

International Journal of Primatology

Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus* and *Plecturocebus*): Potential correlates, patterns and differences between genera --Manuscript Draft--

Manuscript Number:	IJOP-D-19-00042R4
Full Title:	Terrestrial behavior in titi monkeys (<i>Callicebus</i> , <i>Cheracebus</i> and <i>Plecturocebus</i>): Potential correlates, patterns and differences between genera
Article Type:	Original Article
Keywords:	Callicebinae; ground use; fruit availability; predation risk; sampling effort
Corresponding Author:	João Pedro Souza-Alves, PhD in Zoology Universidade Federal de Pernambuco BRAZIL
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universidade Federal de Pernambuco
Corresponding Author's Secondary Institution:	
First Author:	João Pedro Souza-Alves, PhD in Zoology
First Author Secondary Information:	
Order of Authors:	João Pedro Souza-Alves, PhD in Zoology Italo Mourthe Renato Hilário Júlio César Bicca-Marques Jennifer Rehg Carla Gestich Adriana Acero-Murcia Patrice Adret Rolando Aquino Mélissa Berthet Mark Bowler Armando M. Calouro Gustavo Canale Nayara Cardoso Christini Caselli Cristiane César Renata Chagas Aryanne Clyvia Cintia Corsini Thomas Defler Anneke DeLuycker Anthony Di Fiore

Kimberly Dingess
Gideon Erkenwick
Michele Ferreira
Eduardo Fernandez-Duque
Stephen Ferrari
Isadora Fontes
Josimar Gomes
Frederico Gonçalves
Maurício Guerra
Torbjørn Hugaasen
Stefanie Heiduck
Eckhard W. Heymann
Shannon Hodges
Rosario Huashuayo-Llamocca
Leandro Jerusalinsky
Carlos Kasper
Jenna Lawrence
Teresa Lueffe
Karine Lopes
Jesús Martínez
Fabiano Melo
Mariluce Messias
Mariana Nagy-Reis
Inés Nole
Filipa Paciência
Erwin Palacios
Alice Poirier
Grasiela Porfírio
Amy Porter
Eluned Price
Rodrigo Printes
Erika Quintino
Evandro Reis
Alessandro Rocha
Adriana Rodríguez
Fábio Röhe
Damián Rumiz
Sam Shanee
Marina Santana
Eleonore Setz
Francisco Souza

	Wilson Spironello
	Eméríta Tirado Herrera
	Luana Vinhas
	Kevina Vulinec
	Robert Wallace
	Mrinalini Watsa
	Patricia C. Wright
	Robert J. Young
	Adrian A. Barnett
Order of Authors Secondary Information:	
Manuscript Region of Origin:	BRAZIL
Funding Information:	
Abstract:	<p>For arboreal primates, ground use may increase dispersal opportunities, tolerance to habitat change, access to ground-based resources, and resilience to human disturbances, and so has conservation implications. We collated published and unpublished data from 86 studies across 65 localities to assess titi monkey (<i>Callicebinae</i>) terrestriality. We examined whether the frequency of terrestrial activity correlated with study duration (a proxy for sampling effort), rainfall level (a proxy for food availability seasonality), and forest height (a proxy for vertical niche dimension). Terrestrial activity was recorded frequently for <i>Callicebus</i> and <i>Plecturocebus</i> spp., but rarely for <i>Cheracebus</i> spp. Terrestrial resting, anti-predator behavior, geophagy, and playing frequencies in <i>Callicebus</i> and <i>Plecturocebus</i> spp., but feeding and moving differed. <i>Callicebus</i> spp. often ate or searched for new leaves terrestrially. <i>Plecturocebus</i> spp. descended primarily to ingest terrestrial invertebrates and soil. Study duration correlated positively and rainfall level negatively with terrestrial activity. Though differences in sampling effort and methods limited comparisons and interpretation, overall, titi monkeys commonly engaged in a variety of terrestrial activities. Terrestrial behavior in <i>Callicebus</i> and <i>Plecturocebus</i> capacities may bolster resistance to habitat fragmentation. However, it is uncertain if the low frequency of terrestriality recorded for <i>Cheracebus</i> spp. is a genus-specific trait associated with a more basal phylogenetic position, or because studies of this genus occurred in pristine habitats. Observations of terrestrial behavior increased with increasing sampling effort and decreasing food availability. Overall, we found a high frequency of terrestrial behavior in titi monkeys, unlike that observed in other pitheciids.</p>

1 **Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus* and *Plecturocebus*): Potential correlates,**
2 **patterns and differences between genera**

3

4 João Pedro Souza-Alves, Programa de Pós-graduação em Biologia Animal, Departamento de Zoologia,
5 Universidade Federal de Pernambuco, Recife, Brazil

6 Italo Mourthe, Programa de Pós-graduação em Biodiversidade e Conservação, Universidade Federal do Pará,
7 Altamira, Brazil

8 Renato R. Hilário, Departamento de Meio Ambiente e Desenvolvimento, Universidade Federal do Amapá,
9 Macapá, Brazil

10 Júlio César Bicca-Marques, Departamento de Biodiversidade e Ecologia, Pontifícia Universidade Católica do
11 Rio Grande do Sul, Porto Alegre, Brazil

12 Jennifer Rehg, Department of Anthropology, Southern Illinois University Edwardsville, Edwardsville, United
13 States of America

14 Carla C. Gestich, Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual de
15 Campinas, São Paulo, Brazil

16 Adriana C. Acero-Murcia, Universidade Federal de São Paulo, Programa de Pós-graduação em Ecologia e
17 Evolução, São Paulo, Brazil

18 Patrice Adret, Museo Historia Natural Noel Kempff Mercado, UAGRM, Santa Cruz de La Sierra, Bolivia

19 Rolando Aquino, Universidad Nacional Mayor de San Marcos, Lima, Peru

20 Méliissa Berthet, Department of Comparative Cognition, University of Neuchâtel, Neuchâtel, Switzerland

21 Mark Bowler, School of Science, Technology and Engineering, University of Suffolk, Suffolk, United Kingdom

22 Armando M. Calouro, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Brazil

23 Gustavo R. Canale, Universidade Federal do Mato Grosso, Núcleo de Estudos da Amazônia Matogrossense,
24 Sinop, Mato Grosso, Brazil

25 Nayara de A. Cardoso, Programa de Pós-graduação em Ciências Biológicas, Departamento de Sistemática e
26 Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

27 Christini B. Caselli, Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife,
28 Pernambuco, Brazil

29 Cristiane Cäsar, Museu de Ciências Naturais PUC Minas, Minas Gerais, Brazil

30 Renata R. D. Chagas, Programa de Pós-graduação em Ciências Biológicas, Departamento de Sistemática e
31 Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

32 Aryanne Clyvia, Bicho do Mato Meio Ambiente, Belo Horizonte, Minas Gerais, Brazil

33 Cintia F. Corsini, Programa de Capacitação Institucional, Instituto Nacional da Mata Atlântica, Santa Teresa,
34 Espírito Santo, Brazil

35 Thomas Defler, Departamento de Biología, Universidad Nacional de Colombia, Bogotá D. C., Colombia

36 Anneke DeLuycker, Smithsonian-Mason School of Conservation, Smithsonian Conservation Biology Institute,
37 Front Royal, VA, United States of America

38 Anthony Di Fiore, Department of Anthropology, University of Texas at Austin, Austin, United States of
39 America

40 Kimberly Dingess, Department of Anthropology, Indiana University, Bloomington, United States of America

41 Gideon Erkenwick, Department of Biology, University of Missouri-St. Louis, St. Louis, United States of
42 America

43 Michele Alves Ferreira, Bicho do Mato Meio Ambiente, Belo Horizonte, Minas Gerais, Brazil

44 Eduardo Fernandez-Duque, Department of Anthropology, Yale University, New Haven, United States of
45 America

46 Stephen F. Ferrari, Departamento de Ecologia, Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil

47 Isadora P. Fontes, Secretaria Municipal de Meio Ambiente de Aracaju, Aracaju, Sergipe, Brazil

48 Josimar Daniel Gomes, Anglo American Minério de Ferro Brasil S/A, Minas Gerais, Brazil

49 Frederico P. R. Gonçalves, Programa de Pós-graduação em Sustentabilidade e Tecnologia Ambiental, Instituto
50 Federal de Minas Gerais, Bambuí, Minas Gerais, Brazil

51 Maurício Guerra, Parques Nacionales Naturales de Colombia, Parque Nacional Natural Amacayacu, Leticia,
52 Colombia

53 Torbjørn Haugaasen, Faculty of Environmental Sciences and Natural Resource Management, Norwegian
54 University of Life Sciences, Norway

55 Stefanie Heiduck, Deutsches Primatenzentrum, Göttingen, Germany

56 Eckhard W. Heymann, Deutsches Primatenzentrum, Göttingen, Germany

57 Shannon Hodges, Department of Anthropology, Texas A&M University College Station, Texas, United States
58 of America

59 Rosario Huashuayo-Llamocca, Proyecto Mono Tocón, Moyobamba, San Martín, Peru

- 60 Leandro Jerusalinsky, Centro Nacional de Pesquisa e Conservação de Primatas Brasileiros, Instituto Chico
61 Mendes de Conservação da Biodiversidade, João Pessoa, Brazil
- 62 Carlos Benhur Kasper, Laboratório de Biologia de Mamíferos e Aves, Universidade Federal do Pampa, Campus
63 de São Gabriel, São Gabriel, Rio Grande do Sul, Brazil
- 64 Jenna Lawrence, Department of Ecology, Evolution, and Environmental Biology, Columbia University, New
65 York, United States of America
- 66 Teresa Magdalena Lueffe, Deutsches Primatenzentrum, Göttingen, Germany
- 67 Karine G. D. Lopes, Programa de Pós-Graduação em Zoologia, Pontifícia Universidade Católica do Rio Grande
68 do Sul, Porto Alegre, Brazil
- 69 Jesús Martínez, Wildlife Conservation Society-Bolivia, La Paz, Bolivia
- 70 Fabiano R. de Melo, Instituto de Biociências, Universidade Federal de Goiás, Regional Jataí, Goiânia, *and*
71 Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Brazil
- 72 Mariluce Rezende Messias, Laboratório de Mastozoologia & Vertebrados Terrestres, Departamento de Biologia,
73 Universidade Federal de Rondônia, Porto Velho, Brazil.
- 74 Mariana B. Nagy-Reis, Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual
75 de Campinas, Campinas, São Paulo, Brazil
- 76 Inés Nole, Facultad de Medicina Veterinaria, Universidad Nacional Mayor de San Marcos, Lima, Peru
- 77 Filipa Paciência, Deutsches Primatenzentrum, Göttingen, Germany
- 78 Erwin Palacios, Conservation International-Colombia, Bogotá, Colombia
- 79 Alice Poirier, Department of Life Sciences, Anglia Ruskin University, Cambridge, United Kingdom
- 80 Grasiela Porfírio, Programa de Pós-Graduação em Ciências Ambientais e Sustentabilidade Agropecuária,
81 Universidade Católica Dom Bosco, Campo Grande, Brazil
- 82 Amy Porter, Department of Anthropology, University of California, Davis, CA, United States of America
- 83 Eluned Price, Durrell Wildlife Conservation Trust, Jersey, United Kingdom
- 84 Rodrigo C. Printes, Laboratório de Gestão Ambiental e Negociação de Conflitos, Universidade Estadual do Rio
85 Grande do Sul, São Francisco de Paula, Brazil
- 86 Erika P. Quintino, Laboratório de Primatologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto
87 Alegre, Brasil
- 88 Evandro Amato Reis, Bicho do Mato Meio Ambiente, Belo Horizonte, Minas Gerais, Brazil
- 89 Alessandro Rocha, Núcleo de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

90 Adriana Rodríguez, Conservation International Colombia, Bogotá D.C., Colombia

91 Fábio Röhe, World Conservation Society Brazil, Manaus, Brazil

92 Damián Rumiz, Fundación Simón I. Patiño, Santa Cruz de la Sierra, Bolivia

93 Sam Shanee, Neotropical Primate Conservation UK, Manchester, United Kingdom

94 Marina M. Santana, Departamento de Ecologia, Programa de Pós-graduação em Ecologia e Conservação,
95 Universidade Federal de Sergipe, Brazil

96 Eleonore Z. F. Setz, Departamento de Biologia Animal, Universidade Estadual de Campinas, São Paulo, Brazil

97 Francisco Salatiel C. de Souza, Programa de Pós-graduação em Ecologia e Manejo de Recursos Naturais,
98 Universidade Federal do Acre, Acre, Brazil

99 Wilson Spironello, Grupo de Pesquisa de Mamíferos da Amazônia, Instituto Nacional de Pesquisas da
100 Amazônia, Manaus, Brazil

101 Emérita R. Tirado Herrera, Universidad Nacional de la Amazonía Peruana, Iquitos, Peru

102 Luana Vinhas, Departamento de Biologia, Universidade Católica do Salvador, Bahia, Brazil

103 Kevina Vulinec, Department of Agriculture & Natural Resources, Delaware State University, Dover, United
104 States of America

105 Robert B. Wallace, Wildlife Conservation Society Bolivia, La Paz, Bolivia

106 Mrinalini Watsa, Department of Anthropology, Washington University in Saint Louis, United States of America

107 Patricia C. Wright, Department of Anthropology, State University of New York at Stony Brook, Stone Brook,
108 New York, United States of America

109 Robert J. Young, Department of Biology, University of Salford, Manchester, United Kingdom

110 Adrian A. Barnett, Grupo de Pesquisa de Mamíferos da Amazônia, Instituto Nacional de Pesquisas da
111 Amazônia, Manaus, AM, Brazil *and* Centre for Research in Evolutionary Anthropology, Roehampton
112 University, London, United Kingdom

113

114 **Correspondence author:** J.P. Souza-Alves, Departamento de Zoologia, Universidade Federal de Pernambuco,
115 Av. Prof. Moraes Rego, 1235, Cidade Universitária, 50670-901, Recife, Pernambuco, Brazil. Phone: +55 79
116 8129-8106. E-mail: *souzaalves1982@gmail.com*

117 _____

118 Author Contributions: JPS-A and AAB conceived and designed the experiments. RRH and IM analyzed the
119 data. JPS-A and AAB wrote the first draft of manuscript. All the authors revised the manuscript.

120 **Abstract**

121 For arboreal primates, ground use may increase dispersal opportunities, tolerance to habitat change, access to
122 ground-based resources, and resilience to human disturbances, and so has conservation implications. We
123 collated published and unpublished data from 86 studies across 65 localities to assess titi monkey (*Callicebinae*)
124 terrestriality. We examined whether the frequency of terrestrial activity correlated with study duration (a proxy
125 for sampling effort), rainfall level (a proxy for food availability seasonality), and forest height (a proxy for
126 vertical niche dimension). Terrestrial activity was recorded frequently for *Callicebus* and *Plecturocebus* spp.,
127 but rarely for *Cheracebus* spp. Terrestrial resting, anti-predator behavior, geophagy, and playing frequencies in
128 *Callicebus* and *Plecturocebus* spp., but feeding and moving differed. *Callicebus* spp. often ate or searched for
129 new leaves terrestrially. *Plecturocebus* spp. descended primarily to ingest terrestrial invertebrates and soil.
130 Study duration correlated positively and rainfall level negatively with terrestrial activity. Though differences in
131 sampling effort and methods limited comparisons and interpretation, overall, titi monkeys commonly engaged in
132 a variety of terrestrial activities. Terrestrial behavior in *Callicebus* and *Plecturocebus* capacities may bolster
133 resistance to habitat fragmentation. However, it is uncertain if the low frequency of terrestriality recorded for
134 *Cheracebus* spp. is a genus-specific trait associated with a more basal phylogenetic position, or because studies
135 of this genus occurred in pristine habitats. Observations of terrestrial behavior increased with increasing
136 sampling effort and decreasing food availability. Overall, we found a high frequency of terrestrial behavior in
137 titi monkeys, unlike that observed in other pitheciids.

138

139 **Key words:** Callicebinae, ground use, fruit availability, predation risk, sampling effort

140

141 **Introduction**

142 The ability or propensity of arboreal primates to use the ground varies widely among species (Napier
143 and Napier 1967; Wu 1993; Wu *et al.* 1988). For some primates, this behavior appears to be linked to a species'
144 capacity to disperse between forest fragments by crossing roads or open and disturbed areas, to gain access to
145 vital resources, such as fruit and water, or to a reduction in predation risk associated with the long-lasting
146 presence of human observers (Anderson *et al.* 2007; Ancrenaz *et al.* 2014; Barnett *et al.* 2012a; Campbell *et al.*
147 2005; Cheyne *et al.* 2018; Eppley *et al.* 2016; Grueter *et al.* 2009; Mourthé *et al.* 2007; Nowak *et al.* 2014;
148 Tabacow *et al.* 2009). In this sense, ground use potentially enhances species resilience and its long-term
149 persistence in fragmented landscapes (Jones 2005).

150 Lower canopy forests are likely to provide less food for upper canopy specialists and result in a closer
151 proximity to the ground compared to more stratified forest (Takemoto 2004). Furthermore, by using the ground
152 arboreal primates can expand their niche, allowing them access to a greater diversity of resources (Boyer *et al.*
153 2006; Mesa-Sierra and Pérez-Torres 2017). Strata use is also linked to body size. Small-bodied primates usually
154 concentrate their activities in the lower and middle levels of the forest, thus increasing the chance that ground
155 use will occur (Fleagle 1999). For example, ground use is more common in species of *Pithecia*, which use the
156 forest understory more often and have less specialized diets than in the larger-bodied species of *Chiropotes* and
157 *Cacajao* (Barnett *et al.* 2012a; Boyle *et al.* 2015).

158 Increases in study duration and the length of time devoted to fieldwork activities by researchers (e.g.
159 increased sampling effort) can increase the probability of detecting rare events and unusual behaviors, such as
160 terrestriality (Weatherhead 1986). For example, white-faced sakis (*Pithecia pithecia*) showed high rates of
161 terrestrial behavior during systematic monitoring at Isla Redonda, Lago Guri, Venezuela, but low rates in
162 shorter-term studies (see Table III in Barnett *et al.* 2012a). Similarly, spider monkeys (*Ateles geoffroyi*) showed
163 high rates of terrestrial behavior per hour during approximately 2,000 hours of monitoring, but low rates in ca.
164 500 hours of monitoring (Table I in Campbell *et al.* 2005). Although other factors may influence ground use
165 (such as geophagy and drinking water in spider monkeys: Campbell *et al.* 2005), testing the influence of the
166 extent of sampling effort would improve our understanding of terrestrial behavior in primates.

167 Despite the absence of morphological specializations for terrestriality (Aversi-Ferreira *et al.* 2013),
168 ground use is widespread in Neotropical primates as an occasional, although potentially important, part of their
169 behavioral repertoire. The frequency, duration, and context of terrestriality can vary substantially between
170 Neotropical primate species, and such behavior is relatively more common in genera such as *Cebus* and *Sapajus*
171 (Ottoni and Izar 2008; Porfírio *et al.* 2017), and rarer in such genera as *Cacajao*, *Chiropotes* and *Pithecia*
172 (Barnett *et al.* 2012a) (Table 1). As in other species, the availability of arboreal food resources and forest strata
173 potentially influences the nature and extent of terrestrial behaviors in Neotropical primates (Campbell *et al.*
174 2005; Cant 1992).

175 Among species in the family Pitheciidae, terrestrial behavior in pitheciines (*Cacajao*, *Chiropotes*, and
176 *Pithecia*) is unusual and almost completely restricted to the exploitation of alternative food resources when the
177 availability of highly used arboreal items is low (Barnett *et al.* 2012a). Additionally, it can differ substantially
178 among genera, field sites and populations (Barnett *et al.* 2012a). Variation between study sites is compatible
179 with the hypothesis that local variables, such as food availability, predator density, and traditions influence

180 terrestrial activities and their frequencies (Barnett *et al.* 2012a, 2013). In another pitheciid group, the titi
181 monkeys, the frequency of terrestrial behavior, and variables that potentially contribute to this behavior, remain
182 unknown.

183 Titi monkeys (Pitheciidae, Callicebinae) are small-bodied (ca. 1-kg) platyrrhines that live in groups of
184 2 to 5 individuals, typically including a male-female adult pair and their offspring (Norconk 2011). Previously
185 included in a single genus, *Callicebus*, titi monkeys were recently split into three genera (*Callicebus*,
186 *Cheracebus*, and *Plecturocebus*) based on phylogenetic and divergence-time analyses using molecular data
187 (Byrne *et al.* 2016), and in accordance with long-recognized geographically-based species groupings (van
188 Roosmalen *et al.* 2002). The 35 species currently described (Boubli *et al.* 2019; Byrne *et al.* 2016; Serrano-
189 Villavicencio *et al.* 2017; van Roosmalen *et al.* 2002) are distributed throughout Amazonia into Paraguay, with
190 a discontinuous distribution in eastern Brazil. Titi monkeys inhabit a variety of habitats, ranging from Andean
191 pre-montane forests (e.g., *Plecturocebus oenanthe*: Bóveda-Penalba *et al.* 2009), lowland rainforests (e.g.,
192 *Plecturocebus lucifer*: Kinzey *et al.* 1977), and dry semi-deciduous forests (e.g., *Callicebus barbarabrownae*:
193 Printes *et al.* 2011), to semi-arid Chaco forests (e.g., *Plecturocebus pallescens*: Rumiz 2012). Many species
194 occur in landscapes severely fragmented by human activities (e.g., *Callicebus coimbrai*: Chagas and Ferrari
195 2010; *Plecturocebus moloch*: Michalski and Peres 2005; *Plecturocebus oenanthe*: Bóveda-Penalba *et al.* 2009;
196 Shanee *et al.* 2011; *Plecturocebus grovesi*: Boubli *et al.* 2019). The fruit-based diet of titi monkeys is seasonally
197 complemented with leaves, seeds, flowers, animal prey, or other items depending on the species and population
198 (Bicca-Marques and Heymann 2013). These small-bodied monkeys use all levels of the forest, but are often
199 found in the lower strata (up to 10 m) (Bicca-Marques and Heymann 2013). No comprehensive analysis of
200 terrestrial behavior in titi monkeys has been conducted to date; although members of the group have long been
201 reported to use the ground (Kinzey 1977; Mason 1966). In this study, we collated published and unpublished
202 records of terrestrial behavior on the Callicebinae, aiming to identify important ecological correlates, general
203 patterns, and similarities and differences among taxa and regions. We hypothesized that: [1] opportunities to
204 observe unusual behaviors increase with study effort, thereby we tested the prediction that the number of
205 observations of terrestrial behavior in titi monkeys would be positively correlated with study duration (a proxy
206 for sampling effort); [2] the frequency of terrestrial behavior in titi monkeys increases when arboreal food
207 resources are scarce, thereby we tested the prediction that the frequency of ground use would be negatively
208 correlated with rainfall level (a proxy for habitat-wide fruit availability); and [3] opportunities for ground use by

209 titi monkeys increase with a reduction in vertical niche dimension, thereby we tested the prediction that
210 terrestrial behavior would be negatively correlated with forest height (a proxy for vertical niche dimension).

211

212 **Methods**

213 We collated published and unpublished data on terrestrial activity by wild titi monkeys from 86 studies
214 conducted at 65 locations in South America (Electronic Supplementary Material S1; Figure 1). Our dataset
215 contains considerable methodological variation in data recording and reporting, a common limitation of
216 collaborative studies using collated, multi-author data (e.g. Barnett *et al.* 2012a; Boyle *et al.* 2015).

217 We divided terrestrial activity into seven categories (Table 2). We did not include accidental falling to
218 the ground as this is not an intentional act. However, we considered intentional plummeting to the ground a
219 predator-avoidance strategy.

220

221 **Ethical statement**

222 All contributors declared that the studies adhered to the legal requirements of the countries in which the
223 fieldwork was conducted and complied, in each case, with the appropriate ethical requirements of the
224 institutions and governments concerned and adhered to the Code of Best Practices for Field Primatology of the
225 American Society of Primatologists and International Primatological Society
226 (www.asp.org/resources/docs/Code%20of_Best_Practices%20Oct%202014.pdf).

227

228 **Data analysis**

229 We treated each study site as a sampling unit, irrespective of study duration and the number of
230 individuals involved, allocating each one to a behavioral category. Following Mourthé and collaborators (2007),
231 we defined a terrestrial event as that in which one (or more) individual was observed to descend to the ground
232 (or was sighted when already on the ground). For each species, we calculated the number of records of each
233 type of terrestrial activity as a percentage of total terrestrial records (Table 3). Although the frequency of
234 terrestrial behaviors would be a better response variable, we did not have accurate data on sampling effort (i.e.,
235 hours of observation) for each study to allow calculation of such rates. Instead, we used study duration (in
236 months) as a proxy for sampling effort.

237 We used rainfall in the driest quarter of the year (available at WorldClim: Hijmans *et al.* 2005) as a

238 proxy for fruit availability (following Hawes and Peres 2016; Mendoza *et al.* 2017) because for most study sites

239 we lacked comparable data on floristic composition and plant phenology needed to assess the influence of a lean
240 season on terrestrial behavior. We considered driest quarter rainfall a reasonable proxy for seasonality and
241 availability of fruits for most titi monkey species in our study. We obtained information on mean forest height
242 for each study site from the Woods Hole Research Center ([http://whrc.org/publications-data/datasets/detailed-
243 vegetation-height-estimates-across-the-tropics/](http://whrc.org/publications-data/datasets/detailed-vegetation-height-estimates-across-the-tropics/)) to assess the influence of forest height on terrestrial behavior.
244 We extracted estimates of forest height across the tropics using the geographic coordinates of each study site
245 plotted on a 30 x 30 m grid.

246 We computed a Chi-squared test to compare the frequency of different activities performed on the
247 ground between *Plecturocebus* and *Callicebus*. Subsequently, we applied post-hoc Chi-squared tests to detect
248 which activities differed between genera by comparing the frequency of each activity against the frequency of
249 all the other activities. Because we used the same variables in multiple tests, we applied a sequential Bonferroni
250 correction to assess statistical significance and reduce the chance of type I errors (Holm 1979). We did not
251 compare *Cheracebus* with the other genera because of the small number of terrestrial records obtained for
252 members of this genus.

253 We used a Generalized Linear Model (GLM) with a Poisson response distribution to examine whether
254 study duration, rainfall level, and forest height were correlated with the total number of terrestrial records
255 reported in each study. Then, to plot the effect of one variable while controlling for the other, we ran partial
256 models (Velleman and Welsch 1981). We computed partial regressions in three steps: first, we computed GLMs
257 of our response variable (terrestrial activity) against two of our predictors, excluding a given predictor that was
258 explored separately (e.g. terrestrial activity vs. study duration + vegetation height, terrestrial activity vs. rainfall
259 level + vegetation height). In the second step, we computed GLMs of the given independent variable that we
260 explored separately against the other two independent variables. Finally, we plotted the residuals from the first
261 step against the residuals from the second step. We checked visually for compliance with model assumptions
262 through diagnostic plots (Zuur *et al.* 2010), and checked residuals for homoscedasticity using a Shapiro-Wilk
263 test ($W=0.932$, $P=0.133$). We also checked for multicollinearity via a Variance Inflation Factor (keeping all
264 variables with $VIF < 3.0$; Zuur *et al.* 2010), using the package *car* (Fox and Weisberg 2011). We included in
265 these analyses only the 19 systematic studies that contained sufficient information on all variables
266 aforementioned and performed all analyses using R 3.3.0 (R Core Team 2016).

267

268 **Results**

269 Terrestrial behaviors (N = 764 records) were recorded in 72 of the 88 study populations (71%); this
270 includes all five species of *Callicebus* (N = 20 studies, N = 333 records), 48 of 57 populations (84%) of 18
271 species of *Plecturocebus* spp. (N = 57 studies, N = 425 records), and 5 of 6 (83%) populations of four species of
272 *Cheracebus* spp. (N = 6 studies, N = 6 records) (Electronic Supplementary Material S1). Most data (67%) came
273 from non-systematic studies, whereas the remaining (33%) came from systematic studies of titi monkeys.
274 Terrestrial activity was most commonly associated with feeding/foraging and moving/travelling (Table 3). In
275 general, behaviors performed when the titi monkeys were on the ground differed between *Callicebus* spp. and
276 *Plecturocebus* spp. ($\chi^2 = 77.823$, $df = 7$, $P < 0.0001$).

277

278 **Feeding/foraging, moving/travelling, resting, geophagy, and infant retrieval**

279 Feeding and foraging represented 37% of all terrestrial activity records (Table 3). *Callicebus* spp.
280 devoted most of their time exploiting leaves on the ground (new leaves = 49%, mature leaves = 16%), while
281 *Plecturocebus* spp. primarily consumed invertebrates (46%), and *Cheracebus* spp. ate fallen fruits, leaves, seeds
282 and invertebrates (N = 1 record each). *Callicebus* spp. engaged more frequently in feeding/foraging on the
283 ground (48%) than *Plecturocebus* spp. (28%; $\chi^2 = 29.84$, $df = 1$, $P = 0.001$).

284 *Plecturocebus* spp. showed a higher investment in moving/travelling on the ground than did *Callicebus*
285 spp. (40% vs. 16%; $\chi^2 = 29.70$, $df = 1$, $P = 0.001$). This stems from frequent observations of *Plecturocebus*
286 *modestus*, and especially *Plecturocebus olallae* individuals (17.7% of study records) travelling on the ground to
287 reach feeding sites in naturally fragmented forests.

288 Resting on the forest floor was uncommon in all three genera, and did not differ between *Callicebus*
289 spp. and *Plecturocebus* spp. (4% vs. 3%; $\chi^2 = 1.08$, $df = 1$, $P = 0.297$). Rates of geophagy ($\chi^2 = 3.32$, $df = 1$, $P =$
290 0.068) and infant retrieval ($\chi^2 = 0.18$, $df = 1$, $P = 0.665$) also did not differ between the two genera.

291

292 **Social interactions**

293 Several titi monkeys were recorded playing directly on the forest floor and/or on fallen tree trunks.
294 *Plecturocebus oenanthe* descended to the ground to chase and play with tamarins (*Leontocebus leucogenys*) in
295 the San Martin region, Peru, while *Plecturocebus toppini* behaved similarly with tamarins (*Leontocebus*
296 *weddelli* and *Saguinus imperator*) at Los Amigos Biological Station, Peru. Three titi species (*Callicebus*
297 *nigrifrons*, *Callicebus personatus*, and *Callicebus coimbrai*) were observed playing with marmosets (*Callithrix*
298 *aurita*, *Callithrix geoffroyi*, and *Callithrix jacchus*, respectively) in southeastern and northeastern Brazil.

299 Playing behavior was observed in nearly identical proportions in *Callicebus* spp. and *Plecturocebus* spp. (13%
300 and 11%, respectively; $\chi^2 = 1.70$, $df = 1$, $P = 0.191$).

301

302 **Antipredator behaviors**

303 Predators were reported as common at 16 of 20 sites (80%) of *Callicebus* spp., four of five *Cheracebus*
304 spp. sites (80%), and 33 of 56 *Plecturocebus* spp. sites (59%) (Electronic Supplementary Material S1).

305 Individuals of all three genera were observed using the forest floor to escape from potential aerial predators (e.g.
306 hawks, eagles), and humans. Frequencies of antipredator behavior on the ground were similar for *Callicebus*
307 spp. and *Plecturocebus* spp. (1% for both; $\chi^2 = 0.52$, $df = 1$, $P = 0.467$).

308

309 **Correlates of terrestrial behavior in titi monkeys**

310 We found that, overall, study duration and rainfall level correlated with terrestrial activity ($R^2 = 0.29$).
311 As predicted, the longer a study, the higher the number of records of titi monkeys on the ground (Figure 2a). In
312 addition, the lower the rainfall (high seasonality and low fruit availability during lean seasons), the higher the
313 frequency of ground use (Figure 2b). Forest height, however, did not correlate with ground use (Table 4).

314

315 **Discussion**

316 Our findings demonstrated that, overall, callicebines are more likely to use the ground than are other
317 pitheciine genera (Barnett *et al.* 2012a), although there was considerable variation in the extent and nature of
318 terrestrial behaviors. While more than half of the species of each genus was observed using the ground level,
319 there was substantial between-species, population-specific, and context-dependent variation in the frequencies at
320 which titi monkeys performed activities on the ground. These findings should be interpreted with caution due to
321 the limitations of our collated data set, including variation in sampling efforts and methods. However, we found
322 interesting patterns of ground use in titi monkeys. Such variation could result from several factors, including
323 phylogenetic, seasonal, and biogeographic differences between study sites, local density of predators (Campbell
324 *et al.* 2005), and local traditions (*sensu* Tabacow *et al.* 2009).

325 Feeding/foraging was the most frequent activity performed on the ground by *Callicebus* spp. and
326 *Cheracebus* spp. and the second most frequent activity by *Plecturocebus* spp. Fleshy fruit is the main food type
327 in the diet of titi monkeys, whereas new and mature leaves and invertebrates are typically exploited during lean
328 periods, and thus are characterized as alternative foods (Bicca-Marques and Heymann 2013). Leaves and

329 invertebrates are protein-rich foods, with high concentrations of lipids in the latter (Lambert 2011). Therefore,
330 we suggest that descending to the ground to search for these resources during lean periods is likely to be linked
331 to the need to obtain nutrients. The high number of records of feeding on the ground by titi monkeys suggests
332 that the benefits of descending from the canopy to access food resources outweighs the potential costs of
333 increased predation risk and handling difficulties (Treves 2000).

334 The geophagy recorded for *Plecturocebus* spp. and *Callicebus* spp. can be related to one of several
335 benefits (or a combination of them) resulted from ingestion of soil, including mineral supplementation, antacid
336 action, toxin absorption, endoparasite control, and/or antidiarrheal agents (Krishnamani and Mahaney 2000;
337 Setz *et al.* 1999). Forest ground levels have a higher concentration than the canopy of old and dead bark under
338 which insects can hide (Li 2007), and may be locally rich in clay and mud areas (e.g. mineral licks) (Blake *et al.*
339 2010; Lee *et al.* 2010; Voigt *et al.* 2008). Geophagy is also relatively common among other Amazonian
340 pitheciids, such as *Chiropotes* spp. and *Pithecia* spp. (Ferrari *et al.* 2008), possibly due to high levels of dietary
341 plant-based tannins, which is linked to the generally poor soils of the region. Other animals, such as frugivorous
342 bats, non-pitheciid primates, and parrots also eat clay to alleviate the effects of plant alkaloids or as an
343 alternative source of nutrients (Blake *et al.* 2010; Bravo *et al.* 2008; Brightsmith *et al.* 2008).

344 Moving/travelling on the ground is a major component of terrestriality in primates. Primates may travel
345 through open areas to disperse between habitat patches or feeding sites (Li 2007). Such behaviors, however, are
346 often accompanied by the enhanced risk of predation (Barnett *et al.* 2015; Galetti and Sazima 1996) and
347 exposure to parasites (Nunn and Altizer 2006). Moreover, vegetation type, diet and distribution of food
348 resources influence arboreal primate decisions to use the ground, for example, Bolivian endemic titi monkeys
349 occur in naturally fragmented forests, particularly *P. olallae* and regularly travel on the ground to move between
350 forest patches (Kirkpatrick and Long 1994; Li 2007; Martinez and Wallace 2011; Su *et al.* 1998). When
351 necessary, titis travel to find new suitable habitat or to reunite with a groups (Ferrari *et al.* 2013a,b). However,
352 the nature of the causative factors behind the higher frequency of moving/traveling in *Plecturocebus* spp.
353 compared to *Callicebus* spp. remain unclear. Overall, more detailed analyses are required to assess which
354 habitat attributes and matrix elements affect the likelihood of ground use by titi monkeys for moving/traveling
355 activities.

356 The rarity of resting on the ground by titi monkeys may also result from increased predation risk
357 (Eppley *et al.* 2016; Mourthé *et al.* 2007) and/or exposure to parasites (Nunn and Altizer 2006), although resting
358 on the ground can also provide thermoregulatory benefits, as suggested for bamboo lemurs (*Hapalemur*

359 *meridionalis*, Eppley *et al.* 2016) and chimpanzees (*Pan troglodytes*, Takemoto 2004). At all study sites,
360 terrestrial predators were potentially present (Electronic Supplementary Material S1). For example, felids and
361 tayra can be found at Manu National Park, Peru (Endo *et al.* 2010), cougar, boa snakes and pit-vipers at Fazenda
362 Trapsa, northeastern Brazil (Chagas *et al.* 2010), and tayra, ocelot and cougar at RPPN Santuário do Caraça,
363 southeastern Brazil (Talamoni *et al.* 2014). Furthermore, the forest floor may also harbor a variety of infective
364 parasite stages released in feces, vomit, blood or urine, that increase the risk of infection (Nunn *et al.* 2000).

365 Similar to other activities performed on the ground, playing exposes titi monkeys to terrestrial
366 predators while hampering their ability to be vigilant. This limitation can be compensated for by an increase in
367 vigilance by those group members that remain in the canopy, as suggested for squirrel monkeys (*Saimiri*
368 *boliviensis*, Biden *et al.* 1989), golden lion tamarins (*Leontopithecus rosalia*, Oliveira *et al.* 2006), and black-
369 fronted titi monkeys (*Callicebus nigrifrons*, C. Gestich, *pers. obs.*). The interspecific play observed between
370 *Plecturocebus* spp. and various callitrichids may also benefit interacting individuals in a similar way, in addition
371 to a dilution effect resulting from the increase in the number of potential prey (Delm 1990). Although we do not
372 have data on predator density at each study site, carnivorous mammals and snakes were present at all sites
373 where play was recorded. Despite these risks, play on the ground is often recorded in titi monkeys (Kinzey
374 1981), other pitheciids (Barnett *et al.* 2012a), and atelids (Campbell *et al.* 2005; Mourthé *et al.* 2007).

375 Finally, despite the increased risk of predation by terrestrial carnivores on the ground, the forest floor
376 can also serve as an escape route for titis from arboreal and aerial predators, conspecific chasing, and humans
377 (Table 3), as reported for other Neotropical primates (*Ateles* spp., Julliot 1994; *Brachyteles hypoxanthus*,
378 Mourthé *et al.* 2007; *Cacajao* spp., *Chiropotes* spp. and *Pithecia* spp., Barnett *et al.* 2012a, 2012b; *Cebus* spp.,
379 Gilbert and Stouffer 1995). This escape strategy can be an extension of plummeting into the lower vegetation, a
380 common response of small and medium-sized primates (ca. 2-8 kg) to the presence of aerial predators (Barnett
381 *et al.* 2017, 2018; Mourthé and Barnett 2014). Under such circumstances, the additional danger of meeting other
382 predators is likely to be temporarily offset in the presence of an imminent threat.

383

384 **Correlates of terrestrial behavior in titi monkeys**

385 We found that both study duration and rainfall level (surrogates for sampling effort and resource
386 availability, respectively) correlated with ground use by titi monkeys. Longer study duration increased
387 likelihood of observing rare behaviors (Weatherhead 1986). Nevertheless, five out of 19 systematic studies did
388 not report ground use in Callicebinae, suggesting that the extended contact with human observers does not

389 always facilitate observations of terrestriality. Such variation is compatible with the hypothesis that other factors
390 (probably local ones) are more influential than human contact. Changes in resource distribution and availability
391 influence habitat choice (Camaratta *et al.* 2017; Mourthé 2014), resource selection and foraging strategies
392 (Nagy-Reis and Setz 2017), and forest strata use (Ding and Zhao 2004) by primates. Titi monkeys may also
393 adjust diet composition in response to variations in fruit availability and often use the lower forest strata (0.5 to
394 10 m) during periods of fruit scarcity (Acero-Murcia *et al.* 2018; Bicca-Marques and Heymann 2013; Caselli
395 and Setz 2011; Souza-Alves *et al.* 2011). Whilst terrestrial behavior in titi monkeys was correlated with fruit
396 scarcity (this study), some primate species do not seem to follow this pattern. Although significant, the estimates
397 of our models were low (Table 4), implying that an increase of 200 months in study duration or a decrease of
398 200 mm of rainfall in the driest quarter is required to record one additional observation of terrestrial behavior in
399 titi monkeys. However, such a decrease in rainfall in the driest quarter may not be feasible in regions where it is
400 lower than 200 mm. Additionally, the more common presence of open-canopy forests in these regions probably
401 explains why their titis use the ground more frequently (Deguchi *et al.* 2006).

402 Titi monkeys have a wide distribution in South America, occurring in forests that vary greatly in height
403 and canopy connectivity (Electronic Supplementary Material S1). Independent of height and canopy
404 connectivity, titi monkeys usually explore the lower strata in disturbed forests (Bicca-Marques and Heymann
405 2013). This proximity to the ground together with food scarcity in the canopy can help to explain their
406 terrestriality. However, alternative factors, such as predation risk, might explain why titi monkeys seem to avoid
407 the ground at some sites. The identification of the drivers of terrestriality in New World monkeys remains a
408 subject for future continued research.

409

410 **Conclusion**

411 Titi monkeys engage in a variety of activities on the ground, which are more frequent in populations
412 inhabiting more marked seasonal environments and those studied for longer periods. There is a clear difference
413 in the pattern of ground use between *Callicebus* spp. (Atlantic forest titi monkeys) and *Plecturocebus* spp.
414 (Amazonian titi monkeys). Whereas *Callicebus* spp. showed a higher frequency of feeding/foraging for food
415 resources on ground, *Plecturocebus* spp. moved/travelled more frequently on the ground, probably to find
416 alternative food sources and to cross forest clearings. Although *Callicebus* spp. occur in highly fragmented
417 landscapes more frequently than do *Plecturocebus* spp., *Callicebus* species appear to move/travel less than
418 *Plecturocebus* on the ground. For *Cheracebus* spp., we cannot assess whether infrequently observed ground use

419 reflects lower sampling efforts or other more subtle methodological differences between studies, or instead
420 represents a genuine genus-specific propensity for less-frequent terrestriality. The possible ecological and
421 behavioral specialization of *Cheracebus* spp. to *terra firme* forests (van Roosmalen *et al.* 2002), that have high
422 and well-stratified canopies (Defler 1994; Lawler *et al.* 2006), along with the basal position of this clade within
423 callicebines (Byrne *et al.* 2016), suggests that they share a low level of terrestriality, similar with pitheciines.
424 Further investigation is needed to appropriately address differences in moving/travelling behavior between
425 *Plecturocebus* spp. and *Callicebus* spp.; the rarity of terrestrial behavior in *Cheracebus* spp., and to assess
426 whether all titi monkeys share similar levels of behavioral flexibility in disturbed habitats.

427

428 **Conflict of Interest:** The authors declare that they have no conflict of interest.

429

430 **References**

- 431 Acero-Murcia, A., Almario, L. J., García, J., Defler, T. R., & López, R. (2018). Diet of Caquetá titi
432 (*Plecturocebus caquetensis*) in a disturbed forest fragment in Caquetá, Colombia. *Primates*
433 *Conservation*, 32, 1-17.
- 434 Almeida-Silva, B., Guedes, P. G., Boubli, J. P., & Strier, K. B. (2005). Deslocamento terrestre e o
435 comportamento de beber em um grupo de barbados (*Alouatta guariba clamitans* Cabrera, 1940) em Minas
436 Gerais, Brasil. *Neotropical Primates*, 13, 1-3.
- 437 Ancrenaz, M., Sollmann, R., Meijaard, E., Hearn, A. J., Ross, J., et al. (2014). Coming down from the trees: is
438 terrestrial activity in Bornean orangutans natural or disturbance driven? *Scientific Reports*, 4, 4024.
- 439 Anderson, J., Rowcliffe, J.M., & Cowlshaw, G. (2007). Does the matrix matter? A forest primate in a complex
440 agricultural landscape. *Biological Conservation*, 135, 212-222.
- 441 Aversi-Ferreira, R. A. G. M. F., de Abreu, T., Pfrimer, G. A., Silva, S. F., Ziermann, J. M., et al. (2013).
442 Comparative anatomy of the hind limb vessels of the bearded capuchins (*Sapajus libidinosus*) with apes,
443 baboons, and *Cebus capucinus*: with comments on the vessels' role in bipedalism. *BioMed Research*
444 *International*, ID 737358, doi: 10.1155/2013/737358.
- 445 Aximoff, I., & Vaz, S. M. (2016). Bugio-ruivo (Primates, Atelidae) em campos de altitude e com anomalia na
446 coloração no Parque Nacional do Itatiaia, Sudeste do Brasil. *Oecologia Australis*, 20, 122-127.
- 447 Barnett, A. A., Boyle, S., Norconk, M., Palminteri, S., Santos, R. S., et al. (2012a). Terrestrial activity in
448 Pitheciins (*Cacajao*, *Chiropotes* and *Pithecia* spp.). *American Journal of Primatology*, 74, 1106-1127.

449 Barnett, A. A., Almeida, T., Spironello, W. R., Sousa Silva, W., MacLarnon, A., et al. (2012b). Terrestrial
450 foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: is choice of seed patch size
451 and position related to predation-risk? *Folia Primatologica*, 83, 126-139.

452 Barnett, A. A., Bezerra, B. M., Oliveira, M., Queiroz, H., & Defler, T. R. (2013). *Cacajao ouakary* in Brazil and
453 Colombia: patterns, puzzles and predictions. In L. M. Veiga, A. A. Barnett, S. F. Ferrari & M. A. Norconk
454 (Eds.), *Evolutionary biology and conservation of Titis, Sakis and Uacaris* (pp. 179-195). Cambridge:
455 Cambridge University Press.

456 Barnett, A. A., Andrade, E. S., Ferreira, M. C., Garcia Soares, J. B., Fonseca da Silva, V., et al. (2015). Primate
457 predation by black hawk-eagle (*Spizaetus tyrannus*) in Brazilian Amazonia. *Journal of Raptor Research*, 49,
458 105-107.

459 Barnett, A. A., Silla, J. M., de Oliveira, T., Boyle, S. A., Bezerra, B. M., Spironello, W., et al. (2017). Run, hide
460 or fight: anti-predation strategies in Endangered red-nosed cúxiu (*Chiropotes albinasus*, Pitheciidae) in
461 south-eastern Amazonia. *Primates*, 58, 353-360.

462 Barnett, A. A., de Oliveira, T., Soares da Silva, R. F., de Albuquerque Teixeira, S., Todd, L. M., et al. (2018).
463 Honest error, precaution or alertness advertisement? Reactions to vertebrate pseudopredators by red-nosed
464 cuxiús (*Chiropotes albinasus*), a high-canopy Neotropical primate. *Ethology*, 124, 177-187.

465 Biben, M., Symmes, D., & Bernhards, D. (1989). Vigilance during play in squirrel monkeys. *American Journal*
466 *of Primatology*, 17, 41-49.

467 Bicca-Marques, J. C. (1992). Drinking behavior in the black howler monkey (*Alouatta caraya*). *Folia*
468 *Primatologica*, 58, 107-111.

469 Bicca-Marques, J. C., & Calegario-Marques, C. (1995). Locomotion of black howlers in a habitat with
470 discontinuous canopy. *Folia Primatologica*, 64, 55-61.

471 Bicca-Marques, J. C., Muhle, C. B., Prates, H. M., Oliveira, S. G., & Calegario-Marques, C. (2009). Habitat
472 impoverishment and egg predation by *Alouatta caraya*. *International Journal of Primatology*, 30, 743-748.

473 Bicca-Marques, J. C., & Heymann, E. (2013). Ecology and behavior of titi monkeys (genus *Callicebus*). In L.
474 M. Veiga, A. A. Barnett, S. F. Ferrari & M. A. Norconk (Eds.), *Evolutionary biology and conservation of*
475 *Titis, Sakis and Uacaris* (pp. 196-207). Cambridge: Cambridge University Press.

476 Blake, J. G., Guerra, J., Mosquera, D., Torres, R., Loiselle, B. A., & Romo, D. (2010). Use of mineral licks by
477 white-bellied spider monkeys (*Ateles belzebuth*) and red howler monkeys (*Alouatta seniculus*) in eastern
478 Ecuador. *International Journal of Primatology*, 31, 471-483.

479 Boubli, J. P., Byrne, H., da Silva, M. N. F., Silva-Júnior, J., Costa-Araújo, R., et al. (2019). On a new species of
480 titi monkey (Primates: *Plecturocebus* Byrne et al., 2016), from Alta Floresta, southern Amazon. Brazil.
481 *Molecular Phylogenetics and Evolution*, 132, 117-137.

482 Bóveda-Penalba, A., Vermeer, J., Rodrigo, F., & Guerra-Vásquez, F. (2009). Preliminary report on the
483 distribution of *Callicebus oenanthe* on the eastern feet of the Andes. *International Journal of Primatology*,
484 30, 467–480.

485 Boyer, D., Ramos-Fernández, G., Miramontes, O., Mateos, J. L., Cocho, G., et al. (2006). Scale-free foraging by
486 primates emerges from their interaction with a complex environment. *Proceedings of the Royal Society of*
487 *London B: Biological Sciences*, 273(1595), 1743-1750.

488 Boyle, S. A., Thompson, C. L., DeLuycker, A., Alvarez, S. J., Alvim, T. H. G., Aquino, R., et al. (2015).
489 Geographic comparison of plant genera used in frugivory among the pitheciids *Cacajao*, *Callicebus*,
490 *Chiropotes* and *Pithecia*. *American Journal of Primatology*, 78, 493-506.

491 Bravo, A., Harms, K. E., Stevens, R. D., & Emmons, L. H. (2008). Collpas: activity hotspots for frugivorous
492 bats (Phyllostomidae) in the Peruvian Amazon. *Biotropica*, 40, 203–210.

493 Brightsmith, D. J., Taylor, J., Phillips, T. D. (2008). The roles of soil characteristics and toxin adsorption in
494 avian geophagy. *Biotropica*, 40, 766-774.

495 Byrne, H., Rylands, A. B., Carneiro, J. C., Lynch Alfaro, J. W., Bertuol, F., Silva, M. N. F., et al. (2016).
496 Phylogenetic relationship of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy on
497 molecular evidence. *Frontiers in Zoology*, 13, 10. DOI: 10.1186/s12983-016-0142-4.

498 Campbell, A. J., Carvalheiro, L. G., Maués, M. M., Jaffé, R., Giannini, T. C., Freitas, M. A. B., et al. (2018).
499 Anthropogenic disturbance of tropical forests threatens pollination services to açai palm in the Amazon river
500 delta. *Journal of Applied Ecology*, 55(4), 1725-1736.

501 Campbell, C. J., Aureli, F., Chapman, C. A., Ramos-Fernández, G., Matthews, K., Russo, S. E., et al. (2005).
502 Terrestrial behavior of *Ateles* spp. *International Journal of Primatology*, 26, 1039-1051.

503 Cant, J. G. (1992). Positional behavior and body size of arboreal primates: A theoretical framework for field
504 studies and an illustration of its application. *American Journal of Physical Anthropology*, 88, 273–283.

505 Caselli, C. B., & Setz, E. Z. F. (2011). Feeding ecology and activity pattern of black-fronted titi monkeys
506 (*Callicebus nigrifrons*) in a semideciduous tropical forest of Southern Brazil. *Primates*, 52, 351-359.

507 Chagas, R. R. D., & Ferrari, S. F. (2010). Habitat use by *Callicebus coimbrai* (Primates: Pitheciidae) and
508 sympatric species in the fragmented landscape of the Atlantic Forest of southern Sergipe, Brazil. *Zoologia*
509 (Curitiba), 27, 853-860.

510 Chagas, R. R. D., Santos Jr., E. M., Souza-Alves, J. P., & Ferrari, S. F. (2010). Fazenda Trapsa, a refuge of
511 mammalian diversity in Sergipe, Northeastern Brazil. *Revista Nordeste de Biologia*, 19, 35-43.

512 Cheyne, S. M., Supyansyha, Adul, Neale, C. J., Thompson, C., et al. (2018). Down from the treetops: red
513 langur (*Presbytis rubicunda*) terrestrial behavior. *Primates*, doi: 10.1007/s10329-018-0676-5

514 Deffler, T. R. (1994). *Callicebus torquatus* is not a white-sand specialist. *American Journal of Primatology*, 33,
515 149-154.

516 Deguchi, A., Hattori, S., Park, H-T. (2006). The influence of seasonal changes in canopy structure on
517 interception loss: application of the revised Gash model. *Journal of Hydrology*, 318, 80-102.

518 Delm, M. M. (1990). Vigilance for predators: detection and dilution effects. *Behavioral Ecology and*
519 *Sociobiology*, 26(5), 337-342.

520 Dib, L. R. T., Oliva, A. S., & Strier, K. B. (1997). Terrestrial travel in miquis (*Brachyteles arachnoides*)
521 across a forest clearing at the Estação Biológica de Caratinga, Minas Gerais, Brazil. *Neotropical Primates*, 5,
522 8-9.

523 Ding, W., & Zhao, Q. K. (2004). *Rhinopithecus bieti* at Tacheng, Yunnan: diet and daytime
524 activities. *International Journal of Primatology*, 25(3), 583-598.

525 Endo, W., Peres, C. A., Salas, E., Mori, S., Sanchez-Vega, J. L., et al. (2010). Game vertebrate densities in
526 hunted and nonhunted forest sites in Manu National Park, Peru. *Biotropica*, 42(2), 251-261.

527 Eppley, T. M., Donati, G., & Ganzhorn, J. U. (2016). Determinants of terrestrial feeding in an arboreal primate:
528 The case of the southern bamboo lemur (*Hapalemur meridionalis*). *American Journal of Physical*
529 *Anthropology*, 161(2), 328-342.

530 Ferrari, S. F., Veiga, L. M., & Urbani, B. (2008). Geophagy in New World monkeys (Platyrrhini): ecological
531 and geographic patterns. *Folia Primatologica*, 79, 402-415.

532 Ferrari, S. F., & Hilário, R. R. (2012). Use of water sources by buffy-headed marmosets (*Callithrix flaviceps*) at
533 two sites in the Brazilian Atlantic forest. *Primates*, 53, 65-70.

534 Ferrari, S. F., Boyle S. A., Marsh L. K., Port-Carvalho, M., Santos, R. R., et al. (2013a). The challenge of living
535 in fragments. In L. M. Veiga, A. A. Barnett, S. F. Ferrari & M. A. Norconk (Eds.), *Evolutionary biology and*
536 *conservation of Titis, Sakis and Uacaris* (pp. 350-358). Cambridge: Cambridge University Press.

537 Ferrari, S. F., Santos, E. M., Freitas, E. B., Fontes, I. P., Souza-Alves, J. P., Jerusalinsky, L., et al. (2013b).
538 Living on the edge: habitat fragmentation at the interface of the semiarid zone in the Brazilian northeast.
539 In Marsh, L., & Chapman, C. A. (Eds.), *Primates in Fragments: Complexity and Resilience* (pp. 121-135).
540 Springer, New York, NY.

541 Fleagle, J. G. (1999). *Primate adaptation and evolution*. Third Edition. Academic Press.

542 Fox, J., & Weisberg, S. (2011). Package “car” for R software.

543 Galetti, M., & Sazima, I. (2006). Impact of feral dogs in an urban Atlantic forest fragment in southeastern
544 Brazil. *Natureza and Conservação*, 4, 146–151.

545 Gilbert, K. A., & Stouffer, P. C. (1995). Variation in substrate use by white-faced capuchins. *Human Evolution*,
546 10, 265-269.

547 Grueter, C. C., Li, D., Ren, B., Wei, F., Xiang, Z., & van Schaik, C. P. (2009). Fallback foods of temperate-
548 living primates: A case study on snub-nosed monkeys. *American Journal of Physical Anthropology*, 140,
549 700-715.

550 Hawes, J. E., & Peres, C. A. (2016). Patterns of plant phenology in Amazonian seasonally flooded and
551 unflooded forest. *Biotropica*, 48, 465-475.

552 Heymann, E. W., & Nadjafzadeh, M. N. (2013). Insectivory and prey foraging techniques in *Callicebus* – a case
553 of study de *Callicebus cupreus* and comparison with other pitheciids. In L. M. Veiga, A. A. Barnett, S. F.
554 Ferrari & M. A. Norconk (Eds.), *Evolutionary biology and conservation of Titis, Sakis and Uacaris* (pp.
555 215-224). Cambridge: Cambridge University Press.

556 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated
557 climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965-1978.

558 Hilário, R. R., & Mourthé, I. M. (2012). Comparação metodológica de estudos de distribuição vertical de
559 primatas neotropicais. In F. R. de Melo & I. M. Mourthé (Eds.), *A Primatologia no Brasil* (pp. 103-117).
560 Anais do XII Congresso Brasileiro de Primatologia em Belo Horizonte, 2007.

561 Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 65-
562 70.

563 Jones, C. B. (2005). *Behavioral flexibility in primates: Causes and consequences*. New York: Springer.

564 Julliot, C. (1994). Predation of a young spider monkey (*Ateles paniscus*) by a crested eagle (*Morphnus*
565 *guianensis*). *Folia Primatologica*, 63, 75-77.

566 Kinzey, W. G. (1977). Positional behavior and ecology in *Callicebus moloch*. *Yearbook of Physical*
567 *Anthropology*, 20, 248-480

568 Kinzey, W. G., Rosenberger, A. L., Heisler, P. S., Prowse, D. L., & Trilling, J. S. (1977). A preliminary field
569 investigation of the yellow handed titi monkey, *Callicebus torquatus torquatus*, in northern
570 Peru. *Primates*, 18(1), 159-181.

571 Kinzey, W. G. (1981). The titi monkey, genus *Callicebus*. In A. F. Coimbra-Filho & R. A. Mittermeier (Eds.),
572 *Ecology and behavior of Neotropical primates* (pp. 241-276). Rio de Janeiro: Academia Brasileira de
573 Ciências.

574 Kirkpatrick, R. C., & Long, Y. C. (1994). Altitudinal ranging and terrestriality in the Yunnan snub-nosed
575 monkey (*Rhinopithecus bieti*). *Folia Primatologica*, 63(2), 102-106.

576 Krishnamani, R., & Mahaney, W. C. (2000). Geophagy among primates: adaptive significance and ecological
577 consequences. *Animal Behaviour*, 59, 899-915.

578 Lambert, J. E. (2011). Primate nutritional ecology: Feeding biology and diet at ecological and evolutionary
579 scales. In Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M., & Bearder, S. K. (Eds.). *Primates in*
580 *perspective*, 2nd Edn (pp 513–522). Oxford University Press, USA.

581 Lawler, R. R., Ford, S. M., Wright, P. C., & Easley, S. P. (2006). The locomotor behavior of *Callicebus*
582 *brunneus* and *Callicebus torquatus*. *Folia Primatologica*, 77, 228-239.

583 Li, Y. (2007). Terrestriality and tree stratum use in a group of Sichuan snub-nosed monkeys, *Primates*, 48, 197.
584 doi: 10.1007/s10329-006-0035-9.

585 Link, A., Galvis, N., Fleming, E., & Di Fiore, A. (2011). Patterns of mineral lick visitation by spider monkeys
586 and howler monkeys in Amazonia: are licks perceived as risky areas? *American Journal of Primatology*, 73,
587 386-396.

588 Link, A., & Di Fiore, A. (2013). Effects of predation risk on the grouping patterns of white-bellied spider
589 monkeys (*Ateles belzebuth belzebuth*) in Western Amazonia. *American Journal of Physical Anthropology*,
590 150, 579-590.

591 Lee, A. T., Kumar, S., Brightsmith, D. J., & Marsden, S. J. (2010). Parrot claylick distribution in South
592 America: do patterns of “where” help answer the question “why”? *Ecography*, 33(3), 503-513.

593 Martínez, J., & Wallace, R. B. (2011). First observations of terrestrial travel for Olalla’s titi monkey (*Callicebus*
594 *olallae*). *Neotropical Primates*, 18, 49-52.

595 Mason (1966). Social organization of the South American monkey, *Callicebus moloch*: A preliminary report.
596 *Tulane Studies Zoology*, 13, 23-28

597 Mendoza, I., Peres, C. A., & Morellato, L. P. C. (2017). Continental-scale patterns and climatic drivers of
598 fruiting phenology: A quantitative Neotropical review. *Global and Planetary Change*, 148, 227-241.

599 Mesa-Sierra, N., & Pérez-Torres, J. (2017). Calidad estructural y funcional de espacios usados por *Alouatta*
600 *seniculus* em fragmentos de bosque seco tropical (Córdoba, Colombia). *Neotropical Primates*, 23, 9-15.

601 Michalski, F., & Peres, C. A. (2005). Anthropogenic determinants of primate and carnivore local extinctions in
602 a fragmented forest landscape of southern Amazonia. *Biological Conservation*, 124, 383-396.

603 Mourthé, I. M. C. (2014). Response of frugivorous primates to changes in fruit supply in a northern Amazonian
604 forest. *Brazilian Journal of Biology*, 74, 720-727.

605 Mourthé, I. M. C., Guedes, D., Fidelis, J., Boubli, J. P., Mendes, S. L., Strier, K. B. (2007). Ground use by
606 northern muriquis (*Brachyteles hypoxanthus*). *American Journal of Primatology*, 69, 706-712.

607 Mourthé, I. M. C., & Barnett, A. A. (2014). Crying tapir: the functionality of errors and accuracy in predator
608 recognition in two Neotropical high-canopy primates. *Folia Primatologica*, 85, 379-398.

609 Nadjafzadeh, M. N., & Heymann, E. W. (2008). Prey foraging of red titi monkeys, *Callicebus cupreus*, in
610 comparison to sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Physical*
611 *Anthropology*, 135, 56-63.

612 Nagy-Reis, M. B., & Setz, E. Z. F. (2017). Foraging and ranging behavior of black-fronted titi monkeys
613 (*Callicebus nigrifrons*) and their relation to food availability in a seasonal tropical forest. *Primates*, doi:
614 10.1007/s10329-016-0556-9

615 Napier, J.R., & Napier, P. H. (1967). *Handbook of living primates*. Academic, London.

616 Norconk, M. A. (2011). Sakis, uakaris, and titi monkeys: behavioral diversity in a radiation of primate seed
617 predators. In Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M., & Bearder, S. K. (Eds.).
618 *Primates in perspective*, 2nd Edn (pp 122–139). Oxford University Press, USA.

619 Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P., & Hill, R. A. (2014). Human observers impact
620 habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology*, 25, 1199-1204.

621 Nunn, C. L., Gittleman, J. L. & Antonovics, J. (2000). Promiscuity and the primate immune system. *Science*,
622 290, 1168–1170.

623 Nunn, C. L., & Altizer, S. (2006). *Infectious diseases in primates: Behavior, ecology and evolution*. Oxford:
624 Oxford University Press.

625 Oliveira, C. R., Ruiz Miranda, C. R., Kleiman, D. G., & Beck, B. B. (2003). Play behavior in juvenile golden
626 lion tamarins (Callitrichidae: Primates): organization in relation to costs. *Ethology*, 109(7), 593-612.

627 Ottoni, E. B., & Izar, P. (2008). Capuchin monkeys tool use: overview and implications. *Evolutionary*
628 *Anthropology*, 17, 171-178.

629 Pinheiro, T., Ferrari, S. F., & Lopes, M. A. (2013). Activity budget, diet, and use of space by two groups of
630 squirrel monkeys (*Saimiri sciureus*) in eastern Amazonia. *Primates*, 54(3), 301-308.

631 Porfírio, G., Santos, F. M., Foster, V., Nascimento, L. F., Macedo, et al. (2017). Terrestriality of wild *Sapajus*
632 *cay* (Illiger, 1815) as revealed by camera traps. *Folia Primatologica*, 88(1), 1-8.

633 Pozo-Montuy, G., Serio-Silva, J. C., & Bonilla-Sanchez, Y. M. (2011). The influence of the matrix on the
634 survival of arboreal primates in fragmented landscapes. *Primates*, 52, 139-147.

635 Prates, H. M., & Bicca-Marques, J. C. (2008). Age-sex analysis of activity budget, diet, and positional behavior
636 in *Alouatta caraya* in an orchard forest. *International Journal of Primatology*, 29, 703-715.

637 Printes, R. C., Rylands, A. B., & Bicca-Marques, J. C. (2011). Distribution and status of critically endangered
638 blond titi monkey *Callicebus barbarabrownae* of north-east Brazil. *Oryx*, 45, 439-443.

639 R Development Core Team. (2016). *R: A language and environment for statistical computing*. Version 3.3.0.
640 Vienna, Austria: R Foundation for Statistical Computing.

641 Rumiz, D. I. (2012). Distribution, habitat and status of the white-coated titi monkey (*Callicebus pallescens*) in
642 the Chaco-Chiquitano forest of Santa Cruz, Bolivia. *Neotropical Primates*, 19, 8-15.

643 Serrano-Villavicencio, J. E., Vendramel, R. L., & Garbino, G. S. T. (2017). Species, subspecies, or color
644 morphs? Reconsidering the taxonomy of *Callicebus* Thomas, 1903 in the Purus–Madeira interfluvium.
645 *Primates*, 58, 159–167.

646 Setz, E. Z. F., Enzweiler, J., Solferini, V. N., Amendola, M. P., & Berton, R. S. (1999). Geophagy in golden-
647 faced saki monkey, *Pithecia pithecia chrysocephala*, in Central Amazon. *Journal of Zoology* (London), 247,
648 91-103

649 Shanee, S., & Shanee, N. (2011). Observations of terrestrial behavior in the Peruvian night monkey (*Aotus*
650 *miconax*) in an anthropogenic landscape, La Esperanza, Peru. *Neotropical Primates*, 18, 55-58.

651 Shanee, S., Tello-Alverado, J. C., Vermeer, J., & Boveda-Penalba, A. J. (2011). GIS risk assessment and GAP
652 analysis for the Andean titi monkey (*Callicebus oenanthe*). *Primate Conservation*, 26, 17-24.

653 Soini, P. (1987). Ecology of the saddle-back tamarin *Saguinus fuscicollis illigeri* on the Rio Pacaya,
654 northeastern Peru. *Folia Primatologica*, 49, 11-32.

655 Souza, F. S. C., & Calouro, A. M. (2018). Predation of army ants by Toppin's titi monkey, *Plecturocebus*
656 *toppini* Thomas 1914 (Primates: Pitheciidae), in an urban forest fragment in eastern Acre, Brazil. *Primates*,
657 1-6.

658 Souza-Alves, J. P., Fontes, I. P., Chagas, R. R. D., & Ferrari, S. F. (2011). Seasonal versatility in the feeding
659 ecology of a group of titis (*Callicebus coimbrai*) in the northern Brazilian Atlantic forest. *American Journal*
660 *of Primatology*, 73, 1199-1209.

661 Su, Y., Ren, R., Yan, K., Li, J., Zhou, Y., et al. (1998). Preliminary survey of the home range and ranging
662 behavior of golden monkeys (*Rhinopithecus [Rhinopithecus] roxellana*) in Shennongjia National Natural
663 Reserve, Hubei, China. In Jablonski N. G. (Ed.), *The natural history of the doucs and snub-nosed monkeys*
664 (pp. 255-268). London: World Scientific Publishing.

665 Tabacow, F. P., Mendes, S. L., & Strier, K. B. (2009). Spread of a terrestrial tradition in an arboreal primate.
666 *American Anthropologist*, 111, 238-249.

667 Takemoto, H. (2004). Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical
668 forest. *American Journal of Physical Anthropology*, 124, 81-92.

669 Talamoni, S. A., Amaro, B. D., Cordeiro-Júnior, D. A., & Maciel, C. E. M. A. (2014). Mammals of Reserva
670 Particular do Patrimônio Natural Santuário do Caraça, state of Minas Gerais, Brazil. *Check List*, 10(5), 1005-
671 1013.

672 Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, 60(6), 711-
673 722.

674 van Roosmalen, M. G. M., van Roosmalen, T., & Mittermeier, R. A. M. (2002). A taxonomic review of the titi
675 monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi*
676 and *Callicebus stephennashi*, from Brazilian Amazonia. *Neotropical Primates*, 10 (Suppl.), 1-52.

677 Velleman, P. F., & Welsch, R. E. (1981). Efficient computing of regression diagnostics. *The American*
678 *Statistician*, 35(4), 234-242. doi:10.1080/00031305.1981.10479362

679 Voigt, C. C., Capps, K. A., Dechmann, D. K. N., Michener, R. H., & Kunz, T. H. (2008). Nutrition or
680 Detoxification: Why bats visit mineral licks of the Amazonian rainforest. *PLoS ONE* 3(4), e2011. doi:
681 10.1371/journal.pone.0002011.

682 Weatherhead, P. J. (1986). How unusual are unusual events? *The American Naturalist*, 128: 150-154.

- 683 Williamson, E. A., & Feistner, A. T. C. (2003). Habituating primates: processes, techniques, variables and
684 ethics. In J. M. Setchell & D. J. Curtis (Eds.), *Field and laboratory methods in primatology: A practical*
685 *guide* (pp. 25-39). Cambridge: Cambridge University Press.
- 686 Wu, B.Q. (1993). Patterns of spatial dispersion, locomotion, and foraging behavior in three groups of Yunnan
687 snub-nosed langur (*Rhinopithecus roxellana*) on Baimaxue Mountains, northwestern Yunnan Province,
688 China. *Folia Primatologica*, 60:63–71
- 689 Wu, B.Q., Tai, Z., & Ji, W. (1988). A preliminary survey of ecology and behavior on Yunnan snub-nosed
690 monkey (*Rhinopithecus bieti*) group. *Zoological Research*, 9:373–384
- 691 Zuur, A. F., Ieno, E. N., Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical
692 problems. *Methods in Ecology and Evolution*, 1, 3-14.

693

694 **Acknowledgements**

695 All authors acknowledge that they followed the laws of the countries where their research was
696 conducted, and thank the numerous sources that funded, helped and supported the various research projects
697 from which the data were compiled and analyzed. We are grateful to Joanna Setchell and two anonymous
698 reviewers for the valuable consideration in the manuscript.

699

700

701

702

703

704

705

706

707

708

709

710

711

712

713 **Figure legends**

714 Figure 1. Location of (A) the 19 study sites where *Callicebus* spp. and (B) the 46 study sites where *Cheracebus*
715 spp. and *Plecturocebus* spp. were observed engaging in terrestrial behavior (Listed in Electronic Supplementary
716 Material S1). White circles correspond to sites where we recorded up to 10 terrestrial records, white triangles
717 from 11 to 50 records, and white squares are ≥ 51 records. Black symbols represent non-systematic records
718 where terrestrially was recorded, but titi monkeys were not the study targets.

719

720 Figure 2. Partial regressions of the number of terrestrial records in titi monkeys against (A) study duration
721 (controlled for rainfall level and vegetation height), and B) rainfall level (controlled for study duration and
722 vegetation height).

Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus* and *Plecturocebus*): potential correlates, patterns and differences between genera

Acknowledgements

All authors acknowledge that they followed the laws of the countries where their research was conducted, and thank the numerous sources that funded, helped and supported the various research projects from which the data were compiled and analyzed. We are grateful to Joanna Setchell and two anonymous reviewers for the valuable consideration in the manuscript.

João Pedro Souza-Alves, Programa de Pós-graduação em Biologia Animal, Departamento de Zoologia,

Universidade Federal de Pernambuco, Recife, Brazil; souzaalves1982@gmail.com

Italo Mourthe, Programa de Pós-graduação em Biodiversidade e Conservação, Universidade Federal do

Pará, Altamira, Brazil; imourthe@gmail.com

Renato R. Hilário, Departamento de Meio Ambiente e Desenvolvimento, Universidade Federal do

Amapá, Macapá, Brazil; renatohilario@gmail.com

Júlio César Bicca-Marques, Departamento de Biodiversidade e Ecologia, Pontifícia Universidade

Católica do Rio Grande do Sul, Porto Alegre, Brazil; jcbicca@pucrs.br

Jennifer Rehg, Department of Anthropology, Southern Illinois University Edwardsville, Edwardsville,

United States of America; jrehg@siue.edu

Carla C. Gestich, Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual

de Campinas, São Paulo, Brazil; carlagestich@gmail.com

Adriana C. Acero-Murcia, Universidade Federal de São Paulo, Programa de Pós-graduação em Ecologia

e Evolução, São Paulo, Brazil; adriana.carolina.acero@gmail.com

Patrice Adret, Museo Historia Natural Noel Kempff Mercado, UAGRM, Santa Cruz de La Sierra,
Bolivia; patrice.adret@gmail.com

Rolando Aquino, Universidad Nacional Mayor de San Marcos, Lima, Peru; raquinoy2005@yahoo.es

Mélissa Berthet, Department of Comparative Cognition, University of Neuchâtel, Neuchâtel, Switzerland;
melissa.berthet@unine.ch

Mark Bowler, School of Science, Technology and Engineering, University of Suffolk, Suffolk, United
Kingdom; M.Bowler@uos.ac.uk

Armando M. Calouro, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre,
armandocalouro1@gmail.com

Gustavo R. Canale, Universidade Federal do Mato Grosso, Núcleo de Estudos da Amazônia
Matogrossense, Sinop, Mato Grosso, Brazil; grcanale@gmail.com

Nayara de A. Cardoso, Programa de Pós-graduação em Ciências Biológicas, Departamento de
Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil;
nayaraprimatas@gmail.com

Christini B. Caselli, Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife,
Pernambuco, Brazil; ccaselli@gmail.com

Cristiane Cäsar, Museu de Ciências Naturais PUC Minas, Minas Gerais, Brazil; criscasar@gmail.com

Renata R.D. Chagas, Programa de Pós-graduação em Ciências Biológicas, Departamento de Sistemática e
Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil;
renata_deda118@hotmail.com

Aryanne Clyvia, Bicho do Mato Meio Ambiente, Belo Horizonte, MG, Brazil;
aryanneclyvia@yahoo.com.br

Cintia F. Corsini, Programa de Capacitação Institucional, Instituto Nacional da Mata Atlântica, Santa
Teresa, Espírito Santo, Brazil; cintia.corsini@yahoo.com.br

Thomas Defler, Departamento de Biología, Universidad Nacional de Colombia, Bogotá D. C., Colombia;
thomasdefler@gmail.com

Anneke DeLuycker, Smithsonian-Mason School of Conservation, Smithsonian Conservation Biology
Institute, Front Royal, VA, United States of America; adeluyck@gmu.edu

Anthony Di Fiore, Department of Anthropology, University of Texas at Austin, Austin, United States of
America; anthony.difiore@austin.utexas.edu

Kimberly Dingess, Department of Anthropology, Indiana University, Bloomington, United States of
America; kdingess@uemail.iu.edu

Gideon Erkenwick, Department of Biology, University of Missouri-St. Louis, St. Louis, United States of
America; giderk@gmail.com

Michele Alves Ferreira, Bicho do Mato Meio Ambiente, Belo Horizonte, MG, Brazil;
micheleferreira@bichodomato.net.br

Eduardo Fernandez-Duque, Department of Anthropology, Yale University, New Haven, United States of
America; eduardo.fernandez-duque@yale.edu

Stephen F. Ferrari, Departamento de Ecologia, Universidade Federal de Sergipe, São Cristóvão, Sergipe,
Brazil; stephenfferrari@gmail.com

Isadora P. Fontes, Secretaria Municipal de Meio Ambiente de Aracaju, Aracaju, Sergipe, Brazil;
imspfuentes@gmail.com

Josimar Daniel Gomes, Anglo American Minério de Ferro Brasil S/A, Minas Gerais, Brazil;
josimar.gomes@angloamerican.com

Frederico P. R. Gonçalves, Programa de Pós-graduação em Sustentabilidade e Tecnologia Ambiental,
Instituto Federal de Minas Gerais, Bambuí, Minas Gerais, Brazil; fredericopahlm@gmail.com

Maurício Guerra, Parques Nacionales Naturales de Colombia, Parque Nacional Natural Amacayacu,
Leticia, Colombia; guerramauricio@hotmail.com

Torbjørn Haugaasen, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Norway; torbjorn.haugaasen@nmbu.no

Stefanie Heiduck, Deutsches Primatenzentrum, Göttingen, Germany; SHeiduck@dpz.eu

Eckhard W. Heymann, Deutsches Primatenzentrum, Göttingen, Germany; eheyman@gwdg.de

Shannon Hodges, Department of Anthropology, Texas A&M University College Station, Texas, United States of America; rose1283@tamu.edu

Rosario Huashuayo-Llamocca, Proyecto Mono Tocón, Moyobamba, San Martín, Peru; r.huashuayo@monotocon.org

Leandro Jerusalinsky, Centro Nacional de Pesquisa e Conservação de Primatas Brasileiros, Instituto Chico Mendes de Conservação da Biodiversidade, João Pessoa, Brazil; ljerusalinsky@gmail.com

Carlos Benhur Kasper, Laboratório de Biologia de Mamíferos e Aves, Universidade Federal do Pampa, Campus de São Gabriel, São Gabriel, RS, Brazil; cbkasper@yahoo.com.br

Jenna Lawrence, Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, United States of America; j.lawrence@columbia.edu

Teresa Magdalena Lueffe, Deutsches Primatenzentrum, Göttingen, Germany; t.lueffe@stud.uni-goettingen.de

Karine G. D. Lopes, Programa de Pós-Graduação em Zoologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; karine.galisteo@acad.pucrs.br

Jesús Martínez, Wildlife Conservation Society-Bolivia, La Paz, Bolivia; jmartinez@wcs.org

Fabiano R. de Melo, Instituto de Biociências, Universidade Federal de Goiás, Regional Jataí, Goiânia, *and* Departamento de Engenharia Florestal, Universidade Federal de Viçosa, Brazil; fabiano_melo@ufg.br

Mariluce Rezende Messias, Laboratório de Mastozoologia & Vertebrados Terrestres, Departamento de Biologia, Universidade Federal de Rondônia, Porto Velho, Brazil; messias.malu@gmail.com.

Mariana B. Nagy-Reis, Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; mariana.nbreis@gmail.com

Inés Nole, Facultad de Medicina Veterinaria, Universidad Nacional Mayor de San Marcos, Lima, Peru; inesnole@hotmail.com

Filipa Paciência, Deutsches Primatenzentrum, Göttingen, Germany; fmdpaciencia@gmail.com

Erwin Palacios, Conservation International-Colombia, Bogota, Colombia; e.palacios@conservation.org

Alice Poirier, Department of Life Sciences, Anglia Ruskin University, Cambridge, UK; poirier.ac@gmail.com

Grasiela Porfírio, Programa de Pós-Graduação em Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco, Campo Grande, Brazil; grasi_porfirio@hotmail.com

Amy Porter, Department of Anthropology, University of California, Davis, CA, USA; amyporter@ucdavis.edu

Eluned Price, Durrell Wildlife Conservation Trust, Jersey, United Kingdom; Eluned.Price@durrell.org

Rodrigo C. Printes, Laboratório de Gestão Ambiental e Negociação de Conflitos, Universidade Estadual do Rio Grande do Sul, São Francisco de Paula, Brazil;

Erika P. Quintino, Laboratório de Primatologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brasil; erika_estrela@yahoo.com.br

Evandro Amato Reis, Bicho do Mato Meio Ambiente, Belo Horizonte, MG, Brazil; evandroreis@bichodomato.net.br

Alessandro Rocha, Núcleo de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil; le.carpediem.ar@gmail.com

Adriana Rodríguez, Conservation International Colombia, Bogotá D.C., Colombia; adrianarr@hotmail.com

Fábio Röhe, World Conservation Society Brazil, Manaus, Brazil; fabiorohe@gmail.com

Damián Rumiz, Fundación Simón I. Patiño, Santa Cruz de la Sierra, Bolivia; confauna@scbbs.net

Sam Shanee, Neotropical Primate Conservation UK, Manchester, United Kingdom;

samshanee@gmail.com

Marina M. Santana, Departamento de Ecologia, Programa de Pós-graduação em Ecologia e Conservação,

Universidade Federal de Sergipe, Brazil; marinamarquessantana@gmail.com

Eleonore Z. F. Setz, Departamento de Biologia Animal, Universidade Estadual de Campinas, São Paulo,

Brazil; ezfsetz@gmail.com

Francisco Salatiel C. de Souza, Programa de Pós-graduação em Ecologia e Manejo de Recursos Naturais,

Universidade Federal do Acre, Acre, Brazil; salatielclemente@gmail.com

Wilson Spironello, Grupo de Pesquisa de Mamíferos da Amazônia, Instituto Nacional de Pesquisas da

Amazônia, Manaus, AM, Brazil; wrspronello@gmail.com

Emérita R. Tirado Herrera, Universidad Nacional de la Amazonía Peruana, Iquitos, Peru;

toconcolorado@gmail.com

Luana Vinhas, Departamento de Biologia, Universidade Católica do Salvador, Bahia, Brazil;

luavmuniz@gmail.com

Kevina Vulinec, Department of Agriculture & Natural Resources, Delaware State University, Dover,

United States of America; kvulinec@desu.edu

Robert B. Wallace, Wildlife Conservation Society Bolivia, La Paz, Bolivia; rwallace@wcs.org

Mrinalini Watsa, Department of Anthropology, Washington University in Saint Louis, United States of

America; mwatsa@wustl.edu

Patricia C. Wright, Department of Anthropology, State University of New York at Stony Brook, Stone

Brook, New York, United States of America; patricia.wright@ic.sunysb.edu

Robert J. Young, Department of Biology, University of Salford, Manchester, United Kingdom;

R.J.Young@salford.ac.uk

Adrian A. Barnett, Grupo de Pesquisa de Mamíferos da Amazônia, Instituto Nacional de Pesquisas da
Amazônia, Manaus, AM, Brazil *and* Centre for Research in Evolutionary Anthropology,
Roehampton University, London, United Kingdom; adrian.barnett1.biology@gmail.com.

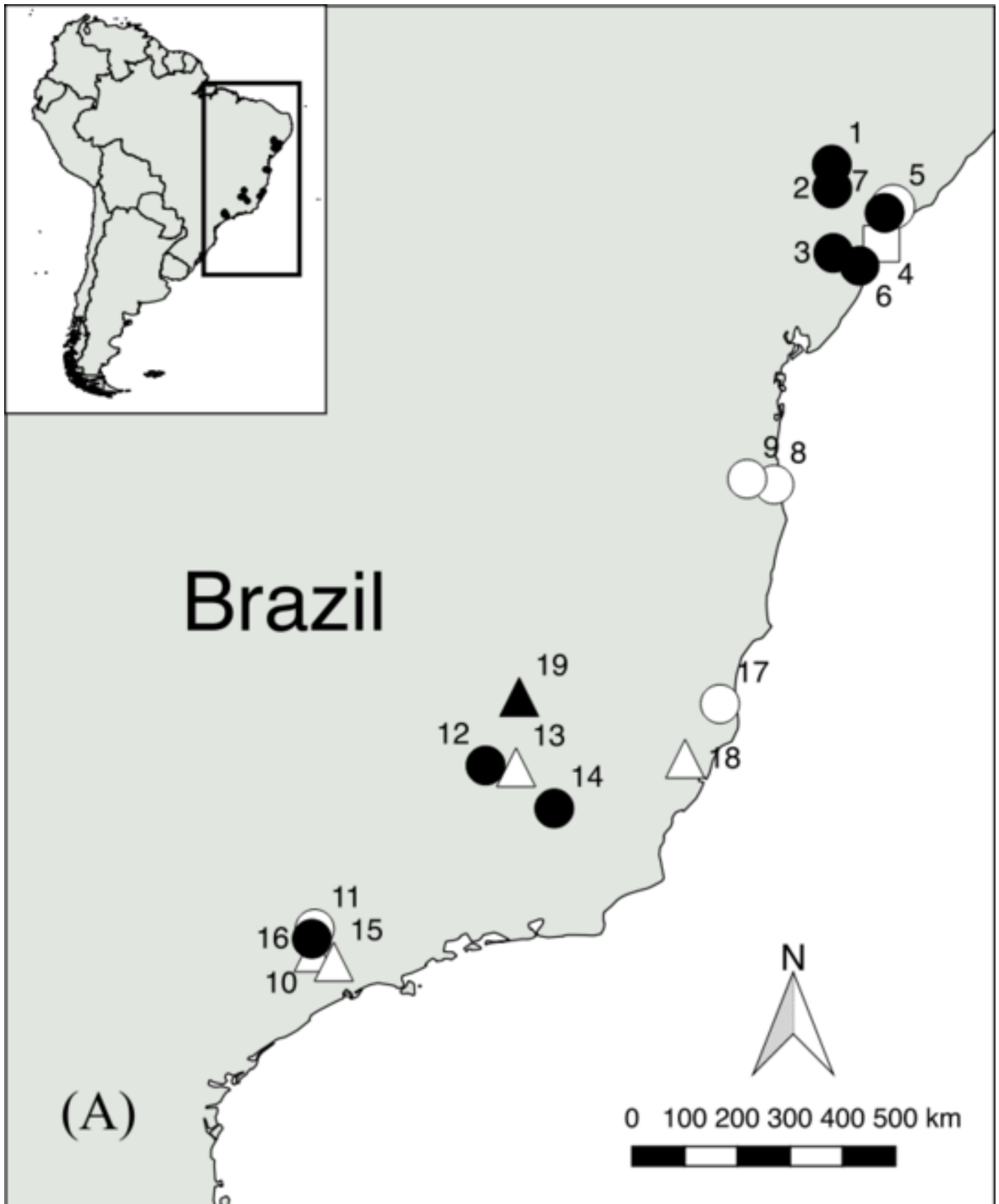
Correspondence author: J.P. Souza-Alves, Departamento de Zoologia, Universidade Federal de
Pernambuco, Av. Prof. Moraes Rego, 1235, Cidade Universitária, 50670-901, Recife, Pernambuco,
Brazil. Phone: +55 79 8129-8106. E-mail: souzaalves1982@gmail.com

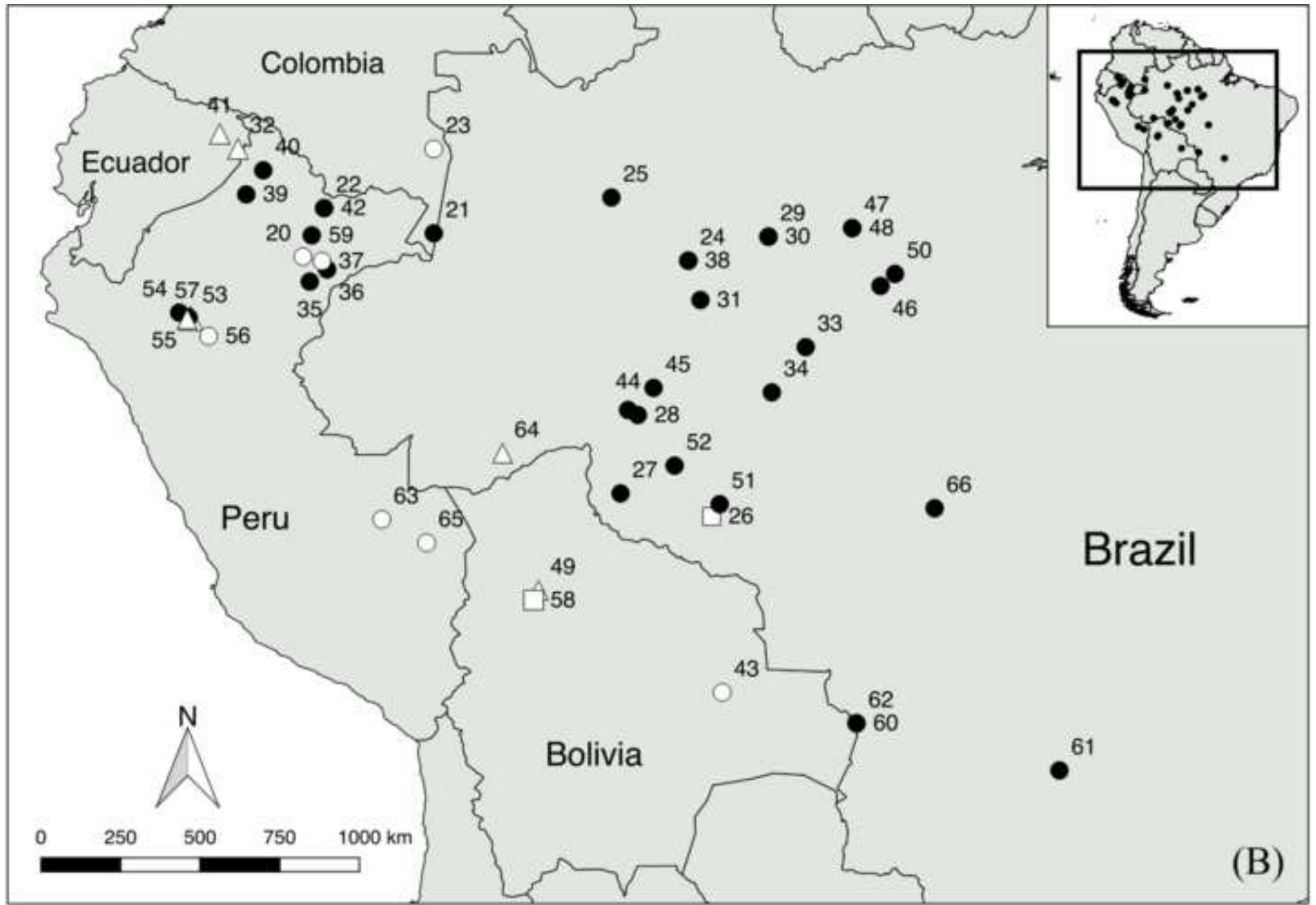
Author Contributions: JPS-A and AAB conceived and designed the experiments. RRH and IM analyzed the data. JPS-A and AAB wrote the first draft of manuscript. All the authors revised the manuscript.

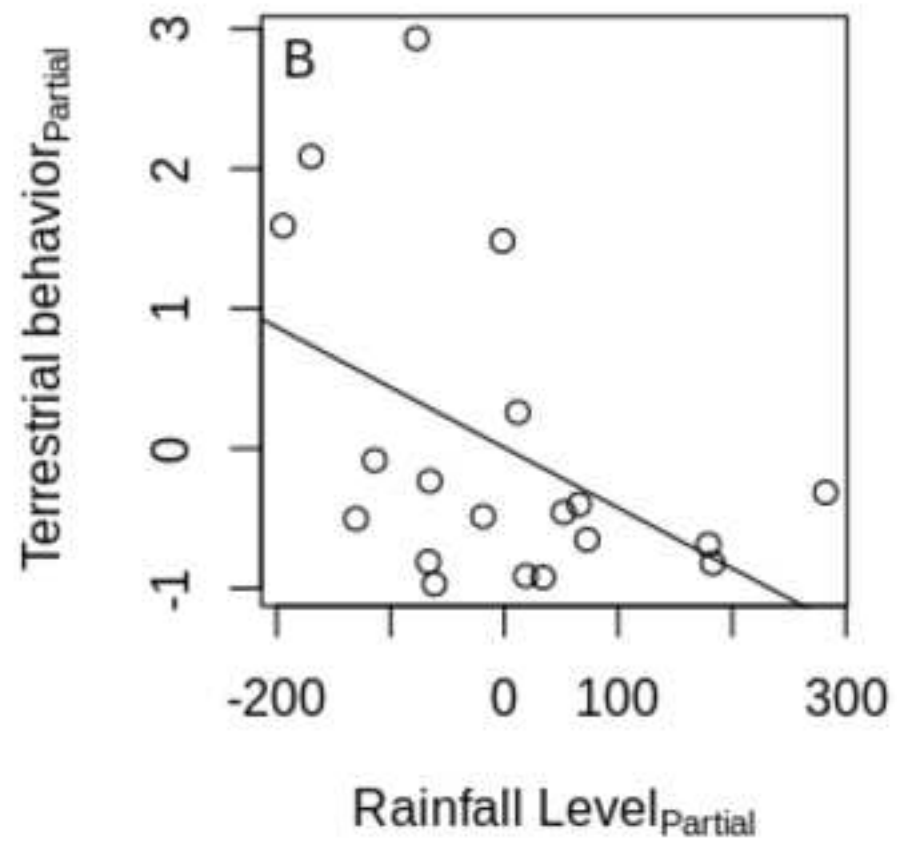
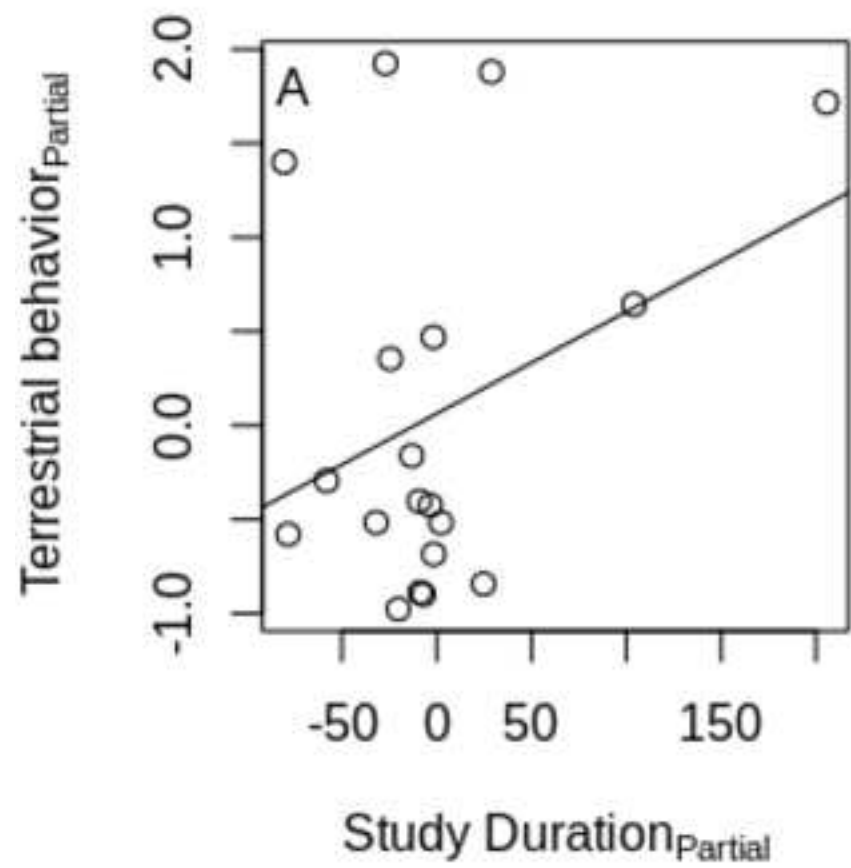
Acknowledgements

All authors acknowledge that they followed the laws of the countries where their research was conducted, and thank the numerous sources that funded, helped and supported the various research projects from which the data were compiled and analyzed. We are grateful to Joanna Setchell and two anonymous reviewers for the valuable consideration in the manuscript.

Supporting Information studies of Callicebinae (*Callicebus*, *Cheracebus* and *Plecturocebus*) analyzed in this review (Appendix S1) are available online.







Tables

Table 1. Ground use by Neotropical primates.

Behavior	Species	Reference
Accessing water sources	<i>Alouatta caraya</i>	Bicca-Marques (1992)
	<i>Alouatta guariba clamitans</i>	Almeida-Silva <i>et al.</i> (2005)
	<i>Ateles</i> spp.	Haugaasen, pers. obs.
	<i>Brachyteles hypoxanthus</i>	Mourthé <i>et al.</i> (2007)
	<i>Callithrix flaviceps</i>	Ferrari and Hilário (2012)
	<i>Sapajus cay</i>	Porfírio <i>et al.</i> (2017)
Visiting mineral licks	<i>Alouatta pigra</i>	Pozo-Montuy and Serio-Silva (2007)
	<i>Alouatta seniculus</i>	Link <i>et al.</i> (2011)
	<i>Ateles</i> spp.	Campbell <i>et al.</i> (2005); Link <i>et al.</i> (2011); Link and Di Fiore (2013)
	<i>Lagothrix flavicauda</i>	S. Shanee, pers. obs.
Exploiting ground-specific food resources	<i>Alouatta caraya</i>	Bicca-Marques <i>et al.</i> (2009)
	<i>Alouatta pigra</i>	Pozo-Montuy and Serio-Silva (2007)
	<i>Cacajao ouakary</i>	Barnett <i>et al.</i> (2012a)
	<i>Cebus yuracus</i>	S. Shanee, pers. obs.
	<i>Plecturocebus torquatus</i>	Kinzey (1977)
	<i>Saguinus mystax</i> and <i>Leontocebus nigrifrons</i>	Nadjafzadeh and Heymann (2008)
	<i>Saimiri sciureus</i>	Pinheiro <i>et al.</i> (2013)
	<i>Sapajus apella</i>	W.R. Spironello, pers. obs.
Crossing canopy gaps, roads or open areas between forest fragments	<i>Alouatta caraya</i>	Prates and Bicca-Marques (2008), G. Porfirio, pers. obs.
	<i>Alouatta guariba clamitans</i>	Aximoff and Vaz (2016); I. Mourthe, pers. obs.; J. C. Bicca-Marques, pers. obs.
	<i>Alouatta macconnelli</i>	I. Mourthe, pers. obs.

	<i>Aotus azarae</i>	M. Svensson and E. Fernandez-Duque, pers. comm.
	<i>Aotus miconax</i>	Shanee and Shanee (2011)
	<i>Brachyteles hypoxanthus</i>	Dib <i>et al.</i> (1997); Mourthé <i>et al.</i> (2007)
	<i>Callithrix penicillata</i>	I. Mourthé, pers. obs.
	<i>Leontocebus illigeri</i>	Soini (1987)
	<i>Plecturocebus cupreus</i>	Nadjafzadeh and Heymann (2008)
	<i>Plecturocebus olallae</i>	Martínez and Wallace (2013)
	<i>Plecturocebus toppini</i>	de Souza and Calouro (2018)
	<i>Mico humeralifer</i>	Barnett <i>et al.</i> (2015)
	<i>Saguinus</i> and <i>Leontocebus</i>	S. Shanee, pers. obs.
	<i>Saguinus mystax pileatus</i>	I. Mourthé, pers. obs.
Escaping from predators	<i>Cebus apella</i>	K. Vulinec, pers. obs.
	<i>Chiropotes</i> spp.	Barnett <i>et al.</i> (2012a,b)
Playing	<i>Brachyteles hypoxanthus</i>	Mourthé <i>et al.</i> (2007)
	<i>Callithrix flaviceps</i>	R. Hilário, pers. obs.
	<i>Leontocebus weddelli</i>	J.C. Bicca-Marques, pers. obs.
	<i>Leontopithecus chrysomelas</i>	C.B. Caselli, pers. obs.
	<i>Saguinus fuscicollis</i>	K. Vulinec, pers. obs.
	<i>Sapajus apella</i>	W.R. Spironello, pers. obs.

Table 2. Categories of behavioral activities performed by titi monkeys on the ground

Behavioral category	Description
Feeding/foraging	Eating/searching for any type of food
Moving/travelling	Local and/or regional locomotion, including navigation between local foraging sites or forest patches
Resting	Inactive
Social interactions	Intraspecific or interspecific agonistic, affiliative and play behaviors
Antipredator behavior	Jumping/descending to the ground to escape predators; hiding
Geophagy	Ingestion of soil not associated with the consumption of prey or plant items
Retrieving fallen infants	Rescue of an infant on the ground (accidental ground use)

Table 3. Number of records (percentages in parentheses) of behaviors performed on the ground by each titi monkey species. Systematic and opportunistic records are pooled here. Asterisks indicate categories whose frequencies differed significantly between *Plecturocebus* and *Callicebus* according to Chi-square tests.

Species	Number (%) of records of terrestrial activity						
	Feeding/ Foraging*	Moving/Travelling*	Resting	Social interactions	Antipredator behavior	Geophagy	Infant retrieval
<i>Callicebus</i>							
<i>C. barbarabrownae</i>	5 (62)	3 (38)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>C. coimbrai</i>	92 (66)	30 (21)	6 (4)	7 (5)	1 (1)	0 (0)	4 (3)
<i>C. melanochir</i>	4 (21)	0 (0)	0 (0)	0 (0)	0 (0)	13 (69)	2 (10)
<i>C. nigrifrons</i>	56 (39)	41 (28)	6 (4)	28 (19)	0 (0)	0 (0)	14 (10)
<i>C. personatus</i>	3 (14)	6 (29)	3 (14)	8 (38)	1 (5)	0 (0)	0 (0)
Total	160 (48)	80 (24)	15 (4)	43 (13)	2 (1)	13 (4)	20 (6)
<i>Cheracebus</i>							
<i>C. lucifer</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
<i>C. lugens</i>	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>C. purinus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>C. torquatus</i>	0 (0)	2 (67)	0 (0)	0 (0)	1 (33)	0 (0)	0 (0)
Total	2 (33)	2 (33)	0 (0)	0 (0)	1 (17)	0 (0)	1 (17)

<i>Plecturocebus</i>							
<i>P. bernhardi</i>	40 (43)	9 (10)	11 (12)	11 (12)	0 (0)	23 (24)	0 (0)
<i>P. brunneus</i>	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)
<i>P. caligatus</i>	2 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. caquetensis</i>	20 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. cinerascens</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. cupreus</i>	4 (57)	1 (14)	0 (0)	0 (0)	2 (29)	0 (0)	0 (0)
<i>P. discolor</i>	10 (30)	4 (12)	0 (0)	1 (3)	1 (3)	4 (12)	13 (40)
<i>P. donacophilus</i>	1 (50)	1 (50)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. dubius</i>	0 (0)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. hoffmannsi</i>	4 (100)	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. modestus</i>	0 (0)	26 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. moloch</i>	0 (0)	1 (25)	1 (25)	1 (25)	0 (0)	0 (0)	1 (25)
<i>P. oenanthe</i>	22 (30)	18 (24)	0 (0)	21 (28)	0 (0)	3 (4)	10 (14)
<i>P. olallae</i>	0 (0)	109 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. ornatus</i>	1 (50)	0 (0)	0 (0)	1 (50)	0 (0)	0 (0)	0 (0)
<i>P. pallescens</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>P. toppini</i>	14 (33)	13 (31)	0 (0)	6 (14)	2 (5)	1 (2)	6 (14)

<i>P. vieirai</i>	3 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total	121 (28)	184 (43)	12 (3)	41 (11)	6 (1)	31 (7)	30 (7)

Table 4. Result of a full Generalized Linear Model relating terrestrial activity in callicebines with three predictive variables. Significant results are in bold.

Variables	Estimate \pm SE	Significance
Study duration	0.0048 \pm 0.0003	< 0.0001
Rainfall	-0.0050 \pm 0.0003	< 0.0001
Forest height	0.0056 \pm 0.0091	0.536



[Click here to access/download](#)

Supplemental File
ESM_1.docx