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Supplemented howler monkeys eat less wild fruits, but do not change their activity budgets

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Abstract

Research on the influence of food supplementation on primate behavior has focused on terrestrial and semiterrestrial species. Its effects on highly arboreal species are poorly known. We assessed the influence of food supplementation on the feeding behavior and activity budget of four adult female and two adult male brown howler monkeys (*Alouatta guariba clamitans*) belonging to two groups (JA and RO) that inhabited periurban forest fragments in southern Brazil. We used the "focal-animal" method during 6–8 full days per month from March to August 2017 (916 h of observation) to record the behavior of the study subjects. The feeding events of the focal individual were recorded using the "all occurrences" method. The supplementation was unevenly distributed during the day and accounted for 5–6% of all feeding events of male and female howlers, respectively. JA always received fruit in a platform, whereas RO had access to fruits and processed foods on roofs and directly from humans. The mean biomass of wild foods ingested by each adult per day was >300% higher than the ingested biomass of supplemented foods (females: 395 vs. 109 g/day; males: 377 vs. 120 g/day), but the ingestion rate of supplemented foods was ca. 400% higher than that of wild foods (females: 17 vs. 4 g/min; males: 19 vs. 5 g/min). The activity budgets of females and males were dominated by resting (66–72%) followed by feeding (18–14%), moving (12–11%), and socializing (2%). We found that food supplementation reduced the ingestion of wild fruits, but it did not affect the howlers' need to ingest a given amount of leaves per day and the time spent resting, feeding, moving, and socializing.

KEYWORDS
Alouatta guariba clamitans, anthropic food, behavioral flexibility, diet, human-wildlife interaction, provisioning

1 | INTRODUCTION

Food supplementation is a relatively common practice to promote wildlife watching in nature reserves (Corcoran et al., 2013; Orams, 2002; Sabbatini, Stammati, Tavares, & Visalberghi, 2008; Sabbatini, Stammati, Tavares, Giuliani, & Visalberghi, 2006), to increase the reproductive success of threatened species (Blanco, Lemus, & García-Montijano, 2011; Robb, McDonald, Chamberlain, & Bearhop, 2008), and to mitigate human-wildlife conflicts (Andreassen, Gundesen, & Storaas, 2005; Barrio, Bueno, & Tortosa, 2010). It also occurs as a consequence of the isolation of animal populations in urban and periurban habitat patches, and their resulting proximity to people (Robb et al., 2008; Rodrigues & Martinez, 2014; Suzin, Back, Garey, & Aguiar, 2017).

Supplemented food, such as fruit, is often more palatable, highly energetic, predictable, available in large amounts, and clustered

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(Boug et al., 2017; Fa, 1992; McLennan & Ganzhorn, 2017; Saj, Sicotte, & Paterson, 1999). Accessing it normally requires less effort to the forager than foraging for wild foods, making it an even more attractive option (Altmann & Muruthi, 1988; El Alami, Van Lavieren, Rachida, & Chait, 2012; Fa, 1992; Orams, 2002; Saj et al., 1999; Sha & Hanya, 2013a; Strum, 2010). Consequently, animals that exploit supplemented resources obtain higher caloric gains than those feeding exclusively on wild foods and they also tend to become satiated and to satisfy their metabolic needs more quickly (McLennan & Ganzhorn, 2017; Saj et al., 1999).

Despite these short-term potential energy- and metabolism-related benefits, long-term food supplementation can bring disadvantages. It can habituate free-ranging animals to the presence of humans (McKinney, Westin, & Serio-Silva, 2015; Newsome & Rodger, 2008; Orams, 2002), making them dependent on anthropic resources (Boug et al., 2017; Newsome & Rodger, 2008; Sha & Hanya, 2013b), and more susceptible to injuries and parasite infections (Becker, Streicker, & Altizer, 2018; Blanco et al., 2011; Longa, 2011; Newsome & Rodger, 2008; Semeniuk & Rothley, 2008; but see Becker, Streicker, & Altizer, 2015). Furthermore, animals feeding on sugar- and fat-rich foods can accumulate body fat and develop higher cholesterol levels (Maréchal, MacLarnon, Majolo, & Semple, 2016a; Pragatheesh, 2011). Finally, intra- and intergroup contest competition between supplemented animals for supplied foods, combined with the proximity to humans, can increase stress levels and aggression among them (Jaman & Huffman, 2013; Maréchal et al., 2016a; Maréchal, Semple, Majolo, & MacLarnon, 2016b; Pragatheesh, 2011; Ram, Ventakatachalam, & Sinha, 2003).

Animals exploiting supplemented food also tend to decrease the distances traveled daily (Boutin, 1990; Sha & Hanya, 2013a) and home range size (Corcoran et al., 2013; Saj et al., 1999; Sha & Hanya, 2013b). Some animals have also changed sleeping sites to areas near supplementation sites (Brotcorne et al., 2014; Strum, 2010). The use of supplements, whether offered directly by humans or obtained from plantations and waste, can also change the activity budget. The times devoted to moving and feeding tend to decrease, while resting and socializing tend to increase (e.g., *Papio cynocephalus*: Altmann & Muruthi, 1988; *Chlorocebus pygerythrus*: Saj et al., 1999; *Macaca sylvanus*: El Alami et al., 2012; *Macaca mulatta* : Jaman & Huffman, 2013). However, some supplemented groups do not change their activity budgets (e.g., *Cebus capucinus*: McKinney, 2011), others increase feeding and reduce resting (e.g., *Papio hamadryas*: Boug, Biquand, Biquand-Guyot, & Kamal, 1994; Boug et al., 2017), and still others reverse their period of activity, becoming more active during the day than their nonsupplemented nocturnal relatives (e.g., *Dasyatis americana*: Corcoran et al., 2013).

Studies on the effects of supplementation on primate behavior have been limited to the comparison of activity budgets of supplemented and nonsupplemented groups (El Alami et al., 2012; Sha & Hanya, 2013a; Unwin & Smith, 2010). To the best of our knowledge, no study has quantified the ingested biomass of supplemented foods and its representation in the daily diet or its short-term influences on the feeding behavior and activity budget of supplemented individuals. In addition, the available information is focused on terrestrial and semiterrestrial species (e.g., *P. hamadryas*: Boug et al., 1994, 2017; *Macaca fascicularis* : Sha & Hanya, 2013a; *C. capucinus*: McKinney, 2011; *Sapajus libidinosus*: Sabbatini et al., 2006, 2008). Therefore, the effects of supplementation on highly arboreal primates are unknown.

The flexibility that enables animals to adjust their behavior to changing environmental conditions has facilitated the survival of primates in human-modified landscapes (Lowry, Lill, & Wong, 2013; McLennan, Spagnoletti, & Hockings, 2017). Howler monkeys (*Alouatta* spp.) are well known among Neotropical primates for their capacity to adapt to habitat restriction in these anthropogenic landscapes (Asensio, Arroyo-Rodríguez, Dunn, & Cristóbal-Azkarate, 2009; Bicca-Marques, 2003, 2017; Chaves & Bicca-Marques, 2013, 2016, 2017; Chaves, Fernandes, Oliveira, & Bicca-Marques, 2019). The adaptation of these highly arboreal monkeys has been related to the adjustment of their folivorous-frugivorous diet (Crockett & Eisenberg, 1987; Neville, Glander, Braza, & Rylands, 1988) to resource availability (Bicca-Marques, 2003; Chaves & Bicca-Marques, 2016). They can exploit food that is common in anthropic environments, such as shrubs, lianas, and alien fruit trees (Asensio et al., 2009; Bicca-Marques & Calegaro-Marques, 1994b; Chaves & Bicca-Marques, 2013, 2016, 2017; Chaves, Bicca-Marques, & Chapman, 2018), and even bird eggs (Bicca-Marques, Muhle, Prates, Oliveira, & Calegaro-Marques, 2009; Bicca-Marques, Silveira, Martins, & Rabelo, 2014). A high level of resting (usually >65%) and a low level of social interaction (<4%) characterize the activity budget of howlers (Bicca-Marques, 2003; Di Fiore, Link, & Campbell, 2011). This activity budget has been related to the consumption of the difficult-to-digest, fiber-rich diet, whose time-consuming microbial fermentation produces short-chain volatile fatty acids that provide a significant amount of howlers' daily energetic demands (Milton, 1979, 1998; Milton & McBee, 1983).

Urbanization of the natural environment and the consequent proximity to humans have facilitated the exploitation of supplemented foods by populations of southern brown howler monkeys (*Alouatta guariba clamitans*). In this study, we (a) describe the pattern(s) of supplemented food consumption by adult female and male southern brown howlers inhabiting periurban forest fragments, (b) estimate the contribution of supplemented foods and wild fruits and leaves to the diet of the study subjects, (c) estimate their activity budgets, and (d) assess whether the use of these foods, the individual's sex, and the interaction of these factors influence the contribution of wild fruits and leaves to their diet and the time devoted to resting, feeding, moving, and socializing.

2 | MATERIALS AND METHODS

2.1 | Study area and groups

We carried out this study in two forest fragments (JA and RO) in the periurban matrix of Vila de Itapuã, Itapuã District, Viamão Municipality, Rio Grande do Sul State, Brazil (Figure 1). We classified

FIGURE 1 Location of the (a) study region and (b) the forest fragments inhabited by the study groups in the Viamão Municipality, Rio Grande do Sul State, Brazil: (c) RO and (d) JA. We delimited the forest fragments based on the groups' home ranges. Source: Google Earth Pro©

this matrix as periurban because it is characterized by sparse human settlements immersed in a landscape with a predominance of rural activities. It is ca. 8 km distant from the nearest neighborhood (Lami) of the nearest town (Porto Alegre). The JA fragment (ca. 148.4 ha, ca. 6.8 ha of which was used by howlers) is ca. 6 km from Vila de Itapuã (30°20′26.33′′S, 51°1′2.37′′W, approximately 76 m a.s.l.). The RO fragment (ca. 12.8 ha, ca. 1.6 ha of which was used by the study howlers) is in the Vila de Itapuã (30°17′3.19′′S, 51°1′6.73′′W, approximately 6.5 m a.s.l.). It is connected to a fragment of ca. 0.5 ha and to the riparian forest of Arroio Chambá. The study region is near the southern limit of the distribution of the species (Culot et al., 2019).

The original vegetation in these areas is subtropical semideciduous forest and is part of the Atlantic Forest (Setubal, Boldrini, & Ferreira, 2011), the most fragmented and endangered Brazilian biome (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). The climate is humid subtropical without a dry season and with rainfall uniformly distributed throughout the year (i.e., type Cfa according to Köppen's classification). The annual mean rainfall varies from 1,100 to 1,300 mm, and the annual mean temperature is 19.5°C. January is the warmest month (mean = 24.5°C) and June is the coldest (mean = 14.9°C; Setubal et al., 2011).

A howler monkey group (hereafter JA) composed of seven individuals (one adult male: M1; two adult females: F1 and F2; three juveniles; one infant) was monitored in the JA fragment. These howlers moved over bamboo bridges installed by local people and fed on both the resources available in the forest and those provided by the landowners.

Another howler group (hereafter RO), whose composition ranged from three to four individuals (one or two adult males: M2 and M3; two adult females: F3 and F4) due to the immigration of M3 in February 2017 and his emigration in June 2017, was monitored in the RO fragment. The howlers in this group spent most of their time in the 1.6-ha area, where they moved over the roofs and walls of houses and on the ground, as reported for another group in the region (Corrêa, Chaves, Printes, & Romanowski, 2018). They also fed on both wild resources available in the altered forest fragments and on the supplements provided by local people. This group was the target of previous studies (J.R. Gonçalves and J.C. Bicca-Marques, unpublished data; VITA group in Bicca-Marques et al., 2014).

The habituation of the study subjects to the presence of researchers and the individual recognition of the adults based on fur color, body size, and presence of scars took place between January and February 2017. The frequent contact with people facilitated the habituation. We highlight that the focus on six adult brown howlers from two periurban groups does not allow to generalize our findings to other age classes, species, and landscapes. However, we provide baseline information for future research. The supplementation of both study groups resulted from the willingness of local people to be closer to the monkeys. Thus, it has no relationship with tourism or a strategy to enhance the survival of howlers.

2.2 | Recording of behavioral data

We followed each group for three to four, consecutive or not, complete days (minimum of 8 h of daily observation) every half month from March to August 2017. We recorded the behavior of the adults M1, M2, F1, F2, F3, and F4 by the "focal-animal" method (Altmann, 1974) with instantaneous records every 20 s in sampling units of 10 min in duration with a 20-min interval between successive focal sampling units. We followed a single focal individual in each data collection day, resulting in a total of 53,912 behavioral records (M1 = 23 days; M2 = 19; F1 = 12; F2 = 10; F3 = 12; F4 = 9).

We recorded all feeding events of the focal individual by the "all occurrences" method (Altmann, 1974). For each feeding event (i.e., when the animal began handling and/or placed the food in its mouth), we recorded the beginning and ending time, food category (wild [i.e., food obtained by the animal in the forest fragment] or supplemented), where and how it was obtained by the animal, food type (fruit, leaf, flower, bread, biscuit, etc.), and the amount ingested (number of bites/mouthfuls of each food item; see Reynoso-Cruz, Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, & Dias, 2016). We calculated the relative contribution of wild fruits and leaves and supplemented items to the diet of brown howlers by dividing the number of feeding records or the biomass ingested of each kind of food by the total number of feeding records or the total biomass ingested by the focal individuals (i.e., frequency method; Fortes & Bicca-Marques, 2005). We collected 5–15 units of each food item after a feeding event and weighed them in the field with 30-, 100-, and 300-g Pesola® scales (precision of 0.25, 1, and 2 g, respectively) to estimate their mean fresh mass (g). When weighing in the field was not possible because the focal individual ate the unique item of its kind available, we estimated the mean mass-consumed based on previous estimates of the same item.

We estimated the daily biomass of ingested wild and supplemented foods with the following formula (Hladik, 1977):

$$I_a = \sum Mm_i \ x \ N_i$$

where I_a is the daily food ingestion (g/day), Mm_i is the mean mass of the mouthfuls and/or the ingested food units (g) of each food item, and N_i is the number of mouthfuls and/or ingested items of each food type. Given potential differences in handling and processing times between supplemented and wild foods, we also calculated their ingestion rates per unit time with the following formula (Nakagawa, 2009):

$$T_a = I_a/t$$

where T_a is the ingestion rate (g/min) and t is the total feeding time (min) on a given food category.

We classified the behavior into resting (inactive, either sitting, or lying), feeding (handling, biting, chewing, and ingesting any type of food), moving (e.g., walking, running, jumping, and climbing), and socializing (vocalization and interaction among two or more conspecifics, such as playing, grooming, aggression, and reproductive behaviors). Other behaviors included defecating, urinating, drinking water, and rubbing the back on the substrate. We calculated the activity budget as the time (min) devoted to each behavior by multiplying the proportion of records of each activity (e.g., the number of feeding records collected during the day divided by the total number of records of all activities recorded on the same day; i.e., by the frequency method, Fortes & Bicca-Marques, 2005) by the total observation time (min) of the focal individual during that day. We estimated the time devoted to resting, feeding, moving, and socializing because the photoperiod at the latitude of our study sites varies by up to 25% during the study months (12 h 41 min in March vs. 10 h 10 min in June), a difference that can bias activity budget estimates based on percentage of diurnal time. We assumed that the focal individual was resting during the unobserved nocturnal period and added this nocturnal resting time to the diurnal resting time to estimate the total time dedicated to resting considering a circadian cycle (24 h = 1,440 min). We also present the pooled activity budget of all adults of each sex and each group from dawn to dusk as the percentage of time for intra- or interspecific comparison with other studies. There are no comparative data on unprovisioned groups for the study region using the focal-animal method. Estimates of the activity budget of unprovisioned adult brown howlers inhabiting three <10-ha forest fragments near the study region based on the scan sampling method (see Chaves & Bicca-Marques, 2017) were 56–63% for resting, 20–28% for feeding, 12–18% for moving, and 1–2% for socializing (Ó.M. Chaves & J.C. Bicca-Marques, unpublished data).

2.3 | Statistical analysis

We used the G test considering the difference between the observed (O) and the expected (E) frequencies of events of ingestion of supplemented food in each daylight hour class (i.e., 6 a.m., 7 a.m ...., 12 noon ..., 6 p.m.) to test the homogeneity of the distribution of the events of consumption of supplements during the day, considering p values corrected by the Williams method to reduce the probability of a type I error (Gotelli & Ellison, 2011). We calculated E in each hour class with sampling because the aforementioned differences in photoperiod precluded it in some hours (e.g., before 7 a.m. and after 6 p.m.) during part of the study. We calculated it based on the respective sampling effort (min) multiplied by the mean rate of supplement consumption (events/min) recorded throughout the study for each group. We grouped the 6–7 a.m. and 5–6 p.m. hour classes to avoid having classes with no observation of supplementation. We run this test in the software BioEstat 5.3 (Ayres, Ayres, Ayres & Santos, 2007).

We tested the influence of daily ingested biomass (g) of supplemented foods, sex (independent variables), and their interaction on the contribution (g) of wild fruits and leaves to the diet and the time (min) devoted to resting, feeding, moving, and socializing (dependent variables) using generalized linear mixed-effects models. We constructed all models using social group and individual ID (nested within-group) as random factors. We previously tested all variables regarding test assumptions. We assessed the statistical significance of each model by comparing the full model (including the fixed effects ingested supplemented biomass, sex, and their interaction) against a null model in which the target fixed effect was removed. We carried out this comparison using a likelihood ratio test (Bates, Maechler, Bolker, & Walker, 2015; Bolker et al., 2009). We identified the best significant model based on the Akaike Information Criteria (AIC). We set a ΔAIC threshold of 6 to consider a model significantly better than the null model (Richards, 2015). We assumed the probabilistic threshold of 95% in all tests. We run these analyses with package "lme4" (Bates et al., 2015) in R 3.5.1 (R Core Team, 2018).

3 | RESULTS

The consumption of supplemented food items by both groups was not uniformly distributed throughout the day (JA: $G = 21.9156$; $df = 10$; $p_{\text{adjusted}} = .0155$; RO: $G = 40.1823$; $df = 10$; $p_{\text{adjusted}} < .0001$). Supplementation at RO occurred mainly in the morning with a peak at 9 a.m., whereas supplementation at JA occurred mostly in the afternoon with a peak at 3 p.m. (Figure 2). JA howlers were always supplemented on a single platform ($n = 91$ events), whereas RO members were supplemented on at least five sites on house roofs (55%, $n = 43$), directly from human hands (40%, $n = 31$), and on trees (2%, $n = 2$). In the remaining two events (2%), the focal individual obtained the supplement from a conspecific. The JA group only received in natura supplements, such as persimmon (*Diospyros kaki*: 49% of the events), guava (*Psidium guajava*: 23%), bergamot (*Citrus* sp.: 14%), melon (*Cucumis* sp.: 12%), butia (*Butia* sp.: 5%), and others (9%). The RO group also received in natura supplements ($n = 77$), such as banana (*Musa* sp.: 31% of the events) and lime (*Citrus* sp.: 3%), in addition to processed food, such as bread (62%), ham (4%), and saltine crackers (3%). In terms of feeding events recorded by the "all occurrences" method, the consumption of supplemented items represented 6.0% of the 1,610 female feeding events and 5.5% of the 1,298 male feeding events.

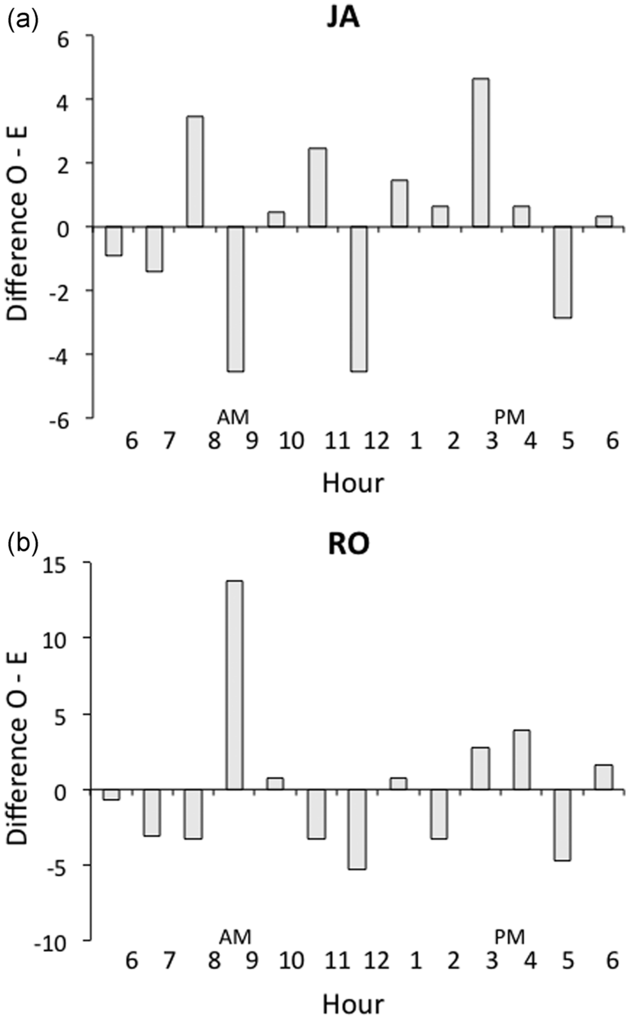

FIGURE 2 Differences between the observed (O) and expected (E) frequencies of supplementation events per hour of groups (a) JA ($N = 91$ events) and (b) RO ($N = 77$) from March to August 2017. Note that the Y scale differs between the graphs

Wild leaves accounted for 72.2% (females) and 57.6% (males) of the focal feeding records, wild fruits accounted for 23.1% (females) and 35.2% (males), and supplemented food items accounted for 4.4% (females) and 6.3% (males). The mean biomass of supplemented foods ingested per day by each adult represented about a quarter of its total food intake (females: 109 g of 468 g; males: 120 g of 454 g). However, the average ingestion rate of supplemented foods was about four times higher than that of wild foods (females: 17 vs. 4 g/min; males: 19 vs. 5 g/min; Table 1).

Adult female and male howlers of both groups devoted the most time to resting, followed by feeding, moving, and socializing (mostly affiliative interactions). This pattern was also found at the group level (Table 2).

The ingested biomass of supplemented foods by howlers and its interaction with the sex of the individual had a negative influence on their consumption of wild fruits, while sex alone did not (Table 3 and Figure 3). On the other hand, the amount of supplemented foods consumed and sex or their interaction did not influence the ingested biomass of wild leaves or the time that howlers devoted to resting, feeding, moving, and socializing (Table 3). Although the AIC of the model of the influence of ingested biomass of supplemented foods on time spent moving is lower than that of the null model (Figure 3), the difference is below the set threshold for significance (Table 3).

4 | DISCUSSION

The adult howlers of the study groups rested most of the time as expected (Bicca-Marques & Calegaro-Marques, 1994a; Koch & Bicca-Marques, 2007; Mendes, 1989; Prates & Bicca-Marques, 2008) and were exposed to different supplements, supplementation regimes, and sites. The range of total fresh biomass ingested per day by the adult howlers is similar to the averages reported by some authors (*A. pigra*: 531 g/day; Aristizabal [2013]; *A. seniculus*: 544 g/day; Edwards [1995]; *A. palliata*: 610 and 782 g/day; Nagy [2001]; Williams-Guillén [2003]), but lower than that found in other studies (*A. pigra*: 1,057 and 1,135 g/day; Amato & Garber [2014]; *A. seniculus*: 1,230 g/day; Gaulin & Gaulin [1982]). Differences in gut capacity resulting from interspecific (Garber,

TABLE 1 Mean ± standard deviation (%) biomass ingested per day (g), time devoted to feeding per day (min) and ingestion rate (g/min) of each major food item category by each focal individual and sex

	F1	F2	F3	F4	Females	M1	M2	Males
Wild fruits								
Biomass	240 ± 142 (45)	182 ± 162 (29)	180 ± 159 (39)	136 ± 159 (31)	185 ± 155 (32)	225 ± 157 (49)	243 ± 156 (37)	233 ± 155 (39)
Time feeding	25 ± 15 (19)	25 ± 17 (17)	25 ± 21 (36)	20 ± 24 (31)	24 ± 19 (22)	21 ± 11 (25)	36 ± 28 (44)	27 ± 22 (31)
Ingestion rate	9 ± 9	7 ± 9	7 ± 8	7 ± 7	8 ± 8	11 ± 14	7 ± 5	9 ± 7
Wild leaves								
Biomass	227 ± 125 (42)	286 ± 118 (46)	153 ± 174 (33)	159 ± 175 (36)	208 ± 155 (36)	121 ± 58 (27)	167 ± 149 (25)	142 ± 110 (24)
Time feeding	102 ± 38 (78)	110 ± 39 (77)	37 ± 25 (53)	36 ± 24 (56)	72 ± 47 (67)	57 ± 24 (67)	36 ± 13 (44)	47 ± 23 (55)
Ingestion rate	2 ± 3	3 ± 3	4 ± 7	4 ± 7	3 ± 3	2 ± 2	5 ± 11	3 ± 5
Total wild*								
Biomass	467 ± 204 (87)	469 ± 165 (75)	335 ± 247 (73)	296 ± 244 (67)	395 ± 222 (69)	346 ± 154 (76)	415 ± 211 (62)	377 ± 183 (63)
Time feeding	127 ± 37 (97)	135 ± 40 (94)	63 ± 33 (89)	57 ± 26 (87)	97 ± 49 (89)	78 ± 25 (92)	71 ± 27 (89)	75 ± 26 (86)
Ingestion rate	4 ± 6	3 ± 4	5 ± 7	5 ± 9	4 ± 4	4 ± 6	6 ± 8	5 ± 7
Supplemented in natura								
Biomass	70 ± 86 (13)	157 ± 110 (25)	33 ± 25 (7)	102 ± 102 (23)	100 ± 99 (17)	109 ± 89 (24)	153 ± 203 (23)	122 ± 127 (20)
Time feeding	4 ± 5 (3)	8 ± 6 (6)	1 ± 1 (1)	4 ± 2 (6)	5 ± 5 (5)	7 ± 4 (8)	3 ± 4 (4)	6 ± 4 (7)
Ingestion rate	17 ± 17	19 ± 18	27 ± 29	27 ± 44	20 ± 19	15 ± 23	52 ± 57	20 ± 31
Supplemented processed								
Biomass	–	–	91 ± 58 (20)	45 ± 15 (10)	79 ± 54 (14)	–	99 ± 86 (15)	99 ± 86 (17)
Time feeding	–	–	7 ± 4 (10)	4 ± 3 (6)	6 ± 4 (6)	–	6 ± 4 (7)	6 ± 4 (7)
Ingestion rate	–	–	13 ± 15	12 ± 5	13 ± 15	–	16 ± 21	16 ± 21
Total supplemented								
Biomass	70 ± 86 (13)	157 ± 110 (25)	98 ± 54 (27)	85 ± 62 (33)	109 ± 86 (31)	109 ± 89 (24)	134 ± 149 (38)	120 ± 118 (37)
Time feeding	4 ± 5 (3)	8 ± 6 (6)	7 ± 4 (11)	5 ± 3 (13)	6 ± 5 (11)	7 ± 4 (8)	5 ± 4 (11)	6 ± 4 (14)
Ingestion rate	17 ± 17	19 ± 18	15 ± 14	18 ± 21	17 ± 18	15 ± 23	26 ± 37	19 ± 29
TOTAL								
Biomass	509 ± 205	587 ± 119	416 ± 210	334 ± 245	468 ± 211	417 ± 187	499 ± 185	454 ± 188
Time feeding	130 ± 37	141 ± 39	68 ± 31	59 ± 27	101 ± 49	82 ± 25	76 ± 26	79 ± 26
Ingestion rate	4 ± 6	4 ± 3	6 ± 7	6 ± 9	5 ± 4	5 ± 7	7 ± 7	6 ± 7

*Includes flowers: females (biomass = 4 ± 4, time feeding = 2 ± 2, ingestion rate = 3 ± 3), males (biomass = 15 ± 13, time feeding = 4 ± 3, ingestion rate = 4 ± 4).

Righini, & Kowalewski, 2015; Van Belle & Bicca-Marques, 2015) or between population body size differences may account for these discrepant estimates.

Supplementation was not uniform throughout the day, and the groups showed distinct peaks of supplemented feeding. The morning RO peak is likely a result of the partially regular schedule of supplementation by local people. In response to this regularity, RO howlers used to sleep near supplementation sites from where they left only after eating the provided food. This group was also highly tolerant of humans, which was not observed in the JA group. The JA supplementation peak in the afternoon was the rule even when the platform was provisioned in the first morning hours. Despite the availability of most of the same fruits provided on the platform (bergamot, *Citrus* sp.; guava, *P. guajava*; butiá, *Butia* sp.) in JA's home range, the supplements represented a significant proportion of the daily food intake of its members as also recorded for RO's members.

Even though the wild food biomass ingested by howlers was greater than the supplemented biomass, its ingestion rate was lower

TABLE 2 Time devoted to each activity (in min and % time) from dawn to dusk by adult females and males and the members of groups JA and RO according to the focal-animal sampling

Activity	min	%	min	%
Sex	Females		Males	
Resting	424	66	462	72
Feeding	117	18	88	14
Moving	75	12	73	11
Socializing	12	2	14	2
(Affiliative)	(9)	(81)	(9)	(66)
(Agonistic)	(<1)	(3)	(0)	(0)
(Other)	(2)	(16)	(5)	(34)
Others	7	2	4	1
Group	JA		RO	
Resting	410	64	476	75
Feeding	127	20	78	12
Moving	89	14	59	9
Socializing	11	2	15	2
(Affiliative)	(8)	(74)	(10)	(73)
(Agonistic)	(<1)	(<2)	(<1)	(<2)
(Other)	(3)	(25)	(4)	(26)
Others	6	1	7	1

than that of supplemented food. This difference in ingestion rate is explained by the greater fresh mass of supplemented foods, which are offered in large amounts, thereby optimizing feeding time, as observed in other studies (Fa, 1992; McLennan & Ganzhorn, 2017; Nakagawa, 2009; Saj et al., 1999).

The finding that the ingestion rate of wild fruits was also higher than that of wild leaves can explain why the amount of supplemented biomass ingested did not influence time devoted to feeding, as leaves are an essential component of the balanced diet exploited by howlers (Ganzhorn et al., 2017; Milton, 1979, 1998; Righini, Garber, & Rothman, 2017). The consumption of a balanced fiber-rich folivorous-frugivorous diet that requires long resting periods to be digested (Ganzhorn et al., 2017; Milton, 1979, 1998) also helps to explain the lack of influence of the contribution of supplemented biomass on time dedicated to resting by adult female and male howler monkeys.

Whereas the weak direct influence of the contribution of supplemented biomass to time dedicated to moving can be related to the need of howlers to move in an environment with a highly discontinuous canopy that demanded displacement over house roofs and walls, electrical wires and even on the ground to reach the single (JA; as also reported by Corrêa et al., 2018) or the scattered (RO) supplementation sites (see El Alami et al., 2012; Sha & Hanya, 2013a), the wide data dispersion (Figure 3) is compatible with the influence of other factors (e.g., distribution and phenology of food sources and weather) on the investment in moving by the study subjects.

Unlike that reported for other species (Altmann & Muruthi, 1988; El Alami et al., 2012; Jaman & Huffman, 2013; Kamal, Boug, & Brain, 1997; Strum, 2010), we did not find an influence of supplemented biomass on time devoted to socializing. Time socializing by adult females and males remained very low overall, with agonistic interactions representing <2% of the study groups' social interactions. The fact that supplements are often offered in amounts sufficient to satiate all group members, as also reported for other species (Altmann & Muruthi, 1988; Jaman & Huffman, 2013; Kamal et al., 1997), can explain this low agonism among howlers. However, the absence of a positive influence of food supplementation on the frequency of affiliative interactions in both groups, particularly in JA, is intriguing. Given the presence of immature individuals in the JA group, it could be expected that these more socially active individuals (see Koch & Bicca-Marques, 2007; Prates & Bicca-Marques, 2008) would socialize more frequently with adults at supplementation sites. Indeed, almost half of this group's social interactions involved adult-immature dyads.

While food supplementation did not influence time devoted to feeding, an increase in the ingestion of supplemented biomass reduced the consumption of wild fruits, but did not alter the ingested biomass of wild leaves. These findings can be explained by howlers' need to maintain a nutritionally balanced diet as mentioned above and the role that fibers play in the digestion process given their slow processing time through the howlers' gut (Milton, 1979, 1981; Nagy & Milton, 1979). The likely energy-richer supplemented food (e.g., carbohydrate-rich fruits and fat-rich processed foods) can lack proteins and micronutrients that are only acquired by ingesting wild food, especially leaves (Ganzhorn et al., 2017; Milton, 1979, 1998; Righini et al., 2017; Silver, Ostro, Yeager, & Horwich, 1998). These needs can decisively preclude howlers from becoming dependent on supplemented foods, at least as far as they do not include leaves. This strategy of maintaining a nutritional balance between supplemented and wild foods was also reported for baboons (*Papio hamadryas*: Boug et al., 2017). A potential reduction in the dispersal of seeds of native species together with the promotion of the dispersal of seeds of alien, potentially invasive, species are undesired side effects of the reduced consumption of wild fruits due to the ingestion of cultivated fruits (Chaves et al., 2018), as this ecosystem role change can alter the vegetation structure of habitat remnants (Sengupta, McConkey, & Radhakrishna, 2015).

On the other hand, similar to the exploitation of cultivated species (Chaves & Bicca-Marques, 2017), food supplementation can also mitigate the seasonal variation in the availability of wild foods, characteristic of low-quality habitat patches (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, & Dias, 2018), thereby facilitating survival and increasing the reproductive success of supplemented animals (Kurita, Sugiyama, Ohsawa, Hamada, & Watanabe, 2008; Maréchal et al., 2016b; Strum, 2010). The births of three infants soon after the end of the study in the winter (two in JA in August and one in RO in September; J. P. Back, pers. obs.) are compatible with such a buffering effect against lean periods. The lack of difference in fecal

TABLE 3 Results of the linear mixed models assessing the influence of the ingested biomass of supplemented food items and sex (independent variables) on time devoted to resting (daytime and diel), feeding, moving, and socializing, and on the ingested biomass of wild fruits and leaves (dependent variables; *df* = 7 in all models)

Dependent variable	Independent variable	β value	SE	χ^2	*p*	AIC (model)	AIC (null)
Wild fruit biomass	Intercept	254.24	27.84				
	Supplemented biomass	−0.94	0.25	18.54	**<.001**	**1,093.80**	
	Sex	7.73	38.27	2.01	.1560	1,107.30	1,106.30
	Interaction	0.56	0.32	12.85	**<.001**	**1,095.50**	
Wild leaves biomass	Intercept	200.21	28.48				
	Supplemented biomass	0.11	0.24	0.00	.9701	1,084.40	
	Sex	−54.57	40.75	2.45	.1174	1,082.00	1,082.40
	Interaction	−0.14	0.30	2.68	.4442	1,085.80	
Time resting (daytime)	Intercept	417.21	39.44				
	Supplemented biomass	0.02	0.08	0.02	.8962	910.82	
	Sex	44.87	24.37	3.03	.0516	907.80	908.84
	Interaction	−0.04	0.11	3.17	.3660	911.66	
Time resting (24 hr)	Intercept	1,227.90	41.86				
	Supplemented biomass	−0.12	0.10	1.77	.1831	937.37	
	Sex	35.76	25.46	2.62	.1054	936.52	937.14
	Interaction	0.06	0.12	4.82	.1854	938.32	
Time feeding	Intercept	115.29	30.74				
	Supplemented biomass	0.03	0.07	0.03	.8728	866.74	
	Sex	−27.32	20.12	2.45	.1178	864.32	864.77
	Interaction	−0.04	0.08	2.76	.4298	868.01	
Time moving	Intercept	70.50	15.89				
	Supplemented biomass	0.08	0.05	3.94	.0470	818.22	
	Sex	−2.61	7.63	0.69	.4052	821.47	820.16
	Interaction	−0.04	0.06	5.10	.1648	821.06	
Time socializing	Intercept	14.37	4.88				
	Supplemented biomass	0.02	0.03	0.67	.4128	701.82	
	Sex	0.00	5.45	0.04	.8424	702.45	700.49
	Interaction	−0.01	0.03	0.83	.8435	705.67	

Note: Significant results are highlighted in bold.
Abbreviations: AIC, Akaike information criteria; SE, standard error.

glucocorticoid metabolites between adult brown howlers inhabiting large (>90 ha) and small (<10 ha) forest fragments in the study region (Chaves et al., 2019) is also compatible with their good health status in these anthropogenic landscapes. However, the regular, long-term addition of anthropic resources to howler diets can have serious consequences for their health and survival. RO howlers, for example, were fed with foods rich in fat, sugar, and salt, which can cause body fat accumulation and its derived health problems (Maréchal et al., 2016a; Newsome & Rodger, 2008; Pragatheesh, 2011).

Food supplementation also brings howlers closer to humans, increasing the risks of electrocution, vehicle collisions, hunting, and predation by domestic dogs (Bicca-Marques, 2017; Chaves & Bicca-Marques, 2017). Indeed, we recorded electrocutions of the three JA juveniles in May 2017. These electrocutions resulted in scars of burnings in legs and tails and deformed or rigid toes. We also recorded several attacks of RO howlers by domestic dogs. Although all attacks were unsuccessful, the absence of immature individuals in this group during the study can reflect their higher vulnerability to these human-related causes of death. Local people reported the deaths of several howlers by electrocution near a supplementation site over the years.

The proximity to domestic animals and the direct contact with humans via supplementation can also increase the exposure to pathogens (Longa, 2011), facilitate two-way disease transmission and increase stress (Maréchal et al., 2016a, 2016b; Newsome & Rodger, 2008; see also Bicca-Marques & Calegaro-Marques, 2014). On the other hand, a nutrient- and energy-balanced supplementation can improve the nutritional status of howlers, strengthen their immune system and, consequently, raise their tolerance to pathogens (Becker et al., 2015). Therefore, future studies should investigate the effects of supplementation on howlers' health (e.g., stress levels, body fat, gut microbiome composition, number of scars and injuries caused by intraspecific aggressions in the feeding area, host-parasite interactions, hair quality, and degree of alopecia; Becker et al., 2015; Maréchal et al., 2016a) and their implications for the long-term survival of these monkeys in habitat patches immersed in periurban or urban landscapes where they experience an intense contact with humans and their resources.

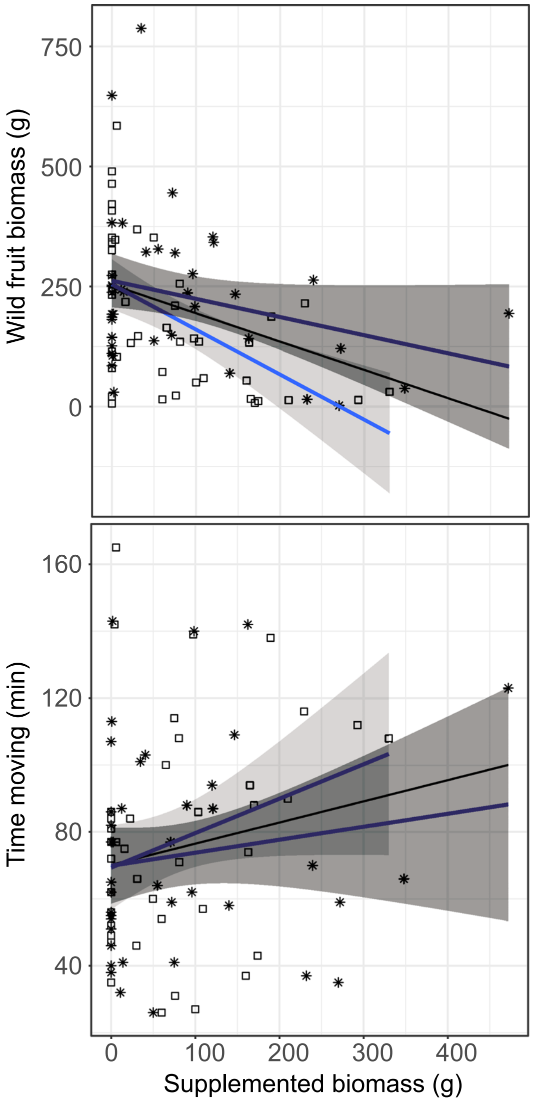

FIGURE 3 Influence of the biomass of supplemented foods ingested per day (independent variable) by adult howler monkeys on the ingested biomass of wild fruits (top) and on time devoted to moving (bottom). The black central line represents the linear mixed model for the entire dataset, whereas the blue upper and lower lines represent the linear mixed models for each sex (squares = females, asterisks = males). Shaded regions are the 95% confidence intervals for each sex

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DATA ACCESSIBILITY

Our dataset is available at https://data.mendeley.com/datasets/nws4gw3ygx/1.

ETHICAL STATEMENT

The Ethics Commission of the Biosciences School of the Pontifical Catholic University of Rio Grande do Sul (Pontifícia Universidade Católica do Rio Grande do Sul—PUCRS) approved this study (project no. 7479—SIPESQ). Data collection followed all ethical and legal guidelines established by the American Society of Primatologists, the appropriate national and institutional standards, and guidelines and the Code of Best Practices for Field Primatology of the International Primatological Society and the American Society of Primatologists. All property owners authorized the execution of this research on their properties and signed a free informed consent form. We highlight that the people who supplemented the howlers were not informed of the specific goals of the research to avoid influencing the supplementation routine.

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