



For emergency only: terrestrial feeding in Coimbra-Filho's titis reflects seasonal arboreal resource availability

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Abstract

Terrestriality in Platyrrhine primates is primarily associated with low arboreal resource availability, low predation risk when on the ground and increased contact time with human observers. To test the relationship between these variables and ground use frequency, we studied a group of endangered Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) in a 14-ha forest fragment in north-eastern Brazil. Terrestriality data were collected on a monthly basis (33 months) using scan sampling procedures from July 2008 to July 2012. Overall, Coimbra-Filho's titi monkeys were recorded during 0.6% of observation time (113 out of 18,164 scans) on the ground. Most of the time on the ground was spent feeding on young leaves (71 records) and the least amount of time on fruits (14 records). Availability of arboreal foods, rainfall, and time of contact with human observers did not influence overall terrestrial behaviour (ground use). However, the timing and nature of the monkeys' terrestrial feeding was strongly related to the absence of arboreal fruit (β -estimate = -3.078) and young leaf (β -estimate = -3.515) food resources. We suggest that terrestrial feeding by Coimbra-Filho's titi monkeys could be an adaptation to low arboreal fruit availability and the exploitation of alternative food resources.

Keywords Arboreal food resources · Brazil · *Callicebus coimbrai* · Human habituation · Predation risk · Predator-sensitive foraging

Introduction

Within the landscape of fear (sensu Laundré et al., 2001; topic review Bleicher 2017), the presence and dispersion of predators may have a profound effect on primate

behaviour. This includes the period when researchers are habituating study animals so that their presence eventually causes minimal stress and impact on the primate study group (Williamson and Feistner 2003). During this time, the presence of humans can affect the behaviour of unhabituated or partially habituated animals, provoking alarm calling (Bezerra and Souto 2008), reducing the time spent feeding, grooming, and resting, and increasing

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vigilance-related behaviours and ranging patterns (Tutin and Fernandez 1991; Cipolletta 2003; Doran-Sheehy et al. 2004). Faecal cortisol levels may also be elevated (Jack et al. 2008), indicating stress—which can reach extreme levels (Shutt et al. 2014). The impacts on primate group dynamics and on the interpretability of study group behaviours are made more complex still by the fact that sex and age cohorts often habituate at different rates (Ando et al. 2008).

However, human presence may also alter the behaviour of habituated groups (Crofoot et al. 2010), including increased frequency of risky behaviours once a group makes the association between human presence and absence of predator species such as canids and felids (Nowak et al. 2014). Furthermore, human presence can act to protect chimpanzees against potential human poachers (Campbell et al. 2011). This “human shield effect” can have profound implications for the ranging behaviours of both prey and predator in a given habitat (Berger 2007). Another effect within the landscape of fear is habituation to human presence. For instance, titi monkeys have been observed to spend more time on a risky behaviour (terrestriality) when the study period was longer (Souza-Alves et al. 2019).

One possible consequence of the changing perception of the landscape of fear as primates become habituated to human presence is the progressive appearance of riskier behaviour patterns, such as decreased vigilance, increased resting, and increased feeding on or near the ground. For example, habituated samango monkeys (*Cercopithecus mitis erythrarchus*) fed closer to the forest floor in the presence of human observers, an occurrence attributed to their increased sense of security under such circumstances (Emerson et al. 2011; Nowak et al. 2014). It has been suggested that behavioural researchers may be perceived as shields against terrestrial predators during such otherwise risky feeding activities (Nowak et al. 2014).

Predator-sensitive foraging characterizes many primates, and is influenced by biological, social, and/or environmental variables (Miller 2002). Primates may reduce foraging success to diminish predation risk (Abrams 1994). For example, baboons (*Papio cynocephalus ursinus*) choose low-quality food to reduce the possibility of predation (Cowlshaw 1997), while golden-backed uacaris (*Cacajao ouakary*) avoid large seed patches near dense vegetation from which felids could ambush them (Barnett et al. 2012a). Other species use alternative routes to obtain high-quality food. Blue monkeys (*Cercopithecus mitis stuhlmanni*), for instance, preferentially consumed fruit on trees with dense foliage, thus avoiding predation by African crowned eagles (*Stephanoetus coronatus*) (Cords 2002). In this sense, primates could use the “human shield effect” to expand their foraging area during seasonal shortages to access high-quality alternative foods (for example, young leaves due to high protein

concentrations: Lambert 2011) that might otherwise be highly risky to obtain.

Although it was found that capuchin monkeys (*Sapajus libidinosus*) living in tropical dry forest spent 44% of their time on the ground (Falótico 2011), where they used stone tools to obtain embedded foods and dig for subterranean resources (Visalberghi et al. 2005), among the almost-entirely arboreal platyrrhines, terrestriality is generally observed only under specific ecological circumstances, such as foraging on ephemeral ground-based food resources, visiting salt or soil licks, or escaping predators (Barnett et al. 2012b; Campbell et al. 2005; Mourthé et al. 2007; Souza-Alves et al. 2019). Overall, terrestrial behaviour in neotropical primates is generally rare, usually constituting less than 5% of the annual time budget of species of the pitheciid genera *Cacajao*, *Chiropotes*, and *Pithecia* (Barnett et al. 2012b). This is considered to be due to the inherently risky nature of such behaviours. However, titi monkeys (*Callicebus*, *Cheracebus*, *Plecturocebus* sensu Byrne et al. 2016) use the forest floor extensively (Souza-Alves et al. 2019). As the presence of human observers tends to make predators more cautious (Muhly et al. 2011; Shannon et al. 2014; Wilmers et al. 2013) and sometimes more nocturnal (Beale and Monaghan 2004), primates in a given region may be expected to show more risk-taking behaviours as the level of habituation increases.

In the present study, we test whether habituation to human presence influenced ground use frequency and on-ground behaviour in a group of Coimbra-Filho's titi monkeys *Callicebus coimbrai*. This endangered primate was described in 1999 (Kobayashi and Langguth 1999), and occurs in small and isolated coastal Atlantic forest fragments in north-eastern Brazil (Jerusalinsky et al. 2006). Individuals can usually be found on the low- and medium-height forest strata feeding primarily on fruit pulp (principally from Myrtaceae, Peraceae, Sapotaceae, and Fabaceae) (Souza-Alves et al. 2011). However, young liana leaves are a major food item when fruit availability is seasonally reduced (Souza-Alves et al. 2011). The time budget is dominated by resting during the hottest parts of the day, followed by feeding and moving (Souza-Alves et al. 2012, 2013). For the current study, we examined a recently habituated *C. coimbrai* group occupying a 14-ha forest fragment in north-eastern Brazil. Since there were potential ground-active predators in the study area (including cougars *Puma concolor* and tiger cats *Leopardus* sp.: see Chagas et al. 2010), we hypothesised that titi monkeys gradually learned to associate the presence of researchers with decreased predation risk. This hypothesis predicted that the cumulative effect of the presence of researchers would result in the titi monkeys engaging more frequently in risky behaviours. We tested this prediction by measuring the frequency of a risky behaviour (terrestriality) over the course of a 33-month study, beginning immediately following the

habituation of the study group. We controlled for the effect of potentially relevant ecological factors, including rainfall, arboreal fruit, and young leaf availability. We predicted that the marked reduction in, or loss of, fear towards humans during the habituation process (i) would result in an increase in ground use. If the prediction above was false, we predicted that (iia) terrestrial behaviour would consist mostly of foraging-related (frugivory and folivory) behaviours, and that (iib) terrestrial behaviour to exploit alternative high-quality food resources (e.g. ground-level young leaves) would occur mostly when preferred food sources (arboreal fruits) were scarce.

Methods

Study site and study group

The study was conducted in a 14-ha forest fragment at Fazenda Trapsa (11° 12' S, 37° 14' W), at the southern region of Sergipe state, north-eastern Brazil (see Souza-Alves 2013 for more detail). The area contained a mosaic of forest compositions of different ages and states of regeneration, including areas burned off in 2008, the year before the study began. The vegetation structure in the study forest fragment conforms to a coastal Atlantic Forest, with a relatively low and well-connected canopy and trees rarely exceeding 15 m in height (Souza-Alves et al. 2014, 2018).

Rainfall data were obtained from information collected by a meteorological station located within a research station, RPPN Caju, run by the state division of the Brazilian Government Agricultural Service (EMBRAPA-Sergipe), located 1 km from the study site. During an 11-year period (2000–2011) the annual mean rainfall was 131 mm (Semarh 2017). In the region, the driest period usually occurs between September and January (mean 49.3 mm), and the rainiest period from February to August (mean 172 mm) (Semarh 2017). The Köppen classification characterizes the regional climate as *As* (tropical zone with dry summer: Alvares et al. 2013).

After 18 days of habituation in June 2009 (see Souza-Alves and Ferrari 2010), we were familiar with the titi monkey study group's ranging pattern. Thus, we were able to monitor the group reliably and continually for 33 months, from July 2009 to July 2011 (25 months), November 2011 to February 2012 (4 months), and April 2012 to July 2012 (4 months), from dawn to dusk (05:00–18:00) during four or five consecutive days per month. Group structure and composition varied across the study period; however, at the end of the study the group contained two adult males, one adult female, and one juvenile female (Table 1). In total, five individuals were observed during the study.

Data collection

Quantitative behavioural data were systematically collected using scan sampling protocols (Altmann 1974), with 1-min scans conducted at 5-min intervals. Typically, the data were collected by two observers (JPS-A and IPF) with the aid of a field assistant. Ground use was recorded when any individual of the study group was in full contact (defined as all limbs touching the ground or within one stride cycle of doing so) with the forest floor. Individuals close to the ground (< 1 m) were not considered instances of ground use. We recorded the following ground-level behavioural categories: feeding (eating any form of ingestible, solid resource), foraging (explicitly moving the head or body in search of food), and non-feeding behaviours (social, move, rest). For feeding, we recorded whether the food item was associated with frugivory, folivory, insectivory, geophagy, or other (e.g. bark, flowers, fungi).

Behavioural data

During group scans we recorded whether an individual was on the ground and the behavioural activity on the ground. Observation times for each individual were quantified in relation to the number of months spent monitoring the group. Although the size of the study group was small (five individuals, not unusual for titi monkeys, see Bicca-Marques and Heymann 2013), in primate studies the validity

Table 1 Study group structure and composition over the observation period

Study chronology	Structure and composition of Coimbra-Filho's titi monkey group				
July 2009	M1	F1	SB1 (Black Face—BF)	I1	
May 2010	M1	F1	BF emigrated	J1	
December 2010	M1	F1	J1	Nb1	
June 2011	M1	F1	SB2	I2	BF returned to the natal group
July 2012	M1		F2	J2	BF (M2)

F adult female, *M* adult male, *SB* sub/adult, *J* juvenile, *I* infant, *Nb* newborn

of behavioural and ecological data is rarely limited by group size per se, as these aspects show strong genetic consistency and phylogenetic inertia (Majolo et al. 2008). More important than group size is the number of observation hours (Setchell and Curtis 2012; Ross and Reeve 2012).

Environmental data

We also documented the monthly availability of arboreal food resources, following the methods of Hilty (1980). Initially, we randomly selected four existing trails each month to serve as transects and monitored them over a width of 10 m (5 m on each side of the trail). We surveyed transects once per month in both directions to quantify the number of trees bearing fruit and new leaves. This method of assessing availability of fruit and young leaves has previously been used with success in the study area (Souza-Alves et al. 2011).

Data analysis

For each month, we quantified the overall frequency of terrestrial behaviour for individual titi monkeys, as well as overall feeding-related behaviours, non-feeding behaviour, folivory, and frugivory. We then used the mean monthly values (\pm SD) of these variables and environmental data in all subsequent analysis.

To test our first prediction, we fitted a generalized least squares (GLS) model using recorded terrestrial frequencies as the dependent variable against observer contact duration, with a temporal correlation structure to account for the repetitive measures of the study group. We also fitted another GLS model, assuming a rationalization of the standard linear equation ($Y = a + b \times 1/X$) to account for an asymptotic relationship (i.e. the number of terrestrial records increases at the beginning of the habituation process, and then remains constant). A sample size-corrected Akaike information criterion (AICc) (Burnham and Anderson 2002) was used to choose the best model. To further explore the frequency of terrestrial behaviour, we fitted a GLS model with a similar temporal correlation structure; however, we used observer contact duration, rainfall level, arboreal fruit, and young leaf production as predictor variables. We adopted GLS models, as they allow for the specification of correlations between the residuals which result from non-independence of observations (repetitive measures of the same group in our case) (Zuur et al. 2009).

Finally, to address our second prediction, we tested the frequency of terrestrial activities against arboreal fruit and young leaf production. Terrestrial behaviour was classified as “non-feeding”, “folivory”, and “frugivory”,

and treated as the dependent variable. We adopted zero-inflated regression models with negative binomial distribution (Cameron and Trivedi 1998) to account for the high number of zeros after splitting the behavioural data into categories. In these models, cumulative observer contact duration was included as offset to control non-independence of observations. All statistical analyses were performed with R version 3.5.0 software (R Core Team 2018). The GLS models were fitted using *nlme* (Pinheiro et al. 2020), the zero-inflated regression models were fitted using *pscl* (Zeileis et al. 2008) and the graphs using *ggplot2* (Wickham 2016) packages.

Results

We observed titi monkeys on the ground in 113 (0.6%) of 18,164 scans conducted across 33 months of monitoring (range of frequency per month: 0–21; mean: $3.2 \pm$ SD 4.8) (Supplementary Material 1). When on the ground, the titi monkey group engaged more frequently in feeding-related behaviours ($2.6 \pm$ SD 4.6 records/month) than non-feeding behaviours ($0.8 \pm$ SD 2.1). In trees, the opposite was true, with the group more frequently displaying non-feeding behaviours ($781 \pm$ SD 187) than feeding-related behaviours ($393 \pm$ SD 126). Of the feeding behaviours, folivory was more common ($2.2 \pm$ SD 3.5 records/month) than frugivory ($0.4 \pm$ SD 1.8). In trees, frugivory was more common ($176 \pm$ SD 107 records/month) than folivory ($62 \pm$ SD 41). We did not see invertebrates being consumed by titi monkeys during periods of terrestrial activity.

The asymptotic model had a better fit than the linear model (Δ AICc = 4.95), but the frequency of terrestrial records was not related to the duration of observer contact (GLS: β -estimate = -0.11 ; $p = 0.211$). This was true after including other predictor variables (availability of arboreal fruit and young leaves, rainfall, human contact) in the model (Fig. 1). The frequency of terrestrial records for titi monkeys was not related to the availability of arboreal fruits (β -estimate = -0.11 ; $p = 0.245$) or arboreal young leaves (β -estimate = -0.09 ; $p = 0.347$), rainfall level (β -estimate = -0.02 ; $p = 0.822$), or human observer contact duration (β -estimate = -0.13 ; $p = 0.174$). Thus, our first prediction (i) was not supported.

When the titis were on the ground, the consumption of fruits (β -estimate = -3.078 ; $p = 0.043$) and young leaves (β -estimate = -3.515 ; $p < 0.001$) showed a negative relationship with arboreal fruit availability (Table 2, Fig. 2). In addition, a negative relationship was found between folivory (β -estimate = -0.815 ; $p = 0.025$) on the ground and availability of arboreal young leaves (Table 2, Fig. 2). Both model results support predictions (iia) and (iib).

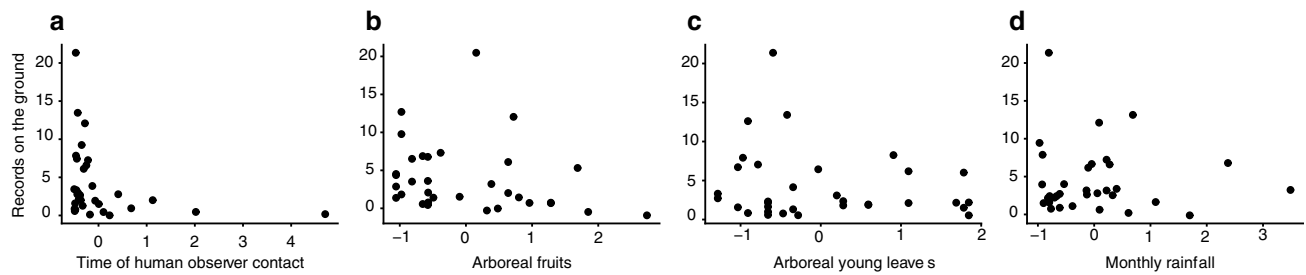


Fig. 1 Response of Coimbra-Filho's titi monkeys terrestrial records to **a** time of human observer contact, **b** arboreal fruits, **c** arboreal young leaves, and **d** monthly rainfall, as indicated by the GLS model. Plots

use partial residuals of the response variable and thus show the effect of a given predictor while controlling the effects of remaining predictors (explaining the negative values)

Table 2 Summary of zero-inflated regression model statistics for the amount of terrestrial non-feeding behaviours, folivory, and frugivory on the ground related to predictor variables: number of arboreal

fruits, number of arboreal leaves, rainfall level, and duration of contact with human observers

Predictor	Terrestrial non-feeding behaviours		Folivory		Frugivory	
	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>
Arboreal fruits	1.820	0.105	0.101	0.919	−2.016	0.043
Arboreal young leaves	−1.837	0.066	−2.227	0.025	−3.319	<0.001
Rainfall	−0.933	0.350	−1.323	0.185	−1.830	0.943

Significant *p* values are in bold

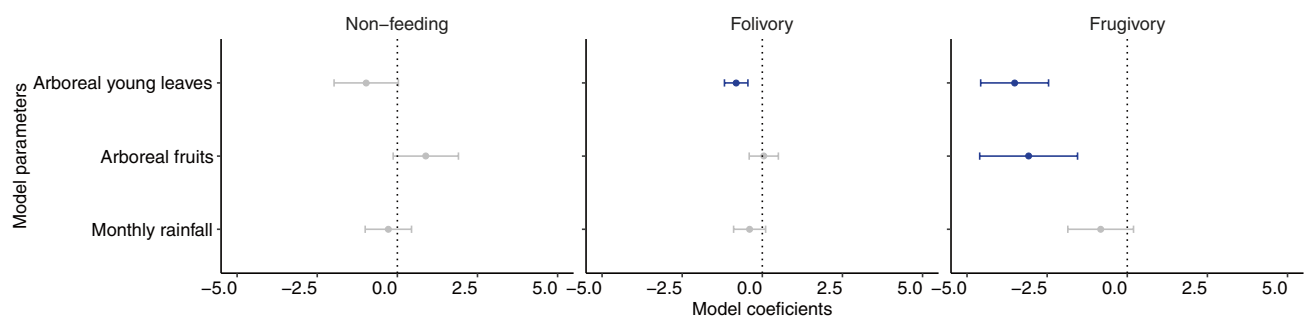


Fig. 2 Beta coefficients (\pm standard errors) of the count models for non-feeding, folivory and frugivory behaviours, when Coimbra-Filho's titi monkeys are on the ground. Significant results are showed in blue

Discussion

We did not find evidence of an association between overall frequency of terrestrial behaviour in the study titi monkey group and availability of arboreal food resources, rainfall level or observer contact duration. However, we found that folivory increased with increasing observer contact duration. In addition, the titi monkeys showed increased frugivory and folivory rates on the ground when arboreal fruits were scarce and increased folivory rates on the ground when young leaves were less available. In this sense, although prediction (i) was not supported, it seems

likely that the scarcity of arboreal fruits, young leaves and human presence drove the monkeys to exploit food on the ground, thereby supporting predictions (iia) and (iib).

The frequency of titi monkey terrestrial behaviour did not increase with increasing observer contact duration. Increasing contact with observers during the habituation process is known to result in more infrequent activities, such as the terrestrial behaviour in several species (*Ateles* spp.: Campbell et al. 2005; *Brachyteles hypoxanthus*: Mourthé et al. 2007, Tabacow et al. 2009; *Presbytis rubicunda*: Cheyne et al. 2018), including titis (*Callicebus*, *Cheracebus*, *Plecturocebus*: Souza-Alves et al. 2019). Although our data do not indicate that titi monkeys are likely to lose their fear of

humans and descend to the ground more often, additional data on terrestrial behaviour with and without the presence of humans may yield different results. Accordingly, a more robust test of the influence of human presence on any terrestrial activity would complement scan sampling with a camera trap system to track terrestrial behaviour, as recently conducted for *Sapajus cay* in Paraguay (Smith and Briggs 2016).

While seasonality seems to be the overriding driver of terrestrial feeding behaviour in titi monkeys, it may not be the case universally. Moreover, folivory was correlated with observer presence. Primates are adept at assessing predation risk (Barnett et al. 2017, 2018; Suscke et al. 2017; Zuberbühler et al. 1999). In the presence of humans, the predation rates on primates are often greatly reduced (Isbell and Young 1993; Kummer 1995; Stanford 1998).

For titi monkeys, consuming fruits and young leaves on or near the ground became a feasible alternative during periods when other resources were in short supply (Souza-Alves et al. 2011). However, in the presence of humans, our monkeys appeared sufficiently confident to come to the ground to exploit additional folivorous resources, such as the leaves of low-growing plants. On burned and open areas, this included exploiting the leaves of a small herb (*Lippia* sp.—Verbenaceae), the low-growing vine *Adenocalymma comosum* (Bignoniaceae), and a shrub (*Paypayrola blanchetiana* Violaceae) (Souza-Alves, JP—unpublished data).

Seed extraction generally involves dental and manual processing of the fruit, and it can be noisy (Overdoff et al. 2002). The fact that leaves rather than fruits were eaten on the ground by titi monkeys may be related to the way in which such foods are eaten, and the differing levels of risk involved. *Adenocalymma comosum* and *P. blanchetiana* leaves needed to be individually plucked from the plant (sometimes done directly with the teeth and lips). In contrast, exploited fallen fruit (e.g. *Passiflora contracta*, Passifloraceae) were individually picked up off the ground and taken up into a tree to be eaten, before another was retrieved from the ground and eaten. Leaves were eaten sequentially on the ground, meaning that the time during which the foraging animal was terrestrial was longer. This, in addition to the fact that dental plucking resulted in periods when a foraging titi monkey could not see predators, made leaf-foraging individuals more vulnerable to both terrestrial and aerial predators (for such encounters between primates and raptors see Barnett et al. 2015). It also appears riskier for titi monkeys to forage on young leaves than fallen fruits. Therefore, it seems that our titi monkeys applied predator-sensitive foraging, using the human shield effect, to safely consume young leaves on the ground.

The use of camera trap systems as a supplementary procedure could provide data on the frequency of risky behaviours such as terrestrial activity before, during, and

after a habituation process (Boyer-Ontl and Pruetz 2014; Bezerra et al. 2014; Porfírio et al. 2017; Cheyne et al. 2018), while also providing information on the presence of potential predators. It is possible that potential predators are not driven away by humans, as proposed in the humans-as-shield hypothesis; this might be especially true for snakes (documented titi predators: Cisneros-Heredia et al. 2005). Moreover, individuals to be studied need to be habituated to the novelty of camera traps in their habitat to reduce curiosity and fear (see Kalan et al. 2019). A further useful supplement would be auto-vocalization registration technology (Heinicke et al. 2015). The distance between observers and study groups at which an animal exhibits discomfort is often used as a measure of the progress of habituation (e.g. Barnett 2010). We suggest that monitoring increases in terrestrial behaviour across observation periods can provide an additional metric by which the level of habituation to human presence may be estimated.

Finally, it should be noted that the titi monkey study group was already habituated, possibly fully so. Thus, any additional time spent with the group would not change the high frequency of feeding/forage behaviours under periods of high and low availability of arboreal food resources. Despite the possibility of predation, using the forest floor seems to be inevitable in the search of alternative food such as leaves. Furthermore, the exploitation of food resources on the ground may be associated with the avoidance of potential predators due to human observer presence (trade-off between foraging and predation risk). Accordingly, we recommend that future studies using the methods proposed above be conducted on initially unhabituated groups. Studies would be further improved if comparisons could be made with partly and fully habituated study groups.

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References

- Abrams PA (1994) Should prey overestimate the risk of predation? *Am Nat* 144:317–328
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–266
- Alvares CA, Stape JL, Sentelhas PC, de Moraes G, Leonardo J, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22:711–728
- Ando C, Iwata Y, Yamagiwa J (2008) Progress of habituation of western lowland gorillas and their reaction to observers in

- Moukalaba-Doudou National Park, Gabon. *Afr Study Monogr* 35:55–69
- Barnett AA (2010) Diet, habitat use and conservation ecology of the golden-backed uacari, *Cacajao melanocephalus ouakary*, in Jaú National Park, Amazonian Brazil. Ph.D. thesis. Roehampton University, London
- Barnett AA, Almeida T, Spironello WR, Sousa Silva W, MacLarnon A, Ross C (2012a) Terrestrial foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: is choice of seed patch size and position related to predation-risk? *Folia Primatol* 83:126–139
- Barnett AA, Boyle SA, Norconk M, Palminteri S, Santos RR, Veiga LM, Alvim THG, Bowler M, Chism J, Di Fiore A, Fernandez-Duque E, Guimarães ACP, Harrison-Levine A, Haugaasen T, Lehman S, MacKinnon KC, Melo FR, Moreira LS, Moura VS, Phillips CR, Pinto LP, Port-Carvalho M, Setz EZF, Shaffer C, Silva LR, Silva SSB, Soares RF, Thompson CL, Vieira TM, Vreedzaam A, Walker-Pacheco SE, Spironello W, MacLarnon A, Ferrari SF (2012b) Terrestrial activity in Pitheciins (*Cacajao*, *Chiropotes* and *Pithecia* spp.). *Am J Primatol* 74:1106–1127
- Barnett AA, Andrade E, Ferreira MC, da Silva VF, Oliveira T (2015) Primate predation by black hawk-eagle (*Spizaetus tyrannus*) in Brazilian Amazonia. *J Raptor Res* 49:105–107
- Barnett AA, Silla JM, de Oliveira T, Boyle SA, Bezerra BM, Spironello WR, Setz EZF, Soares da Silva R, Albuquerque Teixeira S, Todd LM, Pinto LP (2017) Run, hide, or fight: anti-predation strategies in endangered red-nosed cuxiú (*Chiropotes albinasus*, Pitheciidae) in southeastern Amazonia. *Primates* 58:353–360
- Barnett AA, de Oliveira T, Soares da Silva RF, de Albuquerque TS, Tomanek P, Todd LM, Boyle AS (2018) Honest error, precaution or alertness advertisement? Reactions to vertebrate pseudopredators in red-nosed cuxiú (*Chiropotes albinasus*), a high-canopy neotropical primate. *Ethology* 124:177–187
- Beale CM, Monaghan P (2004) Human disturbance: people as predation-free predators? *J Appl Ecol* 41:335–343
- Berger J (2007) Fear, human shields and the redistribution of prey and predators in protected areas. *Biol Lett* 3:620–623
- Bezerra BM, Souto A (2008) Structure and usage of the vocal repertoire of *Callithrix jacchus*. *Int J Primatol* 29:671–701
- Bezerra BM, Bastos M, Souto A, Keasey MP, Eason P, Schiel N, Jones G (2014) Camera trap observations of nonhabituated critically endangered wild blonde capuchins, *Sapajus flavius* (formerly *Cebus flavius*). *Int J Primatol* 35:895–907
- Bicca-Marques JC, Heymann EW (2013) Ecology and behaviour of titi monkey (genus *Callicebus*). In: Barnett AA, Veiga LM, Ferrari SF, Norconk MA (eds) *Evolutionary biology and conservation of titis, sakis, and and uacaris*. Cambridge University Press, Cambridge, pp 196–207
- Bleicher S (2017) The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ* 5:e3772
- Boyer-Ontl KM, Pruetz JD (2014) Giving the forest eyes: the benefits of using camera traps to study unhabituated chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Int J Primatol* 35:881–894
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer Science & Business Media, New York
- Byrne H, Rylands AB, Carneiro JC, Lynch Alfaro JW, Bertuol F, Silva MNF, Messias M, Gorves CP, Mittermeier RA, Farias I, Hrbek T, Schneider H, Sampaio I, Boubli JP (2016) Phylogenetic relationship of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy on molecular evidence. *Front Zool* 13:10
- Cameron C, Trivedi PK (1998) Regression analysis of count data. Econometric society monographs. Cambridge University Press, Cambridge
- Campbell CJ, Aureli F, Chapman CA, Ramos-Fernández G, Matthews K, Russo SE, Suarez S, Vick L (2005) Terrestrial behavior of *Ateles* spp. *Int J Primatol* 26:1039–1051
- Campbell G, Kuehl H, Diarrassouba A, N’Goran PK, Boesch C (2011) Long-term research sites as refuge for threatened and over-harvested species. *Biol Lett* 7:723–726
- Chagas RRD, Santos EM Jr, Souza-Alves JP, Ferrari SF (2010) Fazenda Trapsa, a refuge of mammalian diversity in Sergipe, Northeastern Brazil. *Rev Nord Biol* 19:35–43
- Cheyne SM, Neale CJ, Thompson C, Wilcox CH, Smith YCE, Smith DAE (2018) Down from the treetops: red langur (*Presbytis rubicunda*) terrestrial behavior. *Primates* 59:437–448
- Cipolletta C (2003) Ranging patterns of a western gorilla group during habituation to humans in the Dzanga-Ndoki National Park, Central African Republic. *Int J Primatol* 24:1207–1226
- Cisneros-Heredia DF, León-Reyes A, Seger S (2005) Boa constrictor predation on a titi monkey, *Callicebus discolor*. *Neotrop Primates* 13:11–13
- Cords M (2002) Foraging and safety in adult female blue monkeys in the Kakamega forest, Kenya. In: Miller LE (ed) *Eat or be eaten*. Cambridge University Press, New York, pp 205–221
- Cowlshaw G (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim Behav* 53:667–687
- Crofoot MC, Lambert TD, Kays R, Wikelski MC (2010) Does watching a monkey change its behaviour? Quantifying observer effects in habituated wild primates using automated radiotelemetry. *Anim Behav* 80:475–480
- Doran-Sheehy DM, Greer D, Mongo P, Schwindt D (2004) Impact of ecological and social factors on ranging in western gorillas. *Am J Primatol* 64:207–222
- Emerson SE, Brown JS, Linden JD (2011) Identifying Sykes’ monkeys’, *Cercopithecus albogularis erythrarchus*, axes of fear through patch use. *Anim Behav* 81:455–462
- Falótico T (2011) Uso de ferramentas por macacos-prego (*Sapajus libidinosus*) do Parque Nacional Serra da Capivara—PI. Ph.D. thesis, Universidade de São Paulo, Brazil
- Heinicke S, Kalan AK, Wagner OJ, Mundry R, Lukashevich H, Kühl HS (2015) Assessing the performance of a semi-automated acoustic monitoring system for primates. *Methods Ecol Evol* 6(7):753–763
- Hilty SL (1980) Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12:292–306
- Isbell LA, Young TP (1993) Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Anim Behav* 45:1233–1235
- Jack KM, Lenz BB, Healan E, Rudman S, Schoof VA, Fedigan L (2008) The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *Am J Primatol* 70:490–494
- Jerusalinsky L, Oliveira MM, Pereira RF, Santana V, Bastos PCR, Ferrari SF (2006) Preliminary evaluation of the conservation status of *Callicebus coimbrai* Kobayashi and Langguth, 1999 in the Brazilian state of Sergipe. *Primate Conserv* 21:25–33
- Kalan AK, Hohmann G, Arandjelovic M et al (2019) Novelty response of wild African apes to camera traps. *Current Biol* 29:1211–1217
- Kobayashi S, Langguth A (1999) A new species of titi monkey, *Callicebus* Thomas, from north-eastern Brazil (Primates, Cebidae). *Rev Brasil Zool* 16:531–551
- Kummer H (1995) *Quest of the sacred baboon*. Princeton University Press, Princeton
- Lambert JE (2011) Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (eds) *Primates in perspective*, 2nd edn. Oxford University Press, Oxford, pp 512–522

- Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, USA. *Can J Zool* 79:1401–1409
- Majolo B, de Bortoli VA, Schino G (2008) Costs and benefits of group living in primates: group size effects on behaviour and demography. *Anim Behav* 76:1235–1247
- Miller LE (2002) An introduction to predator sensitive foraging. In: Miller LE (ed) *Eat or be eaten*. Cambridge University Press, New York, pp 1–20
- Mourthé IM, Guedes D, Fidelis J, Boubli JP, Mendes SL, Strier KB (2007) Ground use by northern muriquis (*Brachyteles hypoxanthus*). *Am J Primatol* 69:706–712
- Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M (2011) Human activity helps prey win the predator–prey space race. *PLoS ONE* 6:e17050
- Nowak K, le Roux A, Richards SA, Scheijen CP, Hill RA (2014) Human observers impact habituated samango monkeys’ perceived landscape of fear. *Behav Ecol* 25:1199–1204
- Overdoff DJ, Strait SG, Seltzer RG (2002) Species differences in feeding in Milne Edward’s sifakas (*Propithecus diadema edwardsi*), rufus lemurs (*Eulemur fulvus rufus*), and red-bellied lemurs (*Eulemur rubiventris*) in southern Madagascar: implications for predator avoidance. In: Miller LE (ed) *Eat or be eaten*. Cambridge University Press, New York, pp 126–137
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-149. <https://CRAN.R-project.org/package=nlme>
- Porfirio G, Santos FM, Foster V, Nascimento LF, Macedo GC, Barreto WTG, Fonseca C, Herrera HM (2017) Terrestriality of wild *Sapajus cay* (Illiger, 1815) as revealed by camera traps. *Folia Primatol* 88:1–8
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ross C, Reeve N (2012) Survey and census methods: population distributions and density. In: Setchell JM, Curtis DJ (eds) *Field and laboratory methods in primatology: a practical guide*. Cambridge University Press, Cambridge, pp 111–132
- Semarh (2017) Secretaria de Meio Ambiente e Recursos Hídricos de Sergipe. <https://www.semarh.se.gov.br/biodiversidade/modules/tinyd0/index.php?id=11>. Accessed 26 Sept 2012
- Setchell JM, Curtis DJ (2012) *Field and laboratory methods in primatology: a practical guide*. Cambridge University Press, Cambridge
- Shannon G, Cordes LS, Hardy AR, Angeloni LM, Crooks KR (2014) Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE* 9:e94630
- Shutt K, Heistermann M, Kasim A, Todd A, Kalousova B, Profosouva I, Petrzalkova K, Fuh T, Dicky J-F, Bopalan-zognako J-B, Setchell JM (2014) Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. *Biol Conserv* 172:72–79
- Smith RL, Briggs E (2016) Using camera traps to determine group demography in a Paraguayan population of *Sapajus cay*. *Neotrop Primates* 22:81–88
- Souza-Alves JP (2013) Ecology and life-history of Coimbra-Filho’s titi monkeys (*Callicebus coimbrai*) in the Brazilian Atlantic Forest. PhD Thesis, Universidade Federal da Paraíba, João Pessoa, Brazil
- Souza-Alves JP, Ferrari SF (2010) Responses of wild titi monkeys, *Callicebus coimbrai* (Primates: Platyrrhini: Pitheciidae), to the habituation process. *Zoologia* 27:861–866
- Souza-Alves JP, Fontes IP, Chagas RRD, Ferrari SF (2011) Seasonal versatility in the feeding ecology of a group of titis (*Callicebus coimbrai*) in the northern Brazilian Atlantic Forest. *Am J Primatol* 73:1199–1209
- Souza-Alves JP, Fontes IP, Ferrari SF (2012) Seasonal variation in the activity patterns of a group of *Callicebus coimbrai* in the Atlantic forest of northeastern Brazil. In: *Annals of XXIVth congress of International Primatological Society*. International Primatological Society, Cancún, pp 393–394
- Souza-Alves JP, Ferrari SF, Barbosa MRV, Thomas WW (2014) Diversity of trees and lianas in two sites in the coastal Atlantic Forest of Sergipe, northeastern Brazil. *Check List* 10:709–717
- Souza-Alves JP, Thomas WW, Barbosa MRV (2018) Phytosociology of angiosperms in a highly-fragmented landscape of coastal Atlantic forest in northeastern Brazil. *Rev Nord Biol* 26:124–137
- Souza-Alves JP, Mourthe I, Hilário RR et al (2019) Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus* and *Plecturocebus*): potential correlates, patterns and difference between genera. *Int J Primatol* 40:553–572
- Stanford C (1998) *Chimpanzee and red colobus: the ecology of predator and prey*. Harvard University Press, Cambridge
- Suscke P, Verderane M, de Oliveira RS, Delval I, Fernández-Bolanos M, Izar P (2017) Predatory threat of harpy eagles for yellow-breasted capuchin monkeys in the Atlantic Forest. *Primates* 58:141–147
- Tabacow FP, Mendes SL, Strier KB (2009) Spread of a terrestrial tradition in an arboreal primate. *Am Anthropol* 111:238–249
- Tutin CE, Fernandez M (1991) Responses of wild chimpanzees and gorillas to the arrival of primatologists: behaviour observed during habituation. In: Box HO (ed) *Primate responses to environmental change*. Springer, Dordrecht, pp 187–197
- Visalberghi E, Frigaszy DM, Izar P, Ottoni EB, Lee PC, Moura ACDA (2005) Terrestriality and tool use. *Science* 308(5724):951–953
- Wickham H (2016) *ggplot2: elegant graphics for data analysis*. Springer, New York
- Williamson EA, Feistner AT (2003) Habituating primates: processes, techniques, variables and ethics. In: Setchell JM, Curtis DJ (eds) *Field and laboratory methods in primatology: a practical guide*. Cambridge University Press, Cambridge, pp 25–39
- Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS ONE* 8:e60590
- Zeileis A, Kleiber C, Jackman S (2008) Regression models for count data in R. *J Stat Softw* 27:1–25
- Zuberbühler K, Jenny D, Bshary R (1999) The predator deterrence function of primate alarm calls. *Ethology* 105:477–490
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media, New York

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