

Ranging behavior of black-and-gold howler monkeys (*Alouatta caraya*) in an anthropogenic habitat patch in southern Brazil

Helissandra Mattjie Prates[†], Gabriela Pacheco Hass¹

and Júlio César Bicca-Marques^{1*}

¹Laboratório de Primatologia, Escola de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS 90619-900, Brazil.

[†]In memoriam

*jcbicca@pucls.br

Abstract

Howler monkeys (*Alouatta* spp.) inhabit a wide range of forested environments throughout their distribution. Many aspects of their ecology and behavior are quite conservative (e.g., day range) wherever they live, while others vary predictably in response to habitat size or quality (e.g., home range). We describe the ranging behavior of an *Alouatta caraya* group living in the smallest home range (0.7 ha) known for *Alouatta* spp. and assess whether ambient temperature, time feeding, diet richness, and the contribution of food items in the diet predict day range. We used the instantaneous scan sampling method to record behavioral data during 5 days/month from August 2005 to July 2006 (699 h). The group used an orchard and an isolated clump of trees, and day range (168-599 m) was best explained by average ambient temperature. No significant relationship between day range and any trophic variable was found, suggesting that behavioral thermoregulation played a critical role on the group's ranging behavior.

Resumo

Uso do espaço por bugios-pretos (*Alouatta caraya*) em uma mancha de habitat antropogênico no sul do Brasil

Os bugios (*Alouatta* spp.) habitam uma ampla variedade de ambientes florestais ao longo de sua distribuição. Muitos aspectos de sua ecologia e comportamento são conservadores (e.g., percurso diário) independentemente de onde vivem, enquanto outros variam em resposta à área ou qualidade do habitat (e.g., área de vida). Descrevemos o uso do espaço por um grupo de bugios-pretos habitante da menor área de vida (0,7 ha) conhecida para *Alouatta* spp. e avaliamos se o percurso diário pode ser previsto pela temperatura ambiente, o investimento em alimentação, a riqueza da dieta e o consumo de diferentes itens vegetais. Usamos o método de varredura instantânea para registrar o comportamento durante 5 dias/mês de agosto/2005 a julho/2006 (699 h). O grupo usou um pomar e um conjunto isolado de árvores e o percurso diário (168-599 m) foi melhor explicado pela temperatura ambiente média. Não foram encontradas relações significativas com variáveis tróficas, sugerindo que a termorregulação comportamental desempenhou um papel crítico no percurso diário.

Key words

Palavras-chave

Core area, daily path length, home range, marginal habitat.

Área central, área de vida, habitat marginal, percurso diário.

INTRODUCTION

Human-induced habitat loss and fragmentation represent pervasive negative influences on the conservation of biodiversity (Haddad *et al.* 2015). The reduction in habitat area resulting from these processes promotes changes in population density and increases the vulnerability of isolated animal populations to inbreeding depression, hunting, predation, and diseases (Chapman & Balcomb 1998). Primates are particularly vulnerable to this new scenario (Marsh *et al.* 2003). However, whereas some species disappear from areas below a given expanse threshold, populations of others thrive in habitat patches (sometimes smaller than the normal home range of a single social group) and anthropogenic environments such as urban parks, orchards, and plantations of exotic species (Marsh 2003; Bicca-Marques *et al.* 2009; Duarte *et al.* 2011; Bonilla-Sánchez *et al.* 2012; Marsh & Chapman 2013).

Howler monkeys (*Alouatta* spp.) belong to the latter group (Fortes *et al.* 2015). The capacity of howlers to live in small and degraded forest fragments has been related to the exploitation of an eclectic and flexible folivorous-frugivorous diet (Crockett & Eisenberg 1987; Crockett 1998; Estrada *et al.* 1999, 2002; Bicca-Marques 2003; Chaves & Bicca-Marques 2013, 2016). Habitat restriction appears to influence only a handful of aspects of the ecology and behavior of howler monkeys in predictable ways (Bicca-Marques 2003). Whereas the size of the home range is obviously affected under conditions of space limitation, mean day range is not predicted by fragment size, this result was confirmed in a recent review (Fortes *et al.* 2015).

In *Alouatta*, inter-study analyses have shown that mean day range was positively related to the average number of food species exploited per day (Bicca-Marques 2003) and negatively related to both the degrees of folivory and frugivory (Fortes *et al.* 2015). The positive

relationship reported by Bicca-Marques (2003) is compatible with the expectation that the need of ingesting a diverse and balanced diet and avoiding the consumption of an overload of secondary metabolites modulates day range. On the other hand, the negative relationship between time spent feeding on fruits and day range may be a consequence of foragers “camping” near productive fruiting trees (Fortes *et al.* 2015).

In addition to nutrient balancing and secondary metabolite avoidance, diet selection may favor three other major nutritional goals: energy or nitrogen (protein) maximization and reduction of fiber ingestion (Felton *et al.* 2009 for a review). Diet selection, intergroup mate and resource competition, and predation and infanticide risk are potential drivers of the extent of primate day range (Raño *et al.* 2016). In this respect, habitat patches inhabited by a single group of a particular species represent interesting scenarios for assessing day range in the absence of intergroup competition for mates and resources. Similarly, the influence of predation and infanticide risk on ranging is expected to be negligible if these habitat patches are small and isolated in an anthropogenic matrix. Therefore, single howler monkey groups inhabiting small and isolated habitats offer an opportunity to evaluate the consequences of diet selection on ranging behavior when the effects of other selective pressures are minimal.

Here we describe the ranging behavior of black-and-gold howler monkeys (*Alouatta caraya*) inhabiting the smallest home range so far recorded for a howler monkey group (Fortes *et al.* 2015). Specifically, we describe patterns of use of space and day range, evaluate whether time moving is a reliable proxy of day range, and model the effects of ambient temperature, time feeding, diet richness, and the contribution of fruits, flowers, and leaves to the diet on day range.

MATERIAL AND METHODS

The study was conducted in a 0.7-ha orchard immersed in a landscape dominated by pastures and croplands in Estabelecimento Nossa Senhora da Conceição (29°36'43"S, 56°16'23"W; 86-93 m a.n.s.l.), Alegrete, state of Rio Grande do Sul, Brazil (Figure 1a and B). The climate of the region is humid subtropical (type

Cfa, according to Köppen's classification), characterized by the absence of a dry season and rainfall well distributed throughout the year (Moreno 1961). Average annual rainfall is 1,500 mm. Average annual temperature is 18.6°C with monthly averages ranging from 13.1°C (July) to 26.9°C (January) (IPAGRO 1989).

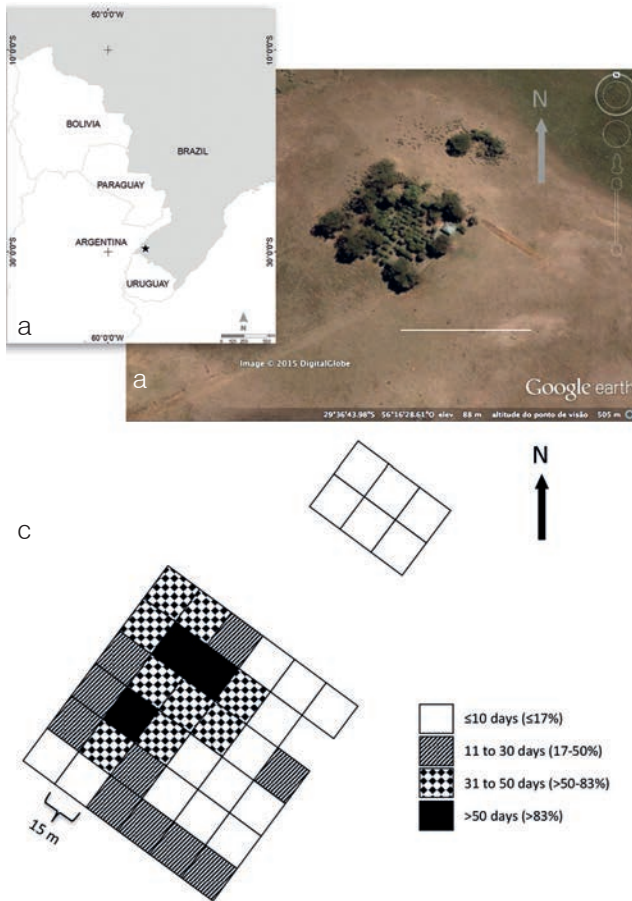


Figure 1. a) Location of the study region (star) in South America. b) Satellite image of the study site, showing the orchard and the isolated clump of trees located at northeast (source: Google Earth®). c) Frequency of use of each imaginary 15 m x 15 m quadrat of the orchard and the isolated clump of trees during the study (N=60 days).

The orchard was composed of 154 trees with diameter at breast height (DBH) ≥ 10 cm that formed an open and discontinuous canopy (Figure 2a; Prates & Bicca-Marques 2008, 2011). All trees were marked with numbered tags. They belonged to seven native and seven exotic species, particularly the exotic *Citrus sinensis* (n=98, Figure 2b) and *Melia azedarach* (n=14), and the native *Parapiptadenia rigida* (n=22) (Prates & Bicca-Marques 2011). The study site is ca. 1.2 km distant from the 2-ha orchard of Estância Casa Branca to the southwest, where Bicca-Marques and collaborators have conducted research on howler monkeys (Bicca-Marques 1990, 1993; Bicca-Marques & Calegato-Marques 1995, 1998; Calegato-Marques & Bicca-Marques 1996; Bicca-Marques *et al.* 2009; Jesus & Bicca-Marques 2012), ca. 0.7 km from a 3-ha woodland to the southeast, and almost 3 km from the nearest gallery forest adjacent to the Itapororó river to the north.



Figure 2. a) External view of the orchard, showing its open and discontinuous canopy. b) View of orange trees in the interior of the orchard. c) Adult female *Alouatta caraya* eating an orange.

According to the owner of the farm, howler monkeys colonized the orchard around 1983, when a dispersing adult female arrived with her infant. The study group (Figure 2c) ranged from 12 to 14 individuals (one or two adult males, three or four adult females, one subadult male, one subadult female, one or two juveniles, and four or five infants) (Prates & Bicca-Marques

2011). The habituation of the group to the researcher (HMP) occurred in July 2005. The identification of its members based on differences in pelage color, size, genitalia, and body marks, such as scars, also occurred during this time. Age-sex classes were classified following Rumiz (1990).

Behavioral data were recorded from dawn to dusk using 5 min instantaneous scan samples (Martin & Bateson 2007) every 15 min during five days per month from August 2005 to July 2006 (total sampling effort=60 days). No observations were made during rainy days. We obtained 26,474 records distributed in 2,805 scan sampling units in 699 h of observation.

Behavior was classified into resting, feeding, moving, socializing, drinking, and defecating/urinating. Although the scan sampling method is not aimed at estimating time spent in a particular behavior, the percentage of records of locomotion during each sampling day was used to estimate time (in min) spent moving. This transformation took into account the total time of daily samples. It was necessary because the photoperiod at the study region varies from *ca.* 10.5 h in July to 14.5 h in January, making longer (e.g., Summer) days resulting in larger sample sizes than shorter (e.g., Winter) days (Bicca-Marques 1991). Therefore, if a constant time is devoted on a daily basis to a particular behavior (e.g., 2 h), its percentage in the activity budget (calculated from the percentage of records) would vary from about 15% to 19% between the shortest and longest days. This artificial 25% increase has the potential of leading to wrong interpretations. The transformation is also supported by the fact that most individuals were recorded in each scan sampling unit (mean=9.4 records/scan sampling unit) and that there were no differences in the number of records per sampling unit within the day.

The size and pattern of use of the home range was estimated by dividing the area of the orchard into 41 imaginary 15 m x 15 m quadrats. The intensity of use of each quadrat took into account the number of sampling days in which it was visited or crossed by the group based on the location of trees. The homogeneity of the

pattern of quadrat use was tested by the Chi-square test expecting equal proportions. All displacements within the orchard that involved at least half of the group members were recorded for estimating day range. The distance between sequentially visited trees was measured for estimating day range. The relationship between day range and percentage of records and time spent moving was evaluated by the Spearman Rank Correlation Coefficient to assess whether the later variables were reliable proxies of the first.

Generalized Linear Mixed Models (GLMM) were used to assess whether average ambient temperature, percentage of activity records spent feeding, percentage of feeding records spent on leaves, flowers or fruits, and diet richness (number of plant species exploited as food sources) were good predictors of day range while taking month and day of data collection as random effects (Bolker *et al.* 2009). Predicting variables (fixed effects) were rescaled (package “scales”, Wickham 2016) and variance inflation factors - VIF (package “car”, Fox & Weisberg 2011) calculated to exclude highly collinear variables from further analysis. All variables ($VIF \leq 3$), except percentage of feeding records spent on leaves ($VIF=14.9$), composed the models.

Functions “fitdist”, “cdfcomp” and “gofstat” were run for selecting the family error distribution that best fits the data (package “fitdistrplus”, Delignette-Muller & Dutang 2015). A total of 24 full models with all possible combinations of null and full models were built (links function of Gamma family: identity, log and inverse) for choosing the best model using the function “glme” (package “lme4”, Bates *et al.* 2015). Full models were compared by the Akaike Information Criterion Second-Order Bias Correction (AICc, Burnham & Anderson 2002; package “bbmle”, Bolker & Core Team 2016). The function “dredge” (package “MuMIn”, Barton 2016) was run to identify the model with the strongest predictive power out of 32 possibilities. All analyses considered an alpha level of 0.05 and were performed in BioEstat 5.0 (Ayres *et al.* 2007) or R 3.3.1 (R Core Team 2016).

RESULTS

The group used the entire area of the orchard in addition to a *ca.* 0.05-ha isolated clump of *P. rigida* and *M. azedarach* trees located 50 m from the orchard.

However, it never used >0.45 ha (=20 quadrats) in the same day. The group also used some parts of the orchard at a higher frequency than others ($\chi^2=684.997$, d.f.=41,

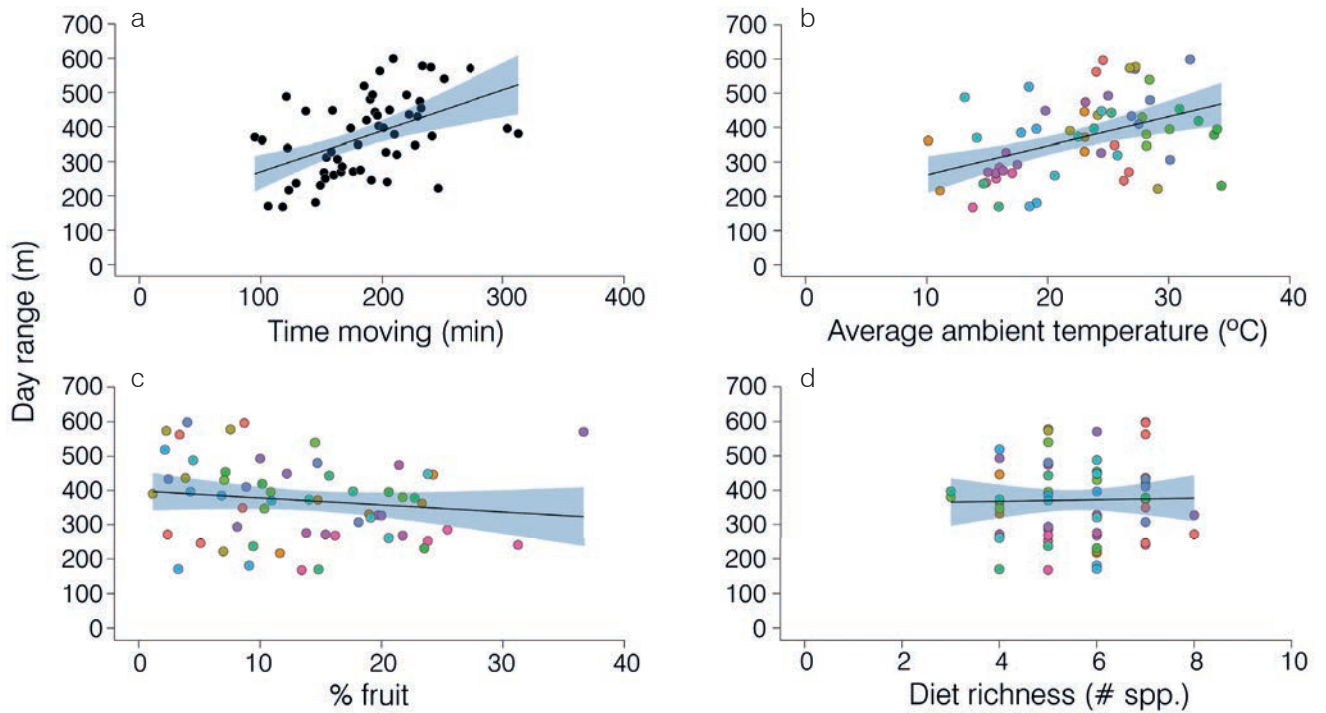


Figure 3. a) Relationship between time spent moving (in minutes) and day range (in meters). (b-d) Day range as a function of ambient average temperature, % fruit and diet richness, respectively. The Gamma regression model (identity link) is shown. Legend: dots, observed data (jitter plot, each month of data collection is represented by a different color); full line, predicted model; shaded area, 95% confidence interval.

$p < 0.0001$). For instance, a core area of 0.27 ha (=12 quadrats) was used during >50% of the days (Figure 1c).

Day range varied from 168 m to 599 m (mean \pm s.d.= 371 ± 116 m, $N=60$). It was strongly correlated with both the percentage of daily records spent

moving ($r_s=0.4944$, $N=60$, $p < 0.0001$) and time spent moving ($r_s=0.5523$, $N=60$, $p < 0.0001$; Figure 3a). The best GLMM model included average ambient temperature, diet richness and percentage of feeding records spent on fruits (Table 1). However, whereas the

Table 1. Best models of multiple logistic regression explaining day range of a black-and-gold howler monkey group in an orchard in southern Brazil, including the estimate and significance of the three variables composing the best model as predictors of day range.

Rank	Model	df	logLik	AICc	Δ_i AICc	w_i
Best model	Average temperature + % fruit + diet richness	7	194.446	-372.7	0.00	0.906
Variable	Estimate	St. Error	t value	$\text{Pr}(> z)$	# models	$\sum w_i$
Intercept	328.19	47.69	6.881	5.94e-12	-	-
Average temperature	199.10	56.46	3.526	0.0004	16	1.00
% fruit	-86.39	62.04	-1.392	0.1638	16	0.91
Diet richness	-62,01	59.58	-1.041	0.2980	16	0.91
2 nd	Average temperature + % feeding + % flower	7	191.786	-367.4	5.32	0.063
3 rd	Average temperature + % flower	6	189.695	-365.8	6.93	0.028
4 th	% feeding	5	185.750	-360.4	12.35	0.002
5 th	Average temperature + % fruit + % flower	7	178.832	-341.5	31.23	<0.001

AICc: corrected Akaike Information Criterion; Δ_i AICc: delta corrected Akaike Information Criterion (difference between the current model and the most parsimonious model); w_i : model selection probability.

Estimate: the sign indicates the direction of the effect of the variable for predicting day range. $\sum w_i$: variable selection probability.

positive relationship between ambient temperature and day range was significant (Figure 3b), the nega-

tive relationships with the two trophic variables were not (Figures 3c and d; Table 1).

DISCUSSION

The distance travelled daily by the group was within the limits described for *Alouatta* spp. (Bicca-Marques 2003; Fortes *et al.* 2015). Therefore, despite inhabiting the smallest known home range for howler monkeys, the area of available habitat was not a good predictor of day range as reported elsewhere (Bicca-Marques 2003). The number of howler monkeys sharing this tiny home range probably played a critical role in howler day range, as group size was shown to have a direct effect on distance traveled (Fortes *et al.* 2015).

The strong positive correlations with both time spent and percentage of records moving confirm that these variables are reliable proxies of day range. This finding was expected because howler monkeys are slow-moving quadrupedal walkers that rarely run during travel (Bicca-Marques & Calegario-Marques 1995; Prates & Bicca-Marques 2008); that is, travel speed is relatively constant. Significant positive correlations between day range and travel time also were recently shown in two groups of brown howler monkeys living in a *ca.* 1,000 ha Atlantic forest fragment in southeast Brazil (Jung *et al.* 2015). These results are compatible with the hypothesis that most events of moving occur while howlers are travelling between food patches. The stronger correlations reported for brown howlers (>0.72 ; Jung *et al.* 2015) compared with the current study may be a consequence of the smaller size of their groups (six and five individuals) and their larger home ranges (5.0 ha and 15.8 ha). Whereas it is easier for fewer individuals to synchronize their activities, this also is necessary for maintaining group cohesion when exploiting a larger area. On the other hand, there was limited need for the black-and-gold howlers of the present study, about half of which were immature, to synchronize their activities to guarantee group cohesion because they were restricted to the boundaries of the orchard.

Although fruit consumption and diet richness composed the best model, the lack of significant relationships between any trophic variable and day range (unlike the results reported by Raño *et al.* 2016 for the same species in Argentina) is explained by the close proximity between all food sources (the longest strai-

ght-line distance between two trees was approximately 110 m) and the very limited diversity of potential foods (only 14 tree species plus a few epiphytes and parasites were present in the orchard). The temporal variation in the consumption of most food items by this highly folivorous ($>80\%$ of feeding records) group did not show a significant relationship to their monthly availability in the orchard. The only exception was mature fruits, whose major source (almost $2/3$ of feeding records on this item) was the highly dominant *Citrus sinensis* (Prates & Bicca-Marques 2011). The overabundance of mature fruits during the fruiting season of *C. sinensis* created a situation equivalent to that found in larger areas where frugivorous primates camp (Strier 1987; Fortes *et al.* 2015), especially because the orange trees were clumped in the center of the orchard. This resource distribution may explain the negative, although non-significant, correlation between the number of feeding records spent on fruit and day range. There was also no evidence that energy or nitrogen (protein) maximization, nutrient balancing, and avoidance of fiber or secondary metabolite ingestion modulated distance travelled by the study group within its spatially restricted home range.

On the other hand, average ambient temperature was a strong predictor of day range. The significant positive relationship between these variables may be related to a thermoregulatory strategy of avoiding heat dissipation during colder days, when howlers decrease their activity (Bicca-Marques 1993) and rest huddled for long periods (Bicca-Marques & Calegario-Marques 1998). The importance of the clumped distribution of orange trees as major fruit sources may also have played a role in this result because orange availability was highest during the coldest months.

Finally, the size of the study group dropped from 13 individuals to only four (two adult males, one adult female, and one subadult female) a few months after the end of this research. According to the owner of the study site (Silva 2007: pers. comm.), most group members may have dispersed to nearby gallery forests. This new, smaller, group size is similar to that found at the site in 1989-1990 (Bicca-Marques & Calegario-Marques

1998). Irrespective of the fate of most study subjects during such a short period of time, their disappearance is compatible with the idea that small fragments have low carrying capacities (Asensio *et al.* 2007). Whether this putative dispersal was triggered by either resource limitation or social intolerance (in this case, based on a comparison of group membership before and after the disappearances it is possible to hypothesize that the social intolerance occurred among adult females and their offspring instead of among adult males), by an interaction of both of these causes or by another factor is an important question that remains unanswered. In sum, the study group did not show abnormal ranging behavior in the orchard despite living in a situation probably near the threshold of the species' tolerance as suggested by Prates & Bicca-Marques (2011).

ACKNOWLEDGMENTS

We thank Mauro Estácio Azambuja da Silva for authorizing this research in his land, the Osório family for its hospitality and logistical support, Alejandro Estrada, Fernando de Camargo Passos and Thaïs Leiroz Codenotti for suggestions on an earlier draft, the editors of this volume for inviting us to contribute and providing critical comments on the first version of this manuscript, Charles Fernando dos Santos for helping us with the GLMM data analysis, Paul A. Garber for revising the manuscript, and Regis A. Lahm and Everton L. Quadros (Laboratório de Tratamento de Imagens e Geoprocessamento/PUCRS) for preparing the map of South America. We also thank the Brazilian National Research Council/CNPq for a M.Sc. studentship to HMP (#131720/2005-8) and a research fellowship to JCBM (#303306/2013-0).

BIBLIOGRAPHY

- Asensio N, Cristobal-Azkarate J, Dias PAD, Veá JJ & E Rodríguez-Luna (2007) Foraging habits of *Alouatta palliata mexicana* in three forest fragments. *Folia Primatologica* 78:141-153.
- Ayres M, Ayres Jr. M, Ayres DL & AAS Santos (2007) *Bio-Estat 5.0: aplicações estatísticas nas áreas das Ciências Biológicas e Médicas*. Instituto de Desenvolvimento Sustentável Mamirauá – IDS/MCT/CNPq. Belém, Brazil. 364 pp.
- Barton K (2016) MuMIn: multi-model inference. R package version 1.15.6. <https://CRAN.R-project.org/package=MuMIn>. (Accessed in 3-IX-2016). 73 pp.
- Bates D, Maechler M, Bolker B & S Walker (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
- Bicca-Marques JC (1990) A new southern limit for the distribution of *Alouatta caraya* in Rio Grande do Sul State, Brasil. *Primates* 31:449-451.
- Bicca-Marques JC (1991) *Ecologia e comportamento de um grupo de bugios-pretos Alouatta caraya (Primates, Cebidae) em Alegrete, RS, Brasil*. MSc dissertation. Universidade de Brasília. Brasília, Brazil. 200 pp.
- Bicca-Marques JC (1993) Padrão de atividades diárias do bugio-preto *Alouatta caraya* (Primates, Cebidae): uma análise temporal e bioenergética. In: Yamamoto ME & MBC de Souza (eds.) *A primatologia no Brasil - 4*. Sociedade Brasileira de Primatologia. Salvador, Brasil. Pp. 35-49.
- Bicca-Marques JC (2003) How do howler monkeys cope with habitat fragmentation? In: Marsh LK (ed.) *Primates in Fragments: Ecology and Conservation*. Kluwer Academic/Plenum Publishers. New York, USA. Pp. 283-303.
- Bicca-Marques JC & C Calegario-Marques (1995) Locomotion of black howlers in a habitat with discontinuous canopy. *Folia Primatologica* 64:55-61.
- Bicca-Marques JC & C Calegario-Marques (1998) Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology* 106:533-546.
- Bicca-Marques JC, Muhle CB, Prates HM, Oliveira SG & C Calegario-Marques (2009) Habitat impoverishment and egg predation by *Alouatta caraya*. *International Journal of Primatology* 30:743-748.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH & JSS White (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127-135.
- Bolker B & Core Team RD (2016) bbmle: tools for general maximum likelihood estimation. R package version 1.0.18. <https://CRAN.R-project.org/package=bbmle>. (Accessed in 3-IX-2016). 30 pp.
- Bonilla-Sánchez YM, Serio-Silva JC, Pozo-Montuy G & CA Chapman (2012) Howlers are able to survive in *Eucalyptus* plantations where remnant and regenerating vegetation is available. *International Journal of Primatology* 33:233-245.
- Burnham KP & DR Anderson (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer-Verlag. New York, USA. 488 pp.
- Calegario-Marques C & JC Bicca-Marques (1996) Emigration in a black howling monkey group. *International Journal of Primatology* 17:229-237.
- Chapman CA & SR Balcomb (1998) Population characteristics of howlers: ecological conditions or group history. *International Journal of Primatology* 19:385-403.
- Chaves ÓM & JC Bicca-Marques (2013) Dietary flexibility of the brown howler monkey throughout its geographic distribution. *American Journal of Primatology* 75:16-29.

- Chaves ÓM & JC Bicca-Marques (2016) Feeding strategies of brown howler monkeys in response to variations in food availability. *PLoS ONE* 11:e0145819.
- Crockett CM (1998) Conservation biology of the genus *Alouatta*. *International Journal of Primatology* 19:549-578.
- Crockett CM & JF Eisenberg (1987) Howlers: variations in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW & TT Struhsaker (eds.) *Primate Societies*. The University of Chicago Press. Chicago, USA. Pp. 54-68.
- Delignette-Muller ML & C Dutang (2015) fitdistrplus: an R package for fitting distributions. *Journal of Statistical Software* 64:1-34.
- Duarte MHL, Vecci MA, Hirsch A & RJ Young (2011) Noisy human neighbours affect where urban monkeys live. *Biology Letters* 7:840-842.
- Estrada A, Juan-Solano S, Martínez TO & R Coates-Estrada (1999) Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *American Journal of Primatology* 48:167-183.
- Estrada A, Mendoza A, Castellanos L, Pacheco R, Belle SV, García Y & D Muñoz (2002) Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. *International Journal of Primatology* 58:45-55.
- Felton AM, Felton A, Lindenmayer DB & WJ Foley (2009) Nutritional goals of wild primates. *Functional Ecology* 23:70-78.
- Fortes VB, Bicca-Marques JC, Urbani B, Fernández VA & TS Pereira (2015) Ranging behavior and spatial cognition of howler monkeys. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B & D Youlatos (eds.) *Howler Monkeys: Behavior, Ecology, and Conservation*. Springer. New York, USA. Pp. 219-255.
- Fox J & S Weisberg (2011) *An R Companion to Applied Regression*. SAGE. Thousand Oaks, USA. 472 pp.
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song DX & JR Townsend (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1:e1500052.
- IPAGRO (1989) *Atlas agroclimático do estado do Rio Grande do Sul*. Secretaria da Agricultura. Porto Alegre, Brazil. 42 pp.
- Jesus AS & JC Bicca-Marques (2012) Acessando a farmacopeia natural dos bugios-pretos. *Revista Brasileira de Plantas Mediciniais* 14:S27-S28.
- Jung L, Mourthe I, Grelle CEV, Strier KB & JP Boubli (2015) Effects of local habitat variation on the behavioral ecology of two sympatric groups of brown howler monkey (*Alouatta clamitans*). *PLoS ONE* 10:e0129789.
- Marsh LK (ed.) (2003) *Primates in Fragments: Ecology and Conservation*. Kluwer Academic/Plenum Publishers. New York, USA. 404 pp.
- Marsh LK & CA Chapman (eds.) (2013) *Primates in Fragments: Complexity and Resilience*. Springer. New York, USA. 537 pp.
- Marsh LK, Chapman CA, Norconk MA, Ferrari SF, Gilbert KA, Bicca-Marques JC & J Wallis (2003) Fragmentation: specter of the future or the spirit of conservation? In: Marsh LK (ed.) *Primates in Fragments: Ecology and Conservation*. Kluwer Academic/Plenum Publishers. New York, USA. Pp. 381-398.
- Martin P & P Bateson (2007) *Measuring Behaviour: An Introductory Guide*. 3rd ed. Cambridge University Press. Cambridge, UK. 176 pp.
- Moreno JA (1961) *Clima do Rio Grande Sul*. Secretaria da Agricultura. Porto Alegre, Brazil. 42 pp.
- Prates HM & JC Bicca-Marques (2008) Age-sex analysis of activity budget, diet and positional behaviour in black-and-gold howler monkey (*Alouatta caraya*). *International Journal of Primatology* 29:703-715.
- Prates HM & JC Bicca-Marques (2011) Vivendo no limite? Dieta de um grupo de bugios-pretos (*Alouatta caraya*) habitante de um pomar. In: Melo FR & Í Mourthé (eds.) *A primatologia no Brasil*, vol. 11. Sociedade Brasileira de Primatologia. Belo Horizonte, Brazil. Pp. 77-91.
- R Core Team (2016) *R: a language and environment for statistical computing reference index version 3.3.1*. R Foundation for Statistical Computing. Austria.
- Raño M, Kowalewski MM, Cerezo AM & PA Garber (2016) Determinants of daily path length in black and gold howler monkeys (*Alouatta caraya*) in northeastern Argentina. *American Journal of Primatology* 78:825-837.
- Rumiz DI (1990) *Alouatta caraya*: Population density and demography in northern Argentina. *American Journal of Primatology* 21:279-294.
- Strier KB (1987) Ranging behavior of woolly spider monkeys, or muriquis, *Brachyteles arachnoides*. *International Journal of Primatology* 8:575-591.
- Wickham H (2016) scales: scale functions for visualization. R package version 0.4.0. <https://CRAN.R-project.org/package=scales>. (Accessed in 3-IX-2016). 46 pp.