




RESEARCH ARTICLE

Trait variation and trait stability in common marmosets (*Callithrix jacchus*) inhabiting ecologically distinct habitats in northeastern Brazil

Paul A. Garber¹  | Christini B. Caselli² | Anna C. McKenney⁶ | Filipa Abreu² |
 Maria Fernanda De la Fuente²  | Arrilton Araújo³ | Maria de Fatima Arruda³ |
 Antonio Souto⁴ | Nicola Schiel²  | Júlio César Bicca-Marques⁵

¹Department of Anthropology and Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, Illinois

²Departamento de Biologia, Laboratório de Etologia Teórica e Aplicada, Universidade Federal Rural de Pernambuco, Recife, PE, Brazil

³Departamento e Fisiologia, Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil

⁴Departamento de Zoologia, Laboratório de Etologia, Universidade Federal de Pernambuco, Recife, PE, Brazil

⁵Escola de Ciências, Laboratório de Primatologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil

⁶Natural Resources and Environmental Sciences, University of Illinois, Urbana, Illinois

Correspondence

Paul A Garber, Department of Anthropology and Program in Ecology, Evolution, and Conservation Biology, 109 Davenport Hall, 607 South Mathews Ave, University of Illinois, Urbana, IL 61801.

Email: p-garber@illinois.edu

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Abstract

Understanding the set of factors that promote and constrain a species' ability to exploit ecologically distinct habitats is central for addressing questions of intraspecific variability in behavior and morphology. In this study, we compared newly collected data with published data on body measurements, group size and composition, daily path length, home range, and reproductive output in wild common marmosets naturally inhabiting two contrasting environments in northeastern Brazil: the Atlantic Forest (AF), which is characterized by high biodiversity and reduced seasonality in food availability and the Caatinga (CAT), which is characterized by a severe hot and dry season lasting from 5 to 11 months, drought-resistant plant species, and reduced primary productivity. Despite marked differences in ecological conditions, CAT marmosets and AF marmosets differed minimally in daily path length, home range, reproductive output, and infant survivorship. CAT marmosets were found to live in smaller groups containing fewer adult females than AF marmosets, and also were characterized by a greater surface area to body mass ratio, a trait that may represent an adaptation to the hot and dry conditions of the Caatinga. We propose that in conjunction with body mass reduction, minor adjustments in behavior, the exploitation of cacti as a source of water and nutrients, and access to exudates as a dependable year-round food resource, common marmosets successfully used the same adaptive pattern to maintain high reproductive output and infant survivorship in exploiting these two ecologically distinct environments.

KEYWORDS

Atlantic forest, Caatinga, intraspecific variability, phylogenetic constraints, surface area to body mass ratio

1 | INTRODUCTION

Understanding the functional significance of morphological and behavioral traits that vary among individuals of the same species living in different habitats offers critical insight into processes of natural selection, adaptation, adaptability, and evolution (Kappeler, Barrett, Blumstein, & Clutton-Brock, 2013; Mitchell-Olds, Willis, & Goldstein, 2007). This is especially important in the study of primate behavior and biology (Strier, 2017). Given their slow life history, large brain size, and ability to learn by watching others, it is generally assumed that individuals in many primate species flexibly alter their behavior, such as diet, activity budget, day range, foraging strategies, group size and cohesion, and frequency of cooperative and competition interactions in response to local or short-term changes in their social and ecological environments (Altmann & Alberts, 2005; Chapman & Rothman, 2009; Kamilar & Baden, 2014; Strier, 2017). Within-species variability also can be driven by natural selection favoring phenotypic diversity among individuals of the same species exposed to alternative environmental conditions (Galligan et al., 2012). For example, populations of gray mouse lemurs (*Microcebus murinus*) inhabiting hotter and drier forests in northwestern Madagascar are characterized by an increase in surface area relative to body mass compared with populations living in cooler and/or wetter forests in southern and western Madagascar (Lahann, Schmid, & Ganzhorn, 2006). Lahann et al. (2006) argue that this change in body proportion represents an adaptive response to dissipating body heat and remaining thermoneutral under hot and dry conditions.

In addition to factors that serve to increase group and subpopulation trait variation, stabilizing selection can act to promote behavioral and biological traits that are fixed or vary minimally in their phenotypic expression (Schradin, 2013). In some cases, these conservative traits constrain or guide behavioral plasticity by limiting the set of effective solutions to a particular ecological or social problem (Garber, Righini, & Kowalewski, 2015). In this regard, Kamilar (2006) examined within-species variation in ecology, behavior (activity budget), diet, and social organization among 27 groups of wild baboons in sub-Saharan Africa (olive baboons, *Papio hamadryas anubis*; yellow baboons, *P. hamadryas cynocephalus*; chacma baboons; *P. hamadryas ursinus*; and Guinea baboons, *P. hamadryas papio*). Although each subspecies is phenotypically distinct in terms of body size and pelage characteristics, based on genetic data and cranial morphometric variation, these populations are argued to represent a single highly polytypic species (Frost, Marcus, Bookstein, Reddy, & Delson, 2003). However, despite the fact that these “savannah baboon subspecies inhabit significantly different environments, their diet, activity budget, and social organization did not exhibit a corresponding distinctiveness” (Kamilar, 2006, pp. 185). That is, members of each population appear to solve alternative ecological and social problems in similar ways. This finding could result from the unifying effects of gene flow across subpopulation boundaries (Kamilar, 2006) or constraints imposed on behavioral plasticity by phylogenetically conservative traits present in baboons that are co-selected for a shared function (Cheverud, 1996). Given

that the set of factors that promote or constrain intraspecific behavioral and biological variability in most primate species remains unclear, understanding the range of variation within a species remains a critical challenge for the study of primate behavior and ecology (Strier, 2017).

In the present study we examined trait variation in common marmosets (*Callithrix jacchus*), a species of New World primate that has been described as exhibiting marked ecological plasticity (Schiel & Souto, 2017), and is widely distributed across northeastern Brazil (Rylands, Coimbra-Filho, & Mittermeier, 2009). Common marmosets live in small, cohesive multi-male multi-female groups (generally 5-10 individuals, but groups of up to 16 individuals have been reported) and are characterized by a set of derived behavioral and biological traits that serve to maximize reproductive output (Digby, Ferrari, & Saltzman, 2011). These include twinning (the twins are dizygotic), the ability to produce two litters per year (due to the absence of lactational anestrus, a breeding female can resume ovulation within days after giving birth and successfully conceive a new pair of twins while nursing her current twin infants), and cooperative infant caregiving, in which principally the adult male group members assist the mother in carrying and provisioning the young (Albuquerque, 1994; Koenig, 1995). In addition, common marmosets are characterized by high levels of within-group female breeding competition. Regardless of the number of adult females present in a group, generally only a single female in each group breeds (but see Yamamoto, Arruda, Alencar, Sousa, & Araújo, 2009 for a discussion of the factors that result in some groups containing multiple breeding females), and the sovereign breeding female can socially and/or hormonally suppress ovulation in subordinate adult females (Tardif et al., 2003). The diet of common marmosets is dominated by plant exudates, ripe fruits, floral nectar, and animal prey (insects and small vertebrates; Abreu, De La Fuente, Schiel, & Souto, 2016; Digby et al., 2011).

Common marmosets naturally exploit two highly distinct habitat types in northeastern Brazil: the Atlantic Forest (AF) and the Caatinga (CAT; Rylands et al., 2009). Compared with the CAT, the AF is characterized by high animal and plant species diversity, an emergent canopy, reduced seasonality in fruit production, and receives up to 2,000 mm of rainfall per year (Santos et al., 2008). Currently, 24 primate species are reported to inhabit this biome (we note, that the northern Atlantic Forest and the southern Atlantic Forest represent two distinct areas of mammalian endemism; Costa, Leite, Fonseca, & Fonseca, 2000; Gonçalves et al., 2018). In contrast, CAT is characterized by an extended hot and dry season lasting from 5 to 11 months per year resulting in a dense herbaceous layer, an attenuated canopy, succulent, deciduous, and drought-resistant plant species, fruit scarcity, and reduced biodiversity (Araújo, Castro, & Albuquerque, 2007). Annual rainfall in CAT averages 620 mm (range, 250–1,200 mm), with no measurable rainfall in some years (Araújo et al., 2007). During the dry season, daytime temperatures often reach or exceed 35°C resulting in high evapotranspiration and extended periods of water and heat stress for local animals and plants (Araújo et al., 2007; Mendes, Rocha, Ribeiro, Perry, & Oliveira,

2004). In addition to common marmosets, four primate species (bearded capuchins, *Sapajus libidinosus*; buff-headed capuchins, *S. xanthosternus*; black-and-gold howler monkeys, *Alouatta caraya*; and blond titi monkeys, *Callicebus barbarabrownae*) range into CAT, but do so at extremely low population densities (Corsini & Moura, 2014; Printes, Rylands, & Bicca-Marques, 2011). The low population density of CAT primates is likely the result of ecological constraints associated with high temperatures, low rainfall, fruit scarcity, and reduced primary productivity (Amora, Beltrão-Mendes, & Ferrari, 2013).

Here, we present newly collected data on body mass, body length, group size, group composition, group biomass, and reproductive output for common marmosets inhabiting the CAT, along with previously published data on group size and composition, day range, and home range area of CAT marmosets (Caselli et al., 2018; De la Fuente, Souto, Sampaio, & Schiel, 2014), and compare these to published data on AF common marmosets (see Supplementary Materials, Table SII and SIII). Our goals are to (a) identify aspects of common marmoset behavior and biology that vary significantly (e.g., phenotypic plasticity) and those that vary minimally (e.g., phylogenetic conservatism) in response to environmental differences in temperature, rainfall, and food availability; and (b) determine the degree to which common marmosets inhabiting these two distinct environments exploit their respective habitats in similar or different ways. To accomplish these goals we test three predictions consistent with assumptions of phenotypic plasticity and biological adaptation:

P1. Given the thermoregulatory benefits associated with efficiently dissipating body heat and conserving water in a hot and dry environment (Blanckenhorn, 2000; Terrien, Perret, & Aujurd, 2011), we expect the ratio of surface area to body mass of CAT marmosets to be higher compared with marmosets living in the AF.

P2. Given reduced primary productivity and increased resource unpredictability in Caatinga (Araújo et al., 2007), we expect that CAT marmosets will exhibit (a) smaller group size, (b) a longer day range, (c) a larger home range, and (d) a lower group biomass than AF marmosets.

P3. Given reduced primary productivity, extremely hot and dry conditions in the Caatinga, and the fact that during pregnancy and lactation females require 40–50% more water (Cain, Krausman, Rosenstock, & Turner, 2006), we expect CAT marmosets to be characterized by (a) a longer interbirth interval (IBI) and (b) have lower infant survivorship than AF marmosets.

2 | METHODS

2.1 | Study sites

We compared data on the behavior, ecology, and body measurements (body mass, head-body length, tail length, and total length [head + body + tail]) of wild common marmosets inhabiting one AF and two CAT field sites in northeastern Brazil; **Nísia Floresta National Forest (NF)**, in the state of Rio Grande do Norte, a 170-ha AF site near the city of Natal (6°05'S, 35°12'W, yearly rainfall

averages 1,295 mm and daytime temperatures rarely if ever exceed 32°C, see Instituto Nacional de Meteorologia-INMET and Araújo et al., 2000 for additional information regarding marmoset behavior and ecology at this site); **Assu National Forest (ASSU)**, a thorn scrub CAT habitat of 518-ha in the state of Rio Grande do Norte (5°34'20"S, 16°54'33"W, yearly rainfall averages 646 mm and daytime temperatures may reach or exceed 35°C during 10 months of the year, see Instituto Nacional de Meteorologia-INMET and Cutrim, 2007 for additional information regarding climatic conditions and marmoset behavior and ecology at this site); and **Baracuhy Biological Field Station (BBFS)**, a 400-ha dry thorn scrub CAT forest near the town of Cabaceiras, (7°31'42"S, 36°17'50"W), in the state of Paraíba. Yearly rainfall at BBFS averages 337 mm, making this site among the driest CAT habitats in northeastern Brazil (Araújo et al., 2007, see De la Fuente et al., 2014 for additional information regarding marmoset behavior and ecology at this site; Figure 1). At BBFS, daytime temperatures can exceed 35°C during 7 months of the year (Instituto Nacional de Meteorologia-INMET).

2.2 | Data collection

Data on common marmoset body measurements were collected through a process of trapping, measuring, marking, and releasing. Between 1991 and 2000, 167 adult marmosets were measured at the AF site of NF. Seven of the marmosets were trapped on two occasions at least 6 months apart, and we included all body mass measurements ($N = 174$) in our analysis to take into account the affect that seasonal changes in resource availability may have on variation in body mass. Body mass data (but not linear body measurements) from these marmosets were previously published (Araújo et al., 2000). At the CAT site of ASSU, 11 adult marmosets were each trapped on a single occasion, weighed, and measured (data collected between 2004 and 2016). Finally, we measured 38 adult marmosets at BBFS, a CAT habitat (data collected between 2014 and 2016). Six adults were trapped on two occasions, at least 6 months apart and in different seasons. As in the case of the NF marmosets, all body mass values ($N = 44$) were included in our analysis. At all field sites, marmosets were trapped during both the wet and dry seasons.

Our trapping procedure at all three field sites involved habituating group members to a large trap baited with bananas, located on a platform approximately 1.5 m above the ground. The trap was divided into 10 separate compartments, each with its own door. We have used this method in the past to successfully trap, mark, and release groups of several tamarin and marmoset species (see Bicca-Marques & Garber, 2004; Garber, Porter, Spross, & Di Fiore, 2016 for additional details concerning our trapping procedure). Once the group was captured, individuals were removed from the trap one at a time and injected intramuscularly in the thigh with Ketamin HCL (50 mg/ml, 0.02 mg for juveniles, and 0.04 mg for adults and subadults). Body measurements were collected using a digital caliper (± 0.1 mm) and body mass was obtained using a digital scale (± 0.1 g). Individuals were classified as adults (> 15 months of age), subadults (12–15 months of age), juveniles (> 4 –11 months of age), or infants

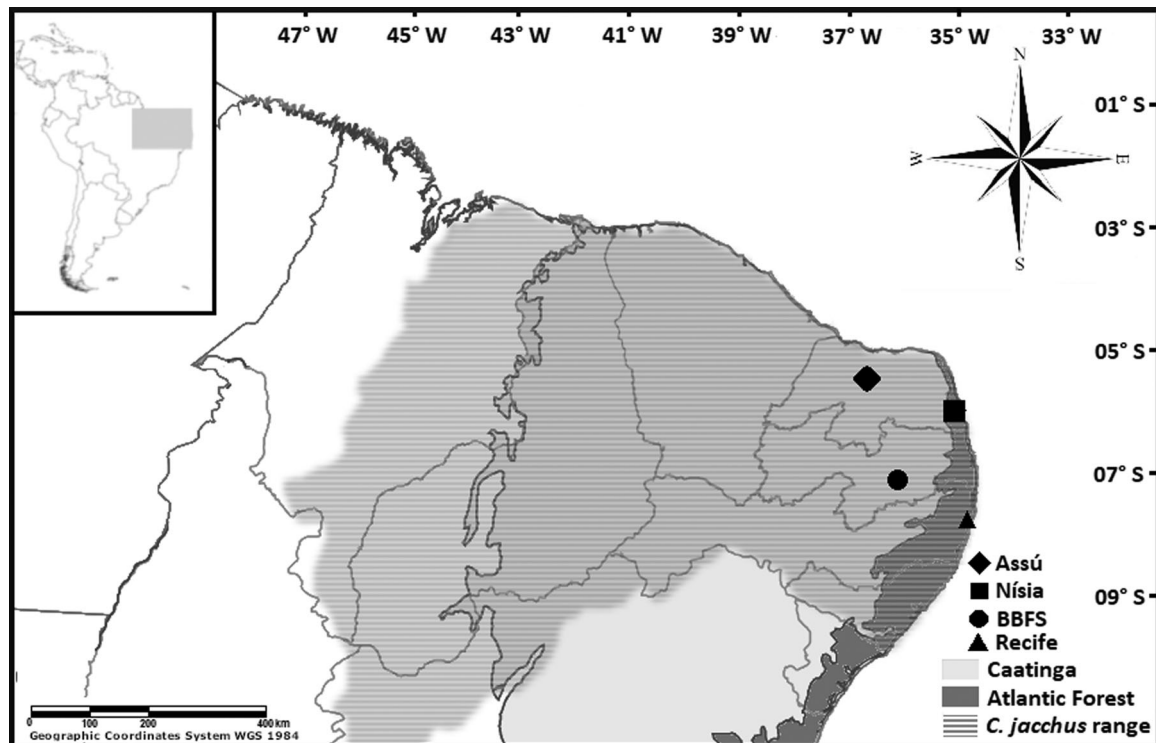


FIGURE 1 Map indicating the distribution of common marmosets and the location and habitat type (Caatinga or Atlantic forest) of the three field sites in northeastern Brazil (Assu National Forest (ASSU), Baracuh Biological Field Station (BBFS), and Nísia Floresta National Forest (NF), at which the common marmosets were trapped, measured, weighed, and studied. Data on common marmoset distribution are from the IUCN (<https://www.iucnredlist.org/>) and the distribution of Caatinga and Atlantic Forest habitats is from the Instituto Brasileiro de Geografia e Estatística (<https://ww2.ibge.gov.br/home/>)

(≤ 4 months of age) based on body mass, body, and genital measurements, and data on deciduous and adult dental eruption sequences (Hershkovitz, 1977; Yamamoto et al., 2009). In the case of several infants and juveniles at BBFS, direct knowledge of their birth date (month/year) was known from data recorded during behavioral observations. After all group members were examined and each had fully recovered from the effects of the tranquilizer, the entire group was released together at the trap site. No marmoset died or showed signs of injury resulting from trapping.

Marmoset trapping and handling procedures were approved by the Ethical Committee on Animal Experimentation (CEUA) of the Federal Rural University of Pernambuco, Brazil (CEUA license number 135/2014 and SISBIO license number 46770-1), and the Federal University of Rio Grande do Norte (SISBIO license numbers 57796, 12218, and 26253). The University of Illinois (IACUC Protocol #14263) approved procedures associated with behavioral observations. This study adhered to the American Society of Primatologists ethical principles for the study of primates.

2.3 | Data analyses

2.3.1 | Body measurements

To assess evidence of between-site differences in the ratio of surface area to body mass, we collected data on body mass, and head-body length (hbl), tail length (tl), and total length (head-tail length; htl;

response variables) in adult male and adult female common marmosets across our three study populations (predictor variables). To avoid ambiguities in determining female reproductive condition (female common marmosets can be both pregnant and lactating at the same time), data on body mass and body measurements of all adult females were pooled for a given field site in all analyses. To conduct inter-site comparisons of body measurements, we adjusted generalized least squares models (GLS) with variance as a covariate because the homogeneity of variance assumption was violated (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We performed a sequential analysis of variance to determine the significance of the predictor variable, retaining the more complete models whenever comparisons indicated that simplification would result in loss of explanatory power (p -value $< .05$; following Zuur et al., 2009). To access differences within the levels of the nominal predictor variables (sex and study site), we used a Tukey's HSD test (THDS-test) as a post hoc pairwise comparison. Whenever outliers were detected, we ran the analyses with and without that individual. We present the results with the single outlier because it did not change our findings.

2.3.2 | Ratio of surface area to body mass

To evaluate our first prediction (P1), we used the square root of body mass multiplied by head-body length divided by 3,537 to calculate each individual's body surface area (BSA) following Wang and Hihara

(2004). We then divided BSA by the individual's body mass to obtain the surface area/body mass ratio (Retamal & Mascie-Taylor, 2018). Given that males and females of the two CAT sites did not differ in their body measurements (see results), we pooled the data for the BBFS and ASSU marmoset population. However, our data set failed to meet the assumptions of normality and homogeneity of variances, and therefore we used a randomization approach to compare the ratio of surface area to body mass between habitats. To do this, we first calculated the absolute difference of the ratio of surface area to body mass between animals inhabiting the AF and the CAT. This was accomplished by randomly selecting half of the AF and the CAT samples (each 100 times) and calculating the mean absolute difference between these habitats to minimize the influence of random sample selection. Then, we compared this difference with the difference expected under the null hypothesis using a two-tailed p -value. The expected random distribution was generated via 1,000 Monte Carlo simulations (Manly, 1997). We note that the formula developed by Wang and Hihara (2004) to calculate BSA has been validated for several mammalian taxa including humans (although validation varies in robusticity depending on the linear measurement used). Moreover, given that we are using the same formula to compare among members of a single species, we feel our results represent a reasonable approximation of CAT and AF common marmoset BSA.

2.3.3 | Group size

Beginning in November 2012, we initiated a series of behavioral, ecological, and demographic studies of the BBFS marmoset population. At BBFS, data on group size were based on direct observations of habituated groups, monthly censuses, and field observations of marked individuals (uniquely beaded identification collars) over a four-year period. To assess the effect of habitat on group size (P2), we compared our newly collected data based on eight CAT groups plus five additional CAT groups from previous studies conducted at BBFS (CAT total = 13) with the published literature on 38 AF groups inhabiting five different field sites (see Table SII in the supplementary material). In those cases in which published studies reported data as the number of group members per month of study, we calculated the mean number of individuals in the group (the mean number of adult males, adult females, and all adults, and the mean group size) across all months of the study. Given that this data set resulted in potential biases and nonindependent samples (e.g., different number of groups studied per field site or data from only one season), we used the same randomization approach as described above and calculated the absolute difference between the size (total number of individuals) and composition (number of adult males and females) of groups inhabiting the AF and the CAT. We then compared this difference with the difference expected under the null hypothesis using a two-tailed p -value. Whenever necessary, we used a false discovery rate (FDR) correction for multiple comparisons, which is less conservative and more powerful than a Bonferroni correction (Benjamini & Hochberg, 1995).

2.3.4 | Daily path length, home range, and group biomass

We also used a randomization approach (see above) to compare daily path length, home range, and group biomass between AF and CAT habitats. We compared published data for AF common marmoset groups (day range = 6 groups; home range = 10 groups), with newly collected data on daily path length ($N = 3$ groups) and published data on home range ($N = 5$ groups) for CAT marmosets at BBFS (see Table SIII in the supplementary material). In addition, we calculated group biomass (the product of the mean adult, subadult, juvenile, and infant body mass based on the number of individuals of each age/sex class in each group divided by the home range occupied by that group) for 10 AF groups (these data are from the literature and include four sites for which data on group size and age/sex composition are available; see Tables SII and SIII in the supplementary material) and five BBFS CAT groups (based on the new data we collected on body mass and the published data on home range for this study site).

2.3.5 | Reproductive output and reproductive success

We collected data on female reproductive output and infant survivorship in six BBFS groups between 2013 and 2016. These data included the birth month, number of offspring born, number of offspring that survived past weaning (4 months of age), and interbirth interval (IBI). We ran a the χ^2 test to compare infant survivorship to weaning in CAT and AF marmosets (AF data from Digby, 1994 and Yamamoto et al., 2009 and were collected at the site of NF) with that expected by chance considering the total number of infants born per site. We also present data from Arruda et al. (2005) on the interbirth interval, across several births, of three common marmoset females resident in two groups at Nisia Floresta.

We performed all analyses in R software version 3.4.1 (R Core Team, 2017) setting the significance level at 5%. We implemented the analyses with the package "nlme" version 3.1.131 (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017), "stats" version 3.4.1 (R Core Team, 2017), "lsmmeans" version 2.30-0 (Lenth, 2016), and "XNomial" version 1.0.4 (Engels, 2015).

3 | RESULTS

3.1 | Body measurements

We compared adult male and female body mass across our three field sites and found that body mass varied by sex and habitat type (GLS: null model vs. full model - including the interaction between sex and study site, $L = 88.86$, $df = 5$, $p < .0001$; full model vs. simplified model - including sex and study site but not the interaction between them, $L = 7.44$, $df = 2$, $p < .05$; Figure 2). There were no differences in adult male body mass across our two CAT field sites and no differences in adult female body mass across our two CAT sites (post hoc THDS-test: $p_s > .05$). Female CAT marmosets, however, were heavier than

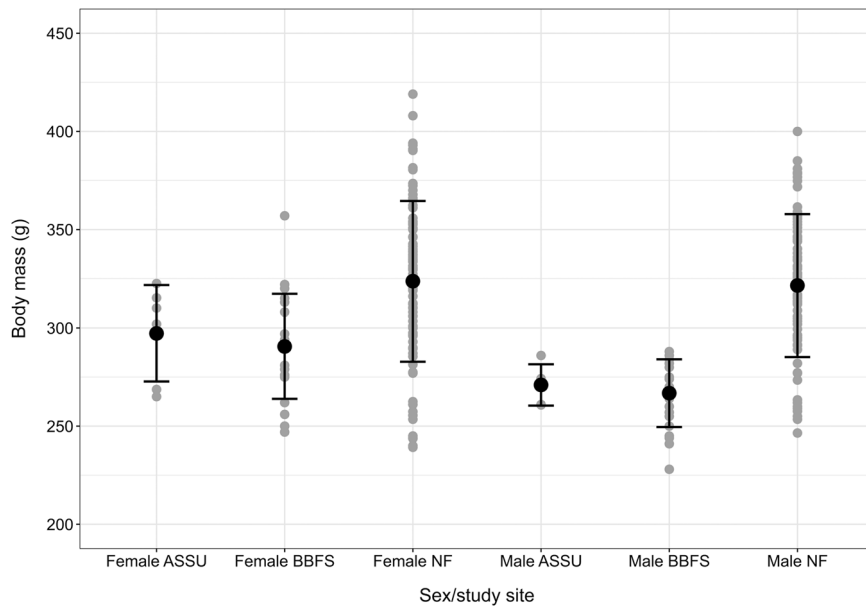


FIGURE 2 Body mass of adult male and female common marmosets inhabiting the Caatinga field sites of Baracuhy Biological Field Station (BBFS) and Assu National Forest (ASSU), and the Atlantic forest field site of Nísia Floresta National Forest (NF). The bars represent the standard deviation, the black circles represent the mean, and the gray circles represent the measurements of each individual

male CAT marmosets (THDS-test: $p_s < .05$, Figure 2). In contrast, although there were no differences in adult male and adult female body mass in the AF (THDS-test: $p = .71$), both male and female AF marmosets were significantly heavier than CAT marmosets. Adult male CAT marmosets weighed 20% less than adult male AF marmosets (AF_{NF} site mean = 321.5 g, SE = 4.1 g, N = 80; CAT_{BBFS} and ASSU sites, mean = 267.5 g, SE = 3.1 g, N = 28; THDS-test: $p < .001$). Similarly, adult females inhabiting CAT weighed 11% less than those inhabiting the AF (AF_{NF} site mean = 323.7 g, SE = 4.3 g, N = 91; CAT_{BBFS} and ASSU sites, mean = 292.1 g, SE = 5.0 g, N = 27; 27THDS-test: $p_s < 0.05$; Figure 2; also see Table S1 for data on common marmoset body mass at other Atlantic Forest sites). In contrast, we found no evidence of differences in head-body length (GLS null model vs. full model: $L = 1.17$, $df = 5$, $p = .95$), tail length ($L = 2.88$, $df = 5$, $p = .72$), and total length ($L = 1.97$, $df = 5$, $p = .85$) between adult males and adult females inhabiting our three study sites (Figure 3).

3.2 | Ratio of surface area to body mass

To test P1, we compared the ratio of surface area to body mass in male and female marmosets across habitat types (Table 1). As a consequence of similar head-body length measurements and a lower body mass (Figures 2,3), marmosets inhabiting the two hot and dry CAT habitats (BBFS+ASSU) were characterized by a higher ratio of surface area to body mass compared with AF marmosets (CAT: $4.4 \times 10^{-3} \pm 2.0 \times 10^{-4}SD$; AF: $4.1 \times 10^{-3} \pm 2.2 \times 10^{-4}SD$; Table 1).

3.3 | Group size, daily path length, home range, and group biomass

To test P2, we compared marmoset group size, daily path length, home range, and group biomass across habitats. Based on 29 censuses of group size and composition, our eight BBFS study

groups' averaged two adult males, two adult females, and a total of six individuals (Table 1). Group sizes varied from two to nine and both the number of adult females per group and the number of adult males per group ranged from one to four. We found that groups contained multiple adult males (N = 16) 55% of the time, and multiple adult females (N = 13) 45% of the time.

In comparison, we found that common marmosets in the AF live in larger groups (mean \pm standard deviation (SD); 8.8 ± 2.7 , N = 38 vs. 5.8 ± 1.0 , N = 13) that contained a greater number of adult females (mean 2.7 ± 1.4 vs. 1.6 ± 0.7) than did CAT marmosets (Table SII supplementary material). The number of adult males per group did not differ across these habitats (mean 2.3 ± 1 in AF vs. 2.0 ± 0.8 in CAT; Table SII). These patterns were supported by statistical comparisons (see Table 1).

Given habitat-specific differences in primary productivity and rainfall, we expected marmosets in CAT to be characterized by increased daily path length, increased home range, and reduced group biomass. Marmoset study groups at BBFS traveled 860 ± 115 m daily (N = 48 daily routes) and occupied a mean home range of 5.3 ± 3.6 ha (see Table SII). The mean number of individuals in these groups was 6 ± 1 marmosets. Data for AF groups available in the literature indicated a mean daily path length of $1,024 \pm 261$ m and a mean home range of 3.9 ± 1.7 ha (N = 6. see Table SIII). The mean size of these groups was 11 ± 2 individuals (note that group size reported here is restricted to the six groups for which calculations of daily path length and home range area are available and therefore differs from that reported earlier for AF marmosets based on a larger sample of groups as presented in Table SII). Daily path length and home range area did not differ between AF and CAT marmosets (Table 1). However, the mean group biomass in CAT was > 50% lower (mean for CAT = 366 g/ha vs. mean for AF = 751 g/ha, $p = .047$) than that of AF marmosets (Table 1).

FIGURE 3 Linear body measurements of adult male and female common marmosets inhabiting the Caatinga field sites of Baracuhy Biological Field Station (BBFS) and Assu National Forest (ASSU), and the Atlantic forest field site of Nísia Floresta National Forest (NF). The bars represent the standard deviation, the black circles represent the mean, and the gray circles represent the measurements of each individual

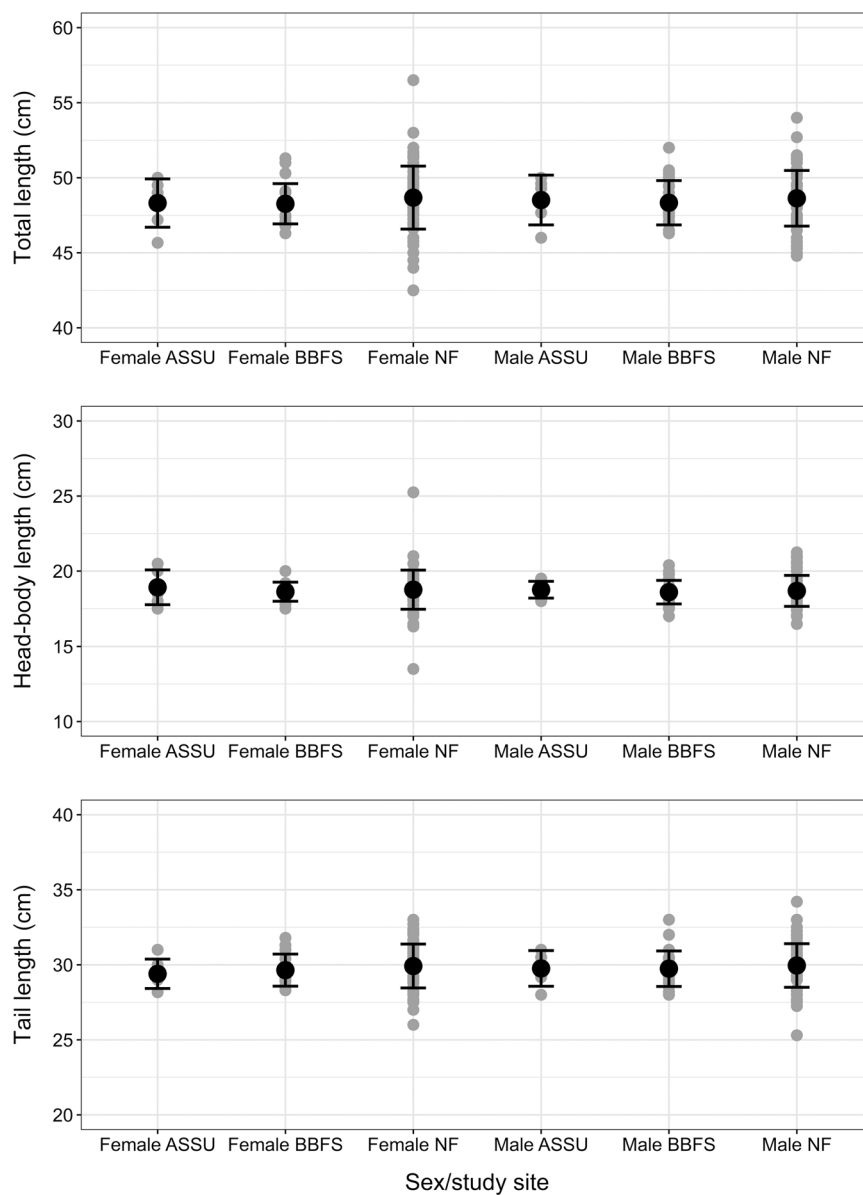


TABLE 1 Comparisons between Caatinga (CAT) and Atlantic Forest (AF) common marmosets based on the ratio of surface area to body mass (S/B ratio), number of adult males, number of females, total group size, path length, home range, and group biomass (g/ha)

	Mean values		Mean differences		<i>p</i>	Corrected <i>p</i>
	CAT	AF	Observed	Expected		
S/B ratio	4.4×10^{-3}	4.0×10^{-3}	3.5×10^{-4}	4.3×10^{-5}	0.001	-
Adult males	1.8	2.1	0.4	0.3	0.270	0.269
Adult females	1.4	2.8	1.0	0.4	0.020	0.023
Group size	5.9	8.3	2.9	0.7	0.000	0.003
Daily path length (m)	860	1,026	178	148	0.346	-
Home range (ha)	5.3	4.1	1.8	1.2	0.260	-
Biomass (g/ha)	366	751	401	173	0.047	-

Note: The mean values presented in this table differ slightly from those based on the raw data presented in Tables SII and SIII of the supplementary material because they are the product of the randomization process used in the statistical comparison.

TABLE 2 Infant survivorship and female reproductive output in common marmosets inhabiting Caatinga vegetation

Female ID	Litters	Infants born		N survived	% Survived ¹
		Assumed	Observed		
Gorda	2	4	4	4	100
Princess	2	4	4	4	100
Entroncada	5	10	9	3	30
Femea	5	10	8	8	80
Mae	3	6	6	5	83
Female UNK	2	4	4	2	50
New group	1	2	2	2	100
Algaroba	1	2	2	1	50
Total	21	42	39	29	69

¹Percentages are based on the number of offspring assumed born.

3.4 | Reproductive output, interbirth interval, and infant survivorship

We documented 21 litters produced by nine adult females at the BBFS CAT field site between 2013 and 2016. Assuming that each birth event produced twin offspring (in three litters we only observed one infant, but we cannot rule out the possibility that a second infant was stillborn or died during the first few days of life), then 29 of 42 (69%) infants survived their first 4 months of life, or beyond the period of weaning (Table 2). If in fact only 39 infants were born in these 21 litters, then infant survivorship to weaning at BBFS approached 75% (29 of 39; Table 2).

To evaluate P3, we compared marmoset reproductive output and infant survivorship at BBFS with data from the AF published by Arruda et al. (2005), Digby (1994), and Yamamoto et al. (2009; see Methods). Based on an analysis of data spanning a 10-year period at the AF site of NF, infant survivorship to weaning averaged 62% (56 of 91 infants). This data set included 11 groups with a single breeding female (70% infant survivorship) and three groups with multiple breeding females (49% infant survivorship for all breeding females in these multiple female breeding groups). An earlier study at the same site reported that 12 of 23 infants (52%) born into three groups survived past weaning. Each of these groups contained two actively breeding females. Overall, we found that infant survivorship to weaning in the BBFS CAT population (~70%) was indistinguishable from that reported for the NF AF population (the χ^2 test: $\chi^2 = 0.26$, $p = .64$).

We also examined evidence of habitat/population differences in female fertility as measured by the length of the interbirth interval (IBI). Across all birth events, the IBI for CAT marmosets at BBFS was 6.9 months ($SD = 1.7$ months, range: 5–8 months, $N = 11$), whereas the IBI for NF AF marmosets averaged 6.3 months ($N = 17$), ranging from a mean of 5.7 months in groups with a single breeding female to a mean of 7.5 months for females in multifemale breeding groups. In addition, the breeding performance of three common marmoset females in two groups at Nisia Floresta indicate that the IBI ranged from 5 to 16 months, with mean values of 5.7 months ($SD \pm 1.3$

months), 7.7 months ($SD \pm 3.8$ months), and 13 months ($SD \pm 2.6$ month). Overall, breeding females in CAT and the AF produced twin offspring at a similar rate.

4 | DISCUSSION

The goal of this study was to examine intraspecific variation in the biology and behavior of common marmosets naturally inhabiting two highly distinct environments in northeastern Brazil: Caatinga, an extremely arid and hot thorn-scrub habitat characterized by low primary productivity; and the wetter and cooler Atlantic Forest, an ecosystem of high animal and plant diversity (Araújo et al., 2007; Santos et al., 2008). Based on hypotheses of phenotypic plasticity and morphological adaptation, we tested three predictions. Our first prediction examined whether in response to the extreme hot and dry conditions of the CAT, marmosets living there are characterized by a higher ratio of surface area to body mass compared with marmosets inhabiting the AF. An increase in the surface area to body mass ratio is expected to result in greater efficiency in water conservation and increased rates of nonevaporative heat loss (Cain et al., 2006). Consistent with this expectation (P1), we found that adult male and adult female marmosets inhabiting two CAT field sites (BBFS and ASSU) were significantly smaller in body mass (mean adult body mass 280 g vs. 323 g), but not in head-body length, compared with conspecifics living in the cooler and wetter AF, resulting in an increased surface area to body mass ratio.

Several theories have been proposed to explain evolutionary changes in body size and shape (Masters, Genin, Silvestro, Lister, & Delperio, 2014). It has been argued that body mass reduction can represent an adaptive response to (a) exploiting an environment of low productivity, (b) exploiting an environment characterized by hyper-unpredictability in food production, (c) selection favoring life history changes associated with increased reproductive output and rapid infant development, or (d) selection favoring changes in allometry designed to more effectively dissipate body heat in a hot and dry environment (Blanckenhorn, 2000; Lahann et al., 2006;

Masters et al., 2014). Body mass reduction has evolved independently in several taxonomically distinct primate lineages, including some human populations (e.g., *Homo floresis*; and several pygmy populations; Ford, 1980; Marroig & Cheverud, 2009; Masters et al., 2014; Perry & Dominy, 2009). In the case of cheirogaleines, Masters et al. (2014) argue that dwarfing is associated with the exploitation of habitats characterized by high levels of resource unpredictability. However, in most species the precise set of factors favoring body mass reduction remains unclear. For common marmosets inhabiting Caatinga, a combination of environmental factors (high temperatures, low rainfall, and decreased primary productivity) and life history traits associated with high reproductive output may offer the strongest explanation (Rylands et al., 2009).

Given an overall reduction in food availability, especially during the extended dry season in Caatinga, we expected CAT marmosets to be characterized by (a) smaller group size, (b) a larger home range and daily path length, and (c) a lower group biomass compared with AF marmosets. This prediction (P2) was partially supported. Groups of CAT marmosets contained 35% fewer individuals, 50% fewer adult females, and exhibited a 49% reduction in relative biomass compared with AF marmosets. However, we found no difference in the daily path length or home range area used by CAT and AF marmosets. At our CAT site (BBFS), we have observed three cases in which groups became unstable and fissioned once they reached nine individuals (unpublished data). And, although factors such as juvenile and subadult mortality and migration affect group size and stability, it appears that by limiting group size and group biomass, CAT marmosets were able to obtain sufficient resources within a home range equal in size to that used by AF marmosets and without increasing their daily path length.

Finally, despite the potential for dietary, heat, and water stress adversely affecting fertility (Prediction 3), reproductively active female marmosets inhabiting the Caatinga maintained the same reproductive output, interbirth interval, and percent infant survivorship as did Atlantic Forest common marmosets. In both environments, a single breeding female commonly gave birth to twin infants two times per year, the mean interbirth interval between habitats varied by an average of only 18 days (from 6.3 months in the AF to 6.9 months in CAT), and infant survivorship to weaning was 52–62% in the AF and 69% in CAT (Digby, 1994; Yamamoto et al., 2009; this study). We note, however, that despite the fact that during 45% of our field censuses BBFS CAT groups contained at least two adult females, only a single female in each group gave birth. This finding contrasts with published studies of AF marmosets at the site of NF, where 6 of 17 groups (35%) contained multiple breeding females (Digby, 1994; Yamamoto et al., 2009).

In several primate taxa, females delay reproduction and increase the interval between successive birth events (IBI) under conditions of limited food availability or reduced access to high quality resources (reviewed in Knott, Thompson, & Wich, 2009). For example, female chacma baboons (*P. ursinus*) living in areas of low food productivity experienced a mean IBI of 38 months, which was 12–14 months longer than for female savannah baboons (*P. anubis* or

P. cynocephalus) inhabiting a wetter and more productive habitat (Lycett, Henzi, & Barrett, 1998). A similar negative relationship between IBI and habitat quality has been documented in vervet monkeys (*Chlorocebus aethiops*; Hauser & Fairbanks, 1988). We found no evidence for an analogous effect on common marmoset fertility.

We also note that based on the published literature, the proportion of time CAT marmosets allocated to traveling (8–9%), feeding/foraging (41–48%), resting (19–28%), and social interactions (16%; Abreu et al., 2016) was similar to the time that AF marmosets allocated to these same activities (traveling: 14–15%, feeding/foraging: 35–48%, resting: 15–30%, and social behavior: 13–16%; Digby & Barreto, 1996), despite exploiting two very different habitats that present distinct challenges related to thermoregulation, water stress, and resource availability. In addition, female reproductive output, fertility (IBI), and infant survivorship were similar across habitats. Thus, our third prediction was not supported.

The question remains, how are common marmosets able to successfully exploit the Caatinga and the Atlantic Forest in the absence of major changes in the behavioral patterns studied here? The ability of common marmosets to buffer against site-specific differences in food availability may relate to a set of derived dental and digestive adaptations (Coimbra-Filho, Rocha, & Pissinatti, 1980; Vinyard et al., 2009) that enable individuals to breakdown difficult-to-digest Beta-linked carbohydrates present in plant exudates (gums and saps; Garber & Porter, 2009). According to Rylands et al. (2009, pp. 53) this specialized complex of traits for exudate feeding evolved in the common ancestor of "*Callithrix jacchus* and *C. penicillata* in highly seasonal and dry forests of the north-east and central Brazil." Exudates account for 28–76% of common marmoset yearly feeding time (Amora et al., 2013; Digby et al., 2011). The high density of exudate trees present in CAT (Amora et al., 2013; Araújo et al., 2007) provide individuals with a predictable and renewable year-round food resource that may serve to offset seasonal perturbations in the availability of other important components of their diet such as fruits, nectar, and arthropod and vertebrate prey (Abreu et al., 2016; Digby et al., 2011; Rylands et al., 2009). Exudates contain a high concentration of water (50–97%, Garber & Porter, 2009), which can be critical for CAT marmosets, especially during the long dry season and for females nursing twin infants.

In addition, the plant family Cactaceae (cacti) is among the most common floristic components of the Caatinga biome (Araújo et al., 2007). The fruits, flowers, and flesh of three species of native cacti (*Pilosocereus pachycladus*, *P. gounellei*, and *Cereus jamacaru*) accounted for 50% of all plant species consumed by common marmosets at BBFS (Abreu et al., 2016). Amora et al. (2013) also report that these same three cacti species were prominent components of the diet of common marmosets inhabiting the CAT site of Grota do Angico Natural Monument, Sergipe, northeastern Brazil. The water content of cacti ranges from 77% to 92% (Nascimento, Moura, Vanconcelos, Maciel, & Albuquerque, 2011). We propose that marmosets have adjusted to spatial and temporal variation in resource availability and water stress in CAT through the targeted exploitation of plant exudates and native cacti. Verification of this hypothesis will require

additional study. However, cacti also represent an important source of water for populations of bearded capuchins (*S. libidinosus*) that inhabit a Caatinga environment (Moraes, Souto, & Schiel, 2014) as well as for hamadryas baboons (*P. hamadryas*) that inhabit a dry desert-like environment in Central Eritrea (Zinner, Peláez, & Torkler, 2001). We note, that at BBFS marmosets lick dew covered leaves and tree bark in the early morning to obtain water (common marmosets in the AF also lick water from leaves) and rest in crevices or openings in large sheltered rocks (F. Abreu pers. obs). These resting sites may be analogous to caves used by chimpanzees in Senegal during periods when outside temperatures can exceed 40°C (Pruetz, 2007).

In conclusion, based on a comparison of newly collected data and published studies, we found that common marmosets inhabiting the Atlantic Forest and common marmosets inhabiting the Caatinga used the same basic adaptive pattern to successfully exploit two highly distinct environments. In both habitats, a single dominant breeding female per group regularly produces twin infants two times per year (although 35% of Atlantic Forest groups contained two simultaneously breeding females, we have no documented cases of more than one breeding female in our CAT marmoset groups), multiple adult males serve as helpers and transport, protect, and provision infants, reproductive output and infant survivorship are high, and individuals gouge holes in tree trunks to regulate the production and availability of exudates. In both habitats, exudates, animal prey (insects and small vertebrates), fruits, and floral nectar represent major components of the diet, and the activity budget, daily path length, and size of the home range occupied varied minimally. We argue that several aspects of common marmoset reproductive, masticatory, and digestive anatomy and behavior are phylogenetically conservative and constrain the expression or variability in other, more labile traits such as group size and composition. And, although future studies will need to test these hypotheses more rigorously, overall common marmosets appear to achieve ecological flexibility by applying the same successful adaptive pattern across a range of habitat conditions. An understanding of behavioral plasticity, trait variation, and the role of phylogenetically conservative traits in influencing a species ability to successfully exploit a range of habitat types offer critical insight into evolutionary processes that drive and constrain primate intraspecific variation.

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ORCID

Paul A. Garber  <http://orcid.org/0000-0003-0053-8356>

Maria Fernanda De la Fuente  <http://orcid.org/0000-0002-4137-2404>

Nicola Schiel  <http://orcid.org/0000-0002-2454-0912>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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