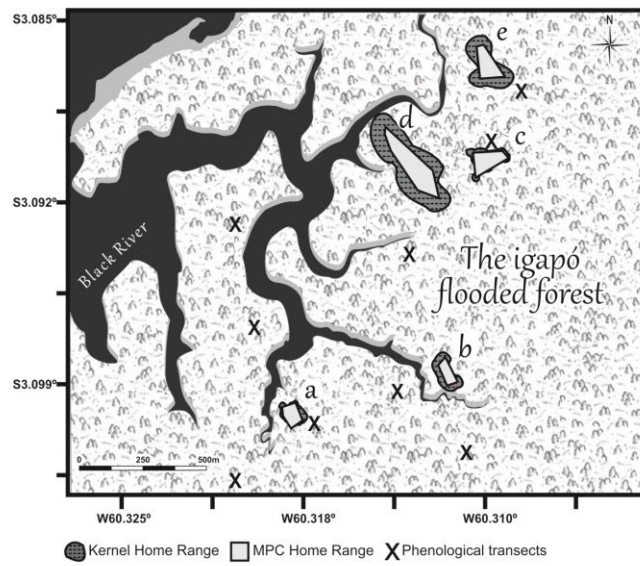


Fig. 2



Fig. 3



Fig. 5

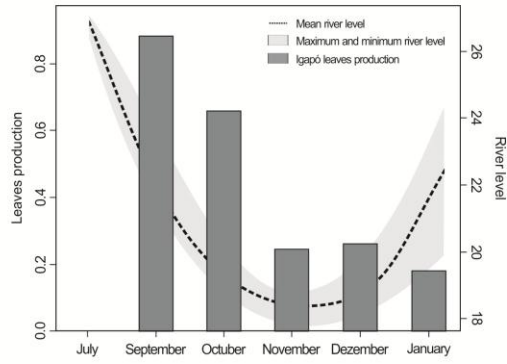


Fig. 6

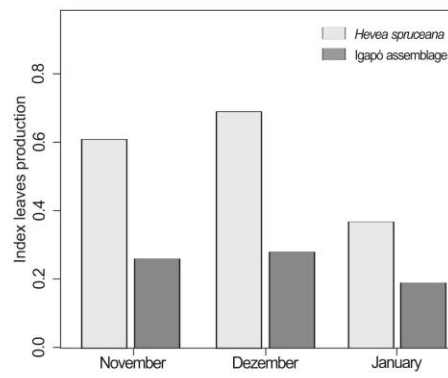
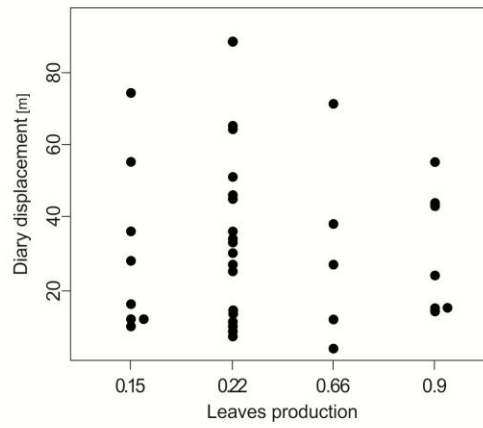


Fig. 7



CONCLUSÃO GERAL

O monitoramento de rádio-telemetria mostrou que as preguiças não deixam o *igapó*, e que são hábeis a permanecer na floresta alagada ao ocupar um nicho ecologicamente inacessível para outros mamíferos. Dentro de um pequeno número de mamíferos, *B. variegatus* pode ser considerada uma espécie com populações especializadas na vida em florestas alagadas. A constante presença das preguiças-comum na floresta alagada, juntamente com sua alta abundância na Amazônia (Eisenberg & Thorington, 1973), pode inclusive explicar o hábito preferencialmente arborícola de onças ao oeste da Amazônia, no qual a preguiça constitui o principal item da dieta (Ramalho & Magnunsson, 2008).

O tamanho da área de vida registrado no presente estudo corresponde ao registrado em outras populações de outros habitats, enquanto, dentro do *igapó*, a extensão do deslocamento diário foi similar para todos os indivíduos. Aparentemente as fêmeas podem cobrir áreas maiores que os machos, um comportamento que pode refletir a organização poligênica da espécie, com fêmeas visitando a área de vida de diversos machos ao longo de seus ciclos reprodutivos (Pauli & Perry, 2012).

Diferente de herbívoros de regiões temperadas, o efeito bottom-up da produção vegetal não alterou o deslocamento das preguiças no *igapó*. Isso ocorre porque as florestas tropicais, mesmo as florestas de *igapó*, são extremamente diversas quando comparadas com regiões temperadas (Pianka, 1966; Klaus, 1992). Para explorar a abrangência de recursos em uma floresta tropical os mamíferos que residem permanentemente no *igapó*, como os macacos uacari - especialistas em florestas alagadas, usam recursos alternativos e mudam a dieta quando o recurso preferencial é escasso (Barnett *et al.*, 2013). Contudo populações de preguiças possuem uma dieta limitada e estável (ver Castro-Sa, 2017; Castro-Sa *et al.*, submitted), e são conhecidas por utilizarem apenas

um pequeno número de espécies arbóreas como alimento (see Table 1: Castro-Sa *et al.*, submitted, and Castro-Sa, 2017). No entanto, a estratégia alimentar das preguiças, que envolve a seleção de espécies produtivas com rápido crescimento, e extensivos movimentos entre elas, reduzem o impacto do efeito bottom-up de um forte pulso sazonal na produção de folhas. Estratégia similar foi registrada em outro mamífero estritamente folívoro com baixo metabolismo, os koalas (Cork *et al.*, 1990), onde o uso do espaço não é intimamente ligado com padrões fenológicos mas sim com necessidades nutricionais e metabólicas (Briscoe *et al.*, 2014; Moore & Foley, 2000). Nós acreditamos que a estabilidade na movimentação das preguiças registrado no presente estudo, mostra que a produção vegetal, mesmo em um ambiente sazonal, não é o principal determinante para o uso do espaço por mamíferos estritamente folívoros com baixo metabolismo. O que também demonstra a alta especialização adaptativa requerida para perpetuar em um ambiente Amazônico com fenologia fortemente sazonal, como as florestas de *igapó*.

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