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Feeding ecology and behavioral adjustments: flexibility of a small neotropical primate (*Callithrix jacchus*) to survive in a semiarid environment

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Abstract Semiarid environments are known for climate extremes such as high temperatures, low humidity, irregular precipitations, and apparent resource scarcity. We aimed to investigate how a small neotropical primate (Callithrix jacchus; the common marmoset) manages to survive under the harsh conditions that a semiarid environment imposes. The study was carried out in a 400-ha area of Caatinga in the northeast of Brazil. During a 6-month period (3 months of dry season and 3 months of wet season), we collected data on the diet of 19 common marmosets (distributed in five groups) and estimated their behavioral time budget during both the dry and rainy seasons. Resting significantly increased during the dry season, while playing was more frequent during the wet season. No significant differences were detected regarding other behaviors. In relation to the diet, we recorded the consumption of prey items such as insects, spiders, and small vertebrates. We also observed the consumption of plant items, including prickly cladodes, which represents a previously undescribed food item for this species. Cladode exploitation required perceptual and motor skills to safely access the food resource, which is protected by sharp spines. Our findings show that common

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² Department of Zoology, Federal University of Pernambuco, Avenida Professor Morais Rego, 1235, Cidade Universitária, CEP: 50670-901 Recife, Pernambuco, Brazil marmosets can survive under challenging conditions in part because of adjustments in their behavior and in part because of changes in their diet.

Keywords Behavior · Time budget · Caatinga · Diet · Cacti

Introduction

The Caatinga, a xerophilous vegetation, represents a semiarid region located in the northeast of Brazil. It occupies an area of approximately 800,000 km² (Araújo et al. 2007). This type of environment is characterized by a climate with high solar radiation, high temperatures, low humidity, and irregular precipitation during a period of three to six consecutive months in the year, resulting in periodic and severe drought (Prado 2003; Araújo et al. 2007; Albuquerque et al. 2012; Medeiros et al. 2012). At the study site, precipitation in the last 86 years ranged from 3.6 to 775.5 mm (Medeiros et al. 2012). The woody vegetation is low and dominated by deciduous trees with thorns, microphyll leaves, and xerophytic adaptations, as well as cacti, bromeliads, and a rich diversity of herbaceous species (Prado 2003; Araújo et al. 2007; Albuquerque et al. 2012). According to Barbosa et al. (2003), the phenology of many plant species in the Caatinga is controlled by precipitation. Therefore, due to both climatic seasonality and rainfall distribution, fleshy fruit represents a relatively scarce resource throughout the dry season (Barbosa et al. 2003; Amorim et al. 2009).

The harsh conditions of semiarid environments, in general, impose significant challenges for mammals in terms of heat stress, thermoregulation, available water, and limited resource availability (Diaz and Ojeda 1999; Albuquerque et al. 2012). In spite of this, at least 156 species of mammals, 12 of which are endemic, inhabit the Caatinga (Albuquerque et al. 2012).

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However, there is no evidence of pronounced physiological adaptations in mammals that inhabit the Caatinga, as has been described for other dry regions (Streilein 1982). Rather, behavioral adaptations have been suggested to be crucial to overcome the constraints and limitations of this environment (Streilein 1982; Albuquerque et al. 2012; De la Fuente et al. 2014); nevertheless, the potential behavioral adjustments that mammals exhibit to survive in the Caatinga are still poorly known. To this regard, Rocha (1995) reported that the endemic rodent Trinomys yonenagae digs holes in dunes during the hottest hours of the day. Moura and Lee (2004) and Moraes et al. (2014) suggested that harsh environmental conditions may have been a factor in leading capuchin monkeys (Sapajus libidinosus) to use tools to gain access to hard-toobtain and hard-to-process food. Additionally, feeding ecology may be adjusted as a strategy to survive in environments (or during seasons) with limited resources (Marshall and Wrangham 2007). Therefore, some mammals inhabiting the Caatinga may include new food items in their diets that are not exploited in other parts of their range (cacti by capuchin monkeys: Moraes et al. 2014; fruit, flower of cacti and leaves by common marmoset: Amora et al. 2013).

The relatively low number of behavioral and ecological studies focused on mammals in the Caatinga may be due to its adverse environmental conditions. Difficulties also derive from the elusive nature and/or night habits of many animals inhabiting this environment (e.g., wild cats, rodents, and bats). However, a small, diurnal group-living primate such as the common marmoset (*Callithrix jacchus*) is more easily studied, therefore offering an important animal model for examining questions regarding the behavioral adjustments used by mammals to exploit this semiarid environment.

The common marmoset is native to different environments in the northeast of Brazil, including the Caatinga (Stevenson and Rylands 1988; Rylands and Faria 1993). This small primate forms groups that range from 3 to 15 individuals in the Atlantic forest and has a hierarchical social structure in which the dominant couple breeds twice a year usually during September, October, and November as well as April, May, and June (Stevenson and Rylands 1988). It has an omnivorous diet, which consists mainly of fruit, insects, exudates (gums and saps), and small vertebrates (Rylands and Faria 1993; Schiel et al. 2010) but may include molluscs in the humid Atlantic Forest (Souto et al. 2007) and leaves in the Caatinga (Amora et al. 2013). Moreover, it is worth pointing out that the teeth and ceca of the common marmoset are adapted for the exploitation of exudates (Nash 1986; Stevenson and Rylands 1988), which represent a difficult-todigest (high in structural carbohydrates) food resource available throughout the year (Araújo et al. 2007). Common marmoset can be habituated to the presence of human observers, a factor that facilitates its study, as documented in several studies conducted in the Atlantic Forest in the last few decades (e.g., Alonso and Langguth 1989; Souto et al. 2007; Bezerra and Souto 2008; Pesendorfer et al. 2009; Schiel et al. 2010; Gunhold et al. 2014).

Despite these advantages, information is limited concerning how these small mammals cope with the difficult conditions of the Caatinga. To date, only two studies have reported on the ecology of common marmosets in a semiarid environment, each with some limitations. Research conducted by Amora et al. (2013) was restricted to the use of previously unknown plant resources as food items. Furthermore, the sample size was small (n=2 to 4 individuals), which may limit the generalization of their findings. De la Fuente et al. (2014) investigated the adjustments of some behavioral patterns of 12 common marmosets in response to temperature fluctuation throughout the day (hourly time analysis). Unfortunately, this study does not provide information on the behavioral time budget of the animals under study.

Given that common marmosets living in the Caatinga environment adjust their behavior throughout the day, we expect adjustments in their behavioral patterns throughout the seasons as well. In order to test this prediction we (i) investigated the diet of 19 individual common marmosets (distributed in five groups) in the Caatinga and (ii) estimated the behavioral time budget of these animals during 3 months of the dry season and 3 months of the rainy season in the study area. Moreover, we described the behavioral strategies used by common marmosets to exploit this challenging environment. Finally, we compared our data with those obtained in previous studies conducted in the humid environment of the Atlantic Forest (e.g., Alonso and Langguth 1989; Souto et al. 2007; Schiel et al. 2010) in order to document the range of behavioral flexibility of this primate species. With our research, we intend to contribute to a better understanding of the importance of behavioral adjustments for the survival of mammals in semiarid environments.

Materials and methods

Study area

This study was carried out in a Caatinga biome at the Fazenda Marimbondo (S 7° 31' 42"–W 36° 17' 50"), located in the state of Paraíba, Northeast of Brazil (video footage of the location available as online supplementary material). This area features the typical vegetation of semiarid environments, high temperatures, and the lowest rainfall index of the Brazilian semiarid region (for further information please see: Nascimento and Alves 2008; De la Fuente et al. 2014). At our study site, the rainy season lasts from February to July, while the dry season lasts from August to January (Medeiros et al. 2012). During our study, the mean maximum temperature in the rainy months was 29.1 °C (highest, 32.3 °C), and

the mean minimum was 19.3 °C (lowest, 14.2 °C); the mean maximum temperature during the dry months was 31.3 °C (highest, 35.2 °C), and the mean minimum was 20.8 °C (lowest, 15.8 °C). The temperatures were obtained from INMET (National Institute for Meteorology—situated in Cabaceiras ~5 km from the study site). During the study period, the mean precipitation in the rainy months (May–July) was 61.8 mm, whereas the mean precipitation in the dry months (September–November) was 13.6 mm (INMET 2015).

Data collection

Behavioral observations were performed by F. Abreu in 2014 for 3 months in the rainy season (May-July) and 3 months in the dry season (September-November) (e.g., Corrêa et al. 2000; De la Fuente et al. 2014; Ferrari and Hilário 2014; Oliveira et al. 2014). The dry and rainy seasons in the Caatinga are in accordance to Medeiros et al. (2012). Observations were conducted during the first 10 days of each month, for a total of 263 h of direct observation. We monitored five groups of C. jacchus, which contained a total of 19 individuals: 14 adults, 2 juveniles, and 3 infants (Table 1). The animals were well-habituated to the observer (distance between the observer to the animals ~ 4 m); hence, the use of binocular was not necessary. Behavioral data was collected according to the focal animal observation method (Altmann 1974; Lehner 1996). In this method, all actions of one animal are continuously recorded for a specified time interval (Altmann 1974; Lehner 1996). We performed 10-min sessions of continuously behavioral records for each individual at a time, throughout their period of diurnal activity (5 am to 5 pm) (De la Fuente et al. 2014). Moreover, ad libitum observations (Altmann 1974; Lehner 1996) were conducted to record off-session feeding events. We observed all groups daily, recording an average of three sessions per individual and changing the observation sequence so that every individual was equally observed at all times of the day.

In the present study, we reported the following behaviors: foraging, gummivory, grooming, locomotion, stationary,

 Table 1
 Composition of the study groups of Callithrix jacchus in the semiarid Caatinga

Age (month)	G 1		G 2		G 3		G 4		G 5	
	Ŷ	8	Ŷ	8	Ŷ	8	Ŷ	8	Ŷ	3
Infant (1–4)	_	1^{a}	_	_	_	_	_	2 ^a	_	_
Juvenile (5–10)	_	_	_	_	2	_	_	_	-	_
Adult (≥11)	1	1	1	1	2	3	1	1	$1(1^{a})$	1
Total of individuals	3		2		7		4		3	

G group

^a Individuals not included in the analyses

resting, and play behavior [foraging—seeking and consuming of food items (except exudates) (De la Fuente et al. 2014); gummivory—gouging holes in trees to obtain and consume exudate (Stevenson and Poole 1976); grooming—parting the fur of another individual to apparently remove particles and/or ectoparasites (e.g., Stevenson and Rylands 1988); locomotion—continuous moving for a distance greater than 3 m at once (Schiel and Huber 2006); stationary—the individual stays still, i.e., performing no apparent activity, for a period of 10–60 s; resting—the individual stays still for more than 60 s (Schiel and Huber 2006); play behavior—a set of playful activities such as hide-and-seek, chase, or wrestling (Stevenson and Poole 1976)].

Whenever possible, we recorded and collected the remains of insects captured by the animals. The insects were identified to the order level. Moreover, all the plant items eaten were recorded. The plant items were collected and subsequently identified by Dr. Elcida de Lima Araújo at the Botany Lab of the Federal Rural University of Pernambuco.

Statistical analysis

Data from 15 individuals were used (a total of 215 h of direct observation) in our analysis. We discarded data from an adult female who disappeared during the study and from those collected on infants younger than 5 months (a total of 48 h of direct observation). These infants were excluded because their behavioral repertoire is not fully developed (Schiel et al. 2010).

A time budget was calculated according to the duration of each behavior, for each season of the year. Since data were not normally distributed, the Wilcoxon's test (Lehner 1996) was used to examine behavioral differences between each season of the year. A Wilcoxon's test also was used to identify differences in the number of insects captured during the dry and rainy seasons. Results at $p \le 0.05$ (two-tailed) were considered significant. All the data were analyzed with the software Instat 3.0 (GraphPad Software, Inc.) and Excel (Microsoft Corporation).

Results

Behavioral time budget

In general, the animals dedicated most of their time to foraging (rainy season, 30.7 %; dry season, 25.6 %), followed by resting (rainy season, 18.6 %; dry season, 27.8 %). The animals foraged mainly on trees or tree-like plants (cacti), and occasionally on the ground. When it rained, the individuals drink water that accumulated in tree holes or by licking the drops that remained on the top of the leaves. During the dry season, we did not observe any event of direct water intake. There was

a significant increase in the time spent resting from the rainy season to the dry season (n=15, W=-92.0, p=0.006) and a significant decrease in the time spent in playful interactions in the dry season (n=15, W=105, p=0.0001) (Table 2). The individuals in our study usually rested on tree branches protected from direct sunlight. All other behavioral patterns did not reveal a significant difference between the seasons.

Food items consumed

In total, we observed 940 feeding events, of which 850 involved animal prey and 90 involved plant items. We found that 797 incidents of prey capture and consumption involved insects (Table 3), and the remaining 53 were directed to the exploitation of lizards (n=32), earthworms (n=14), arachnids (n=6), and bird eggs (n=1). Common marmosets captured and consumed a significantly higher amount of insects during the rainy season (71.3 %) than during the dry season (28.7 %) (n=11, W=66.0, p=0.001).

Six species of plants were consumed: three belonging to the family Cactaceae, two to the family Leguminosae/ Fabaceae, and one to the family *Malvaceae* (Table 4). Of the 90 events of plant feeding, 64 occurred during the rainy season and 24 occurred during the dry season. The animals feed on plant resources one at a time.

The consumption of plant items

Pilosocereus pachycladus Plant description: a cactus up to 10-m tall. It has columnar cladodes presenting areoles with numerous, small, thin spines of 1.8 cm in length and subglobose red to purple fruit (Menezes et al. 2013). Description of the feeding behavior. (1) *Cladode* (Fig. 1a)—the marmoset traveled to a tree in close proximity to the cactus and stood on a branch close (approximately 10 cm) to the tallest cladode. With its hind feet grasping the branch, the individual reached out and carefully held the sides of the cactus spines in both hands and **Table 3**Insects eaten by *Callithrix jacchus* throughout the study periodduring the dry and rainy seasons in the semiarid Caatinga

Order	Rainy season Percentage of captures (absolute value)	Dry season Percentage of captures (absolute value)	
Orthoptera	44.5 (254)	35.8 (80)	
Hymenoptera	11.8 (74)	7.4 (27)	
Coleoptera	7.4 (39)	5.9 (14)	
Lepidoptera	5.3 (30)	0.5 (2)	
Hemiptera	2.1 (13)	2.5 (8)	
Mantodea	2.1 (13)	1.5 (4)	
Isoptera	1.5 (11)	0.0 (0)	
Blatodea	1.0 (6)	2.5 (4)	
Odonata	0.4 (2)	0.0 (0)	
Diptera	0.2 (1)	0.0 (0)	
Unidentified	23.8 (125)	44.1 (90)	
Total of captures	100 (568)	100 (229)	

bit directly into the upper area of the cladode (apparently by choosing the most suitable region to start biting, i.e., damaged areas without or with few or broken spines), extracting small pieces that were then ingested. Then, one by one, all the members of the group performed the same procedure consecutively, alternately eating a portion of the cladode. (2) *Fruit*—the individual moved to a branch close to the fruit, grabbed the fruit with both forelimbs, and used its mouth to bite into the fruit and ingested small pieces at a time.

Cereus jamacaru (Fig. 1b) Plant description: a cactus up to 6m tall. It has upright cladodes presenting areoles 2–4 cm apart from each other with long prickly cylindrical spines up to 6cm long; it produces ellipsoid red to magenta fruit and white flowers (Rocha and Agra 2002; Menezes et al. 2013). Description of the feeding behavior. 1) *Cladode*—the individual stood with both hind feet on the cactus, in the upper area of

Table 2	Comparison of the behaviora	al time budget of Callin	<i>trix jacchus</i> in the semiario	d Caatinga, between the o	irv and rain	v season

	e ,			
Behavior	Rainy season Total sample time [%] (total sample time [hour])	Dry season Total sample time [%] (total sample time [hour])	W	p value
Foraging	30.7 (29.31)	25.6 (30.39)	46	0.21
Gummivory	17.7 (16.90)	15.8 (18.81)	36	0.33
Resting	18.6 (17.77)	27.8 (33.04)	-92	0.006
Locomotion	8.3 (7.93)	8.8 (10.48)	16	0.68
Grooming	12.1 (11.53)	14.6 (17.34)	-64	0.07
Play	6 (5.71)	1.4 (1.72)	105	0.0001
Stationary	6.6 (6.19)	6 (6.93)	-2	0.97
Total in percentage (total in hours) ^a	100 (95.37)	100 (118.74)	-	-

Statistics: Wilcoxon's test (*W*); values of $p \le 0.05$ are significant

^a Total hours of observations of the 15 individuals used for statistical analysis

 Table 4
 Plant items eaten by

 Callithrix jacchus in the semiarid
 Caatinga

Family	Scientific name	Part consumed	Events	Number of animals that consumed a plant item
Cactaceae	Pilosocereus pachycladus	Fruit	3	3
		Cladode	16	8
	Pilosocereus gounellei	Fruit	7	4
		Flower	3	3
	Cereus jamacaru	Fruit	10	9
		Flower	2	1
		Cladode	2	2
Leguminosae/Fabaceae	Prosopis juliflora ^a	Fruit	35	8
	Tamarindus indica ^a	Fruit	4	2
Malvaceae	Herissantia tiubae	Flower	8	3

^a Exotic plant

the cladode, among the spines. Next, the animal placed its hands onto the cladode, biting a spot that lacked spines and ingesting the stem. 2) *Fruit*—the individual stood on the cladode among the spines close to the fruit. In order to feed, the animal bit into the outer portion of the fruit, exposing its pulp. It discarded the outer portion, and then, using one of its hands, it grabbed the inner portion of the fruit and put it in its mouth. 3) *Flower*—the individual stood among the spines of the cladode close to the flower and, holding the flower with both forelimbs, removed a piece with its mouth and moved away to a nearby tree to feed.

Pilosocereus gounellei (Fig. 1c) Plant description: a cactus up to 4-m tall. Its areoles are 1 cm apart from each other and exhibit long cylindrical and rigid spines up to 15 cm in length, with a central and bigger acicular spine. The plant has 17-cm long white tubular flowers, succulent, and sub-globose and laterally dehiscent fruit (Rocha and Agra 2002; Menezes

Fig. 1 Some of the plant items consumed by *Callithrix jacchus* in the study site. **a** Cladode of *P. pachycladus*. **b** Fruit of *C. jamacaru*. **c** Flower of *P. gounellei* et al. 2013). Description of the feeding behavior. 1) *Fruit* the marmoset stood on a branch close to the fruit, grabbed the fruit with both hands, and ingested small pieces at a time. 2) *Flower*—the marmoset stood on a branch close to the flower and proceeded as described for the consumption of the flower of *Cereus jamacaru*. Afterwards, other individuals approached the flower and proceeded alternately in the same way.

Prosopis juliflora (exotic plant) Plant description: A thorny tree native to Central and South America (country of Peru) up to 12-m tall (Pasiecznik et al. 2001). Its fruit is indehiscent, has an elongated shape, and is divided into compartments each containing a seed (Burkhart 1976). Description of the feeding behavior: *fruit*—the animal stood on a branch in order to reach the pod hanging vertically down. The fruit was consumed in two ways: (i) the marmoset ate the pod without pulling it away from the branch; (ii) the animal pulled the pod away from the



branch and bit it, removing a piece for consumption. Both procedures were conducted several times for the same fruit.

Tamarindus indica (exotic plant) Plant description: a tree native to Africa about 25-m tall. It produces brown indehiscent and woody fruit measuring from 5 to 15 cm in length (Sousa et al. 2010). Description of the feeding behavior: *fruit*—the individual traveled to the periphery of the canopy near to the fruit, grabbed the fruit with both hands without pulling it away from the tree, bit directly into the fruit, and ingested small pieces at a time. Feeding was observed only on unripe fruit.

Herissantia tiubae Plant description: a perennial plant, with flowers having white petals, yellow anthers, and grandular-viscous trichomes (Silva et al. 2013). Description of the feeding behavior: *flower*—the individual reached a spot in the canopy close to the flower, grabbed it by the peduncle with both hands, and consumed all of the petals at once and discarded the calyx.

Discussion

From the seven different behavioral patterns under analysis (foraging, gummivory, resting, locomotion, grooming, play, stationary), two of them (resting and play) showed significant differences the between dry and wet seasons in Caatinga. The pronounced change in resting behavior appears to be an adjustment to the high temperatures during the dry season in the study site (up to 35.2 °C). Such behavioral adjustments may represent an important strategy to cope with thermal stress during the hottest hours of the day, as has been reported in other primates (baboons: Stelzner 1988; common marmosets: De la Fuente et al. 2014; chimpanzees: Pruetz and Bertolani 2009). De la Fuente et al. (2014) have addressed the problem of how the duration of resting is affected by hourly temperatures in common marmosets and found a significant increase in resting during the hotter hours of the day. Our results complement the study conducted by De la Fuente et al. (2014) and indicate that marmosets increased time spent resting in the hot dry season relative to the cooler rainy season in the Caatinga. Unfortunately, a more precise comparison with the Atlantic Forest is difficult since the study conducted by Alonso and Langguth (1989) did not present an analysis of seasonal variation in activity budget. Nonetheless, common marmosets in the Caatinga devoted a similar percentage of time to resting in the rainy season (18.6 %) as compared to common marmosets reported in the Atlantic Forest (18 %) by Alonso and Langguth (1989). As for stationary behavior, which is a short pause the animal displays between activities, there were no observed differences in time budget between the two seasonal periods. This behavior is of very short duration

(<1 min) and appeared to play no major role in reducing thermal stress in the marmosets. Stationary behavior was not measured in the Alonso and Langguth (1989) study.

Regarding playing behavior, the fact that it occurred more frequently in the rainy than in the dry season is likely explained by the presence of more infants (five infants vs. two infants) during the rainy season. Moreover, as observed in our study, the presence of infants can promote the engagement of adults in this kind of social activity (e.g., Ingram 1977; Stevenson and Poole 1982). Thus, a greater number of infants in the rainy than in the dry season probably resulted in more adult participation in play, as well as more frequent play, hence increasing the difference we observed between seasons. The lower temperatures during the rainy season (mean minimum temperature, 19.3 °C) also may have contributed to increased physical activity such as playing (e.g., Barber 1991). A comparison with the Atlantic Forest marmosets is not possible as data on play behavior in this environment are unavailable.

Foraging, the search and consumption of food items (except gummivory), was one of the most frequent activities in common marmosets (C. jacchus) inhabiting the Caatinga. Interestingly, we found no differences in the time budget for this behavior between seasons, despite strong seasonal shifts in rainfall and the availability of fruits, flowers, and presumably insects. Moreover, our finding that foraging accounted for 30.7 % of Caatinga marmoset activity in the rainy season is similar, in terms of percentage, to the 36 % obtained in the Atlantic Forest (Alonso and Langguth 1989), despite marked differences in habitat and plant species composition between both environments. We believe that such behavioral consistency, across seasons in Caatinga and between Caatinga and Atlantic Forest, is a consequence of the high metabolic costs of small body size in mammals, causing them to require a constant pattern of food intake (Schmidt-Nielsen 1997; Passamani 1998; Menárd et al. 2013).

As for the consumption of trunk exudates in the dry and rainy seasons, our findings reported no seasonal differences, supporting a previous study conducted by Amora et al. (2013). This also is a noteworthy finding, whose verification is important as the marmosets' ability to gouge holes in trees to obtain exudates makes this food resource available to them throughout the year (Araújo et al. 2007). We expected that, in response to both water stress and the limited availability of fruits during the hot dry season, common marmosets would increase gummivory. Studies of the nutrient content of gums consumed by tamarins and callimicos, close relatives of marmosets, indicate that gums contain 52-95 % water (Porter et al. 2009). The results obtained both in our study and in that conducted by Amora et al. (2013) may be related to hydric stress during the dry season, which could decrease the water content of gums and result in an increase in the concentration of tannins or other compounds (Pizzi and Cameron 1986).

Tannins are known to adversely affect palatability, bind with proteins that make them unavailable to the forager, and to reduce herbivory (Monteiro et al. 2005). This phenomenon might well affect marmosets, keeping gum consumption relatively constant across seasons, even though the availability of other food types varies considerably. Regarding a comparison between the Caatinga and Atlantic Forest, the percentage of time devoted for gummivory is similar in both environments (Atlantic Forest, 15 %; Caatinga, 17.5 and 15.8 %, wet and dry seasons, respectively). Although we certainly do not dispute the importance of gummivory as part of the diet of common marmosets, our results coupled with previous findings suggest a limit for the use of this resource, even when inhabiting a challenging environment.

Regarding grooming, this behavior was consistent across seasons in our study (12.1 and 14.6 %, rainy and dry seasons, respectively) and was comparable to that reported for Atlantic Forest marmosets (15 %) (Alonso and Langguth 1989). It seems that this activity, which helps maintain group cohesion (Dunbar and Shultz 2007), is important to the extent of not showing remarkable variation between the seasons in the Caatinga, and also between the Caatinga and Atlantic Forest environments.

Similarly to grooming, locomotion did not show significant differences between seasons (8.3 and 8.8 %, rainy and dry seasons, respectively). It is known that common marmosets travel to the borders of their territories as a function of vigilance (against other competing marmoset groups) and visit several different feeding sites to both obtain food (Alonso and Langguth 1989) and access to mating opportunities (Lazaro-Perea 2001). Possibly, the lack of a difference between seasons in the Caatinga is due to the exploitation of a small home range throughout the entire year. Nevertheless, common marmosets seem to adjust this behavior in another ways: De la Fuente et al. (2014) observed that these small mammals in the Caatinga increased locomotion during the cooler hours of the day. Thus, it is likely that our common marmosets also behaved in such a fashion to avoid heat stress and/or compensate for longer resting periods during the dry season. A comparison between the percentages of this activity spent in the Caatinga and Atlantic Forest also shows similar results (Atlantic Forest, 11 %; Alonso and Langguth 1989), a factor that further supports the assumption that common marmosets demonstrate consistency in time devoted to locomotion across different forests.

The diet of common marmosets in the Caatinga included a wide range of food types including vertebrates (small lizards and bird eggs), invertebrates (including spiders), fruit, flowers, gums, and cladodes, consistent with the idea of a generalist feeder, as documented in the Atlantic Forest (Stevenson and Rylands 1988; Rylands and Faria 1993; Schiel et al. 2010). However, cladode consumption is described here for the first time, which enhances the adaptability and flexibility of

common marmosets living in this environment. The limited consumption of insects during the dry period (28.7 % dry season vs. 71.3 % wet season) was probably due to the decrease of invertebrate biomass in semiarid environments in this season (Vasconcellos et al. 2010). Their inclusion in the diet is extremely important, as it provides both water for thermoregulation and energy for daily activities (Arnold and Drawe 1979; Mellink and Riojas-López 2002).

Cactus consumption presents problems as these plants are usually protected by numerous sharp spines (Theimer and Bateman 1992; Rangel and Mellink 1993). Overcoming this challenge requires a perception of the problem as well as proper body dexterity to access the resource without getting injured. Studies of wild common marmosets in the Atlantic Forest have documented that these small primates possess both complex cognitive capacities (Hasley et al. 2006; Gunhold et al. 2014) and enhanced motor skills (Souto et al. 2007; Schiel et al. 2010) associated with fine manual dexterity and object manipulation. Our results suggest that these abilities are important for the success of this species in obtaining a crucial amount of food and water in such a semiarid environment. Of course, common marmosets are not the only animals that successfully exploit these plants; however, a few mammals are able to do so easily. For example, cattle breeders based in semiarid environments are aware of livestock that will usually reject plants protected by long and sharp spines; thus, they have to eliminate the spines prior to providing forage for their animals (Mizrahi et al. 1996). On the other hand, some mammals such as the collared peccary (Pecari tajacu) and some rodents (e.g., Neotoma albigula) inhabiting semiarid regions also feed on cacti, avoiding plant species that contain long sharp spines (Theimer and Bateman 1992; Rangel and Mellink 1993). Common marmosets and capuchin monkeys (Sapajus sp.: Moraes et al. 2014) are able to survive in the Caatinga by having the cognitive ability and manual dexterity that enable them to obtain a nutritionally adequate diet while avoiding plant mechanical defenses.

Streilein (1982) suggested that behavioral adaptability is one way to explain the presence of mammals in the extensive semiarid region of the Caatinga. Common marmosets do not dig holes to escape the heat nor do they use tools to gain access to food items as capuchins do. However, they show a number of behavioral adjustments to cope with the semiarid conditions. Most importantly, and unlike many other animals, common marmosets are not considered pests, do not harm domestic animals, and are commensal with the human presence in Caatinga. Thus, this species of nonhuman primate represents a good model to better understand how a mammal without unique physiological adaptations to semiarid conditions can survive in such an environment.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards and practices of the institution at which the studies were conducted. The study was approved by the Ethics Committee for Animals Use (CEUA) of the Federal Rural University of Pernambuco (license number 135/2014).

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