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ORIGINAL ARTICLE

Uses of nonhuman primates by humans in northeastern Brazil

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Abstract

Humans have used non-human primates (hereafter referred to as primates) as food source, medicine, parts of rituals, pets, and models for various studies worldwide. Here we investigated the extent of the use of primates by humans in three areas in northeastern Brazil, the country's most impoverished region. We carried out our study in three biomes (Caatinga, Cerrado, and Atlantic Forest). The results showed that humans exploited all five primate species occurring in the study sites: *Callithrix jacchus*, *Sapajus flavius*, *Sapajus libidinosus*, *Alouatta belzebul*, and *Alouatta ululata*. They used the primates as a food source, as pets and medicines, and for leisure. Despite socioeconomic differences in the study areas, we found similarities in the use of primates. Larger primates were targeted for meat, whereas the small common marmosets were targeted as pets. We found conflicting interactions between humans and bearded capuchins due to crop raiding, but no such conflict was found between humans and blonde capuchins, reflecting the differences in crop type, pattern, and tradition in the sites. *A. ululata* was used as medicine. We suggest that environmental education actions in the study areas should focus on (i) raising awareness among local people of the ecological importance of primates, (ii) providing alternative activities to hunting whenever possible, and (iii) minimising conflicts.

Keywords Hunting · Pet trade · Ethnoprimatology · Ethnozoology

Introduction

There is a vast cummulative knowledge on primate behavioural ecology resulting from a long history of interactions between humans and other primates. These interactions also threaten many species' survival (Alves and Souto 2011; Chi et al. 2014; Ramos et al. 2016; Fernandes-Ferreira and Alves 2017). Overhunting to obtain animals and their parts has led to a severe decline in several animal populations (Ripple et al. 2016; Constantino 2019). The body size of a species plays an essential role in the choices considered by the hunters. Hunters prefer to capture large animals (Cullen et al. 2001). Such prey may be easier to detect and provide a more substantial meat reward (Peres 1990; da Silva Neto et al. 2017). This targeted selection can lead to local extinction of various medium-sized and large species, including primates, directly affecting ecological services such as dispersal of large seeds (Peres 1990; Barboza 2013; Alves et al. 2016a; Constantino 2019).

Scientists have used traditional and local ecological knowledge to understand humans' interactions with their environments (Gray et al. 2017). Traditional ecological knowledge (TEK) can be defined as information, practice,

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and belief, culturally transmitted from generation to generation (Berkes 1993; Berkes et al. 1995). Although traditional ecological knowledge may incorporate local ecological knowledge (LEK) it may also include recently created knowledge shared among the local resource users (Charnley et al. 2007). TEK and LEK have been used to guide management and conservation strategies for several species, including common eider (*Somateria mollissima sedentaria*), harlequin ducks (*Histrionicus histrionicus*), hammerhead sharks (*Sphyrna* spp.), and golden langurs (*Trachypithecus geei*) (Gilchrist et al. 2005; Rasalato et al. 2010; Alves 2012; Thinley et al. 2019).

TEK and LEK have also been useful for obtaining new information on the distribution and abundance of species including the Caatinga howler monkey (*Alouatta ululata*), snub-nosed monkey (*Rhinopithecus strykeri*), forest elephant (*Loxodonta cyclotis*), and terrestrial tortoise (*Testudo graeca*) (Anadón et al. 2010; Rasalato et al. 2010; Chi et al. 2014; Freire Filho et al. 2018; Brittain et al. 2020). Nutrition, clothing, tools, medicine, magical and religious rituals are contexts where humans use primate parts (Alves 2012; Alves and Rosa 2012; Casanova et al. 2014; Peres 1990). For example, in popular medicine, humans have used howler monkey parts in northeastern Brazil to treat whooping cough, sore throat, and asthma to cure such illnesses, a person may drink water using the hyoid bone as a cup in a religious ritual (Alves et al. 2013). In Amazonian upland forest sites, large-bodied primates (i.e. *Alouatta*, *Ateles*, and *Lagothrix*) are an important source of meat for the local communities (Peres 1990). In some tribes of Ghana (Africa), both *Colobus vellerosus* and *Cercopithecus campbelli lowei* are considered children of the gods that protect the villages (Appiah-Opoku 2007; Alves et al. 2016b). In Guinea-Bissau, chimpanzees (*Pan troglodytes verus*) are considered distant family members and also blacksmiths that God punished because they did not rest on Sundays, and thus were condemned to live in the forest (Casanova 2008; Casanova et al. 2014).

The precarious socioeconomic conditions of northeastern Brazil, as shown by the municipal human development index (IPEA 2016), are in part responsible for local humans' regular use of wildlife, including primates (e.g., de Melo et al. 2014; da Silva Santos et al. 2019). Understanding how these humans use primates in northeast Brazil will help us in achieving one of the five aims of the Brazilian National Action Plan for the Conservation of the Primates of the Northeast—PANPriNE (federal decree Nº 242 of March 26, 2018). The aim focuses on characterising hunting and harvesting of the primates targeted by the action plan. Three of six targeted primates by the PANPriNE occur in our study areas: the Caatinga howler monkey (*Alouata ululata*), blonde capuchins (*Sapajus flavius*), and red-handed howler monkeys (*Alouata belzebul*). Other two species, not targeted by the action plan, also occur in the study sites: bearded capuchins (*Sapajus libidinosus*) and common marmosets (*Callithrix jacchus jacchus*). The International Union for Conservation of Nature (IUCN) categorises Caatinga howler monkeys and blonde capuchins as endangered (Fialho et al. 2021; Valença-Montenegro et al. 2021a, respectively). Red-handed howlers are classified as vulnerable (Valença-Montenegro et al. 2021c), bearded capuchins as near threatened (Martins et al. 2021), and common marmosets as a "least-concern" species (Valença-Montenegro et al. 2021b).

Here, we aimed to investigate the extent of human use of primates in northeastern Brazil. We sought to understand whether primates were hunted, consumed, and/or used as pets in the region. We also evaluated whether the region's socioeconomic profile influenced the use of primates by humans. We predicted that medium-sized primate species in the studied sites would be hunted for bushmeat, whereas small primates would be kept as pets. We also predicted that people living in more urbanised regions with better socioeconomic backgrounds would use primates in less contexts than people who live in poorer and less urbanised regions.

Methods

Studied sites

We carried out our study in three regions (Fig. 1), comprising three biomes (Caatinga, Cerrado, and Atlantic Forest) in northeastern Brazil.

Region 1 (Caatinga): the northwestern area of the State of Ceará, between the municipalities of Santana do Acaraú (3°27′ S, 40°12′ W) and the Ibiapaba mountain (4°17′ S, 41°5′ W) range, totaling 11 municipalities visited. Region 1 comprises flat areas (Caatinga shrub) and humid enclaves (humid forest enclaves). The humid enclaves are characterised by high altitudes (750–900 m), steep slopes, high rainfall (the annual mean above 1100 mm), low temperatures (24–26 °C), and excellent conditions for agriculture (Bragagnolo et al. 2017). Agriculture is the main activity in these regions: horticulture, coffee, rice, and sugarcane plantations (Bragagnolo et al. 2017). Livestock farming is present in the region on a smaller scale and is restricted to the flatter regions (Bragagnolo et al. 2017). Caatinga howler monkey, (common marmoset), and bearded capuchin occur in region 1.

Region 2 (Caatinga and Cerrado): the north-central area of the state of Piauí, between the municipalities of Castelo do Piauí (5°19′ S, 41°33′ W) and Valença do Piauí (6°24′ S, 41°44′ W). We sampled eight municipalities. The semiarid climate is typical of these regions (da Silva et al. 2017), where we encounter areas with semi-deciduous trees and dry forest areas (arboreal Caatinga), and

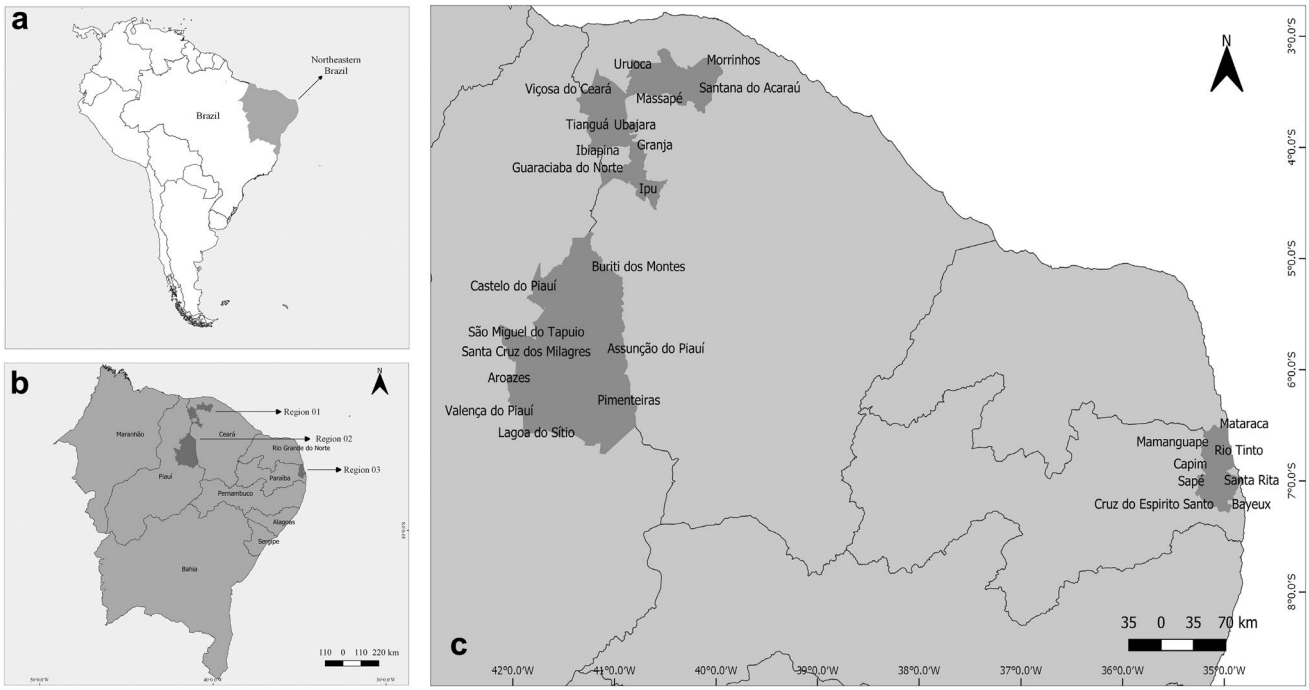

Fig. 1 Study areas. **a** Map showing the northeastern region of Brazil. **b** Location of the study areas inside northeastern Brazil: region 1 in the northwestern area of Ceará state in the Caatinga biome; region 2 in the north-central area of Piauí state in the Caatinga and Cerrado biomes; and region 3 on the northern coast of Paraíba state in the Atlantic Forest biome. **c** The municipalities that make up each region studied

some parts have typical Cerrado forest features (Freire-Filho personal observation). This region has high annual mean temperatures (28–30 ºC), low humidity (60–65%), high evapotranspiration (1400–1550 mm), high evaporation (2000–2500 mm), and low and irregular precipitation (annual mean 800–1000 mm) (Gomes et al. 2005). Although agriculture is also conducted in the region, livestock raising (goats and cattle) is the main activity. Caatinga howler monkeys, common marmosets, and bearded capuchins occur in region 2.

Region 3 (Atlantic Forest): the northern coast of Paraíba, between the municipalities of Santa Rita (7°8′ S, 34°57′ W) and Mamanguape (6°50′ S, 35°8′ W). Region 3 covers remnants of the Atlantic Forest, 'restinga' forest, and mangroves. The climate is tropical and rainy, with a short dry season. The average annual temperature is 25.5 ºC (23.7 ºC in July and 26.8 ºC in February). The average annual rainfall is 1725 mm; 86.2% of the total is concentrated between February and August, with December being the driest month (32 mm), and two peaks in May (289 mm) and July (255 mm) (Cunha et al. 2003). Sugar and alcohol agribusiness, mineral extraction, fishing, agriculture, and livestock are the main economic activities developed in the region (PTDRS 2010). Red-handed howler monkey, blonde capuchin, and common marmoset occur in region 3.

Survey methods

We conducted semi-structured interviews (Huntington 2000) in all three study sites because such a technique allows for flexibility in the conversation between the interviewer and the interviewee (Alves et al. 2014). This approach has been used in several ethnoprimatological studies investigating the attitudes and perceptions of humans towards primates (e.g., Nekaris et al. 2013; Casanova et al. 2014; Rocha and Fortes 2015; Torres Junior et al. 2016; Waters et al. 2019). We asked whether subjects wanted to participate in the present study, and confidentiality was guaranteed. Researchers only conducted interviews if the respondent verbally agreed and was comfortable participating in the study. Interviews started after we read a free consent term.

The semi-structured interviews initially took the shape of an informal conversation about the local fauna, and then we started focusing on primates. Questions focused on aspects related to the primates in the study sites (i.e., *S. flavius*, *A. belzebul*, *A. ululata*, *S. libidinosus*, and *C. jacchus*). Despite the format of an informal conversation, we were guided by a list of questions as detailed in Table 1. For instance, we first asked whether the respondent knew of hunting practices in the area (e.g., do people poach or kill monkeys here?/were or are monkeys hunted here?), and in the case of positive answers, we then asked for the reasons hunting occurred

Table 1 Primate use in three regions in northeast Brazil

Questions	Responses	Percentages of responses		
		Region 1 (Caatinga)	Region 2 (Caatinga/ Cerrado)	Region 3 (Atlantic forest)
Responses about hunting				
Do people poach or kill monkeys here?/were or are monkeys hunted here? (number of respondents: region 1 = 50; region 2 = 62; region 3 = 44)	Yes	48% ($n = 24$)	42% ($n = 26$)	90.9% ($n = 40$)
	No	52% ($n = 26$)	58% ($n = 36$)	6.8% ($n = 3$)
	I don't know	0% ($n = 0$)	0% ($n = 0$)	2.3% ($n = 1$)
What were or are monkeys hunted for? (region 3: 40 respondents)*respondents said more than one use	Eat	NA	NA	92.5% ($n = 37$)
	Sell	NA	NA	0% ($n = 0$)
	Pet	NA	NA	37.5% ($n = 15$)
	Other	NA	NA	0% ($n = 0$)
Which monkeys are poached, killed or caught? (number of respondents: region 1 = 50; region 2: = 62; region 3 = 40)	Bearded capuchin	100% ($n = 50$)	100% ($n = 62$)	NA
	Caatinga howler	34% ($n = 17$)	45% ($n = 28$)	NA
	Common marmoset	0% ($n = 0$)	0% ($n = 0$)	7.5 ($n = 3$)
	Red-handed howler	NO	NO	22.5% ($n = 9$)
	Blonde capuchin	NO	NO	30% ($n = 12$)
	I don't know	0% ($n = 0$)	0% ($n = 0$)	40% ($n = 16$)
Responses about using primates as food sources				
Do people eat monkeys? (number of respondents: region 1 = 50; region 2 = 62; region 3 = 37)	Yes	16% ($n = 8$)	16% ($n = 10$)	13.5% ($n = 5$)
	No	84% ($n = 42$)	76% ($n = 47$)	86.5% ($n = 32$)
	I don't know	0% ($n = 0$)	8% ($n = 5$)	0% ($n = 0$)
Have you eaten monkey meat? (number of respondents: region 1 = 50; region 2 = 62)	Yes	0% ($n = 0$)	10% ($n = 6$)	NA
	No	100% ($n = 50$)	90% ($n = 54$)	NA
Which monkeys were or are eaten by people in this region? (number of respondents: region 1 = 50; region 2 = 62; region 3 = 37)	Bearded capuchin	80% ($n = 40$)	76% ($n = 47$)	NO
	Caatinga howler	75% ($n = 37$)	60% ($n = 37$)	NO
	Common marmoset	0% ($n = 0$)	0% ($n = 0$)	0% ($n = 0$)
	Blonde capuchin	NO	NO	24.3% ($n = 9$)
	Red-handed howler	NO	NO	13.5% ($n = 5$)
	I don't know	0% ($n = 0$)	0% ($n = 0$)	62.2% ($n = 23$)
Which monkeys have you already eaten? (number of respondents: region 1 = 0 respondents; region 2: = 6 respondents)	Bearded capuchin	None	0% ($n = 0$)	NA
	Caatinga howler	None	100% ($n = 6$)	NA
	Common marmoset	None	0% ($n = 0$)	NA
Responses about using primates as pets				
Do people keep monkeys as pets at home? (number of respondents: region 1 = 50; region 2 = 62; region 3 = 40)	Yes	52% ($n = 26$)	63% ($n = 39$)	37.5% ($n = 15$)
	No	18% ($n = 9$)	10% ($n = 6$)	62.5% ($n = 25$)
	I don't know	30% ($n = 15$)	27% ($n = 17$)	0% ($n = 0$)
Do you have or have you ever had a monkey pet? (number of respondents: region 1 = 50; region 2 = 62)	Yes	6% ($n = 3$)	3% ($n = 2$)	NA
	No	94% ($n = 47$)	97% ($n = 60$)	NA
Which monkeys are kept as pets? (number of respondents: region 1 = 50; region 2 = 62; region 3 = 15)	Bearded capuchin	100% ($n = 50$)	100% ($n = 62$)	NO
	Caatinga howler	0% ($n = 0$)	3% ($n = 2$)	NO
	Common marmoset	100% ($n = 50$)	100% ($n = 62$)	53.4% ($n = 8$)
	Red-handed howler	NO	NO	0% ($n = 0$)
	Blonde capuchin	NO	NO	0% ($n = 0$)
	I don't know	0% ($n = 0$)	0% ($n = 0$)	46.6% ($n = 7$)

Table 1 (continued)

Questions	Responses	Percentages of responses		
		Region 1 (Caatinga)	Region 2 (Caatinga/ Cerrado)	Region 3 (Atlantic forest)
Respondents perceptions of primate threats and extinction				
Are monkeys facing extinction? (number of respondents: region 1 = 50; region 2 = 62)	Yes	80% (n = 40)	92% (n = 57)	NA
	No	0% (n = 0)	0% (n = 0)	NA
	I don't know	20% (n = 10)	8% (n = 5)	NA
Which monkeys are disappearing/facing extinction?(number of respondents: region 1 = 50; region 2 = 62). Has the number of monkeys (for each species) decreased?(region 3 = 44 respondents)	Bearded capuchin	0% (n = 0)	0% (n = 0)	NO
	Caatinga howler	100% (n = 50)	100% (n = 50)	NO
	Common marmoset	0% (n = 0)	0% (n = 0)	0% (n = 0)
	Red-handed howler	NA	NA	16% (n = 7)
	Blonde capuchin	NA	NA	25% (n = 11)
	I don't know	NA	NA	59% (n = 26)
Do you think hunting is a threat to the monkeys? (number of respondents: region 1 = 50; region 2 = 62)	Yes	80% (n = 40)	92% (n = 57)	NA
	No	0% (n = 0)	0% (n = 0)	NA
	I don't know	20% (n = 10)	8% (n = 5)	NA
What are the reasons for the decrease? (region 3 = 44 respondents)	Deforestation	NA	NA	61.4% (n = 27)
	Hunting	NA	NA	38.6% (n = 17)
Has the number of monkeys (for each species) increased? (region 3 = 44 respondents)	Blonde capuchin	NA	NA	0% (n = 0)
	Common marmoset	NA	NA	54.5% (n = 24)
	Red-handed howler	NA	NA	31.9% (n = 14)
	I don't know	NA	NA	13.6% (n = 6)
What are the reasons for the increase? (region 3 = 44 respondents)	Marmosets high reproductive rate	NA	NA	36.4% (n = 16)
	Red-handed howler:Guaribas Reserve creation	NA	NA	13.6% (n = 6)
	Gargaú Reserve creation	NA	NA	9% (n = 4)
	Hunting surveillance	NA	NA	20.5% (n = 9)
	Other	NA	NA	9% (n = 4)
	I don't know	NA	NA	11.5% (n = 5)
Respondent perception of humans–primates interactions				
Do people have a pacific or a conflicting interaction with the monkey? (we considered "pacific" when the human contemplates the animal or enjoys its vocalization in the wild or keeps the animal as a pet. We considered "conflicting" when the human hunt, chase and kill the animal). (Number of respondents: region 1 = 50; region 2 = 62; region 3 = 44)	Bearded capuchins:Pacific	6% (n = 3)	4% (n = 2)	NO
	Conflicting	94% (n = 47)	96% (n = 60)	NO
	Caatinga howler:Pacific	100% (n = 50)	100% (n = 62)	NO
	Conflicting	0% (n = 0)	0% (n = 0)	NO
	Common marmosets:Pacific	100% (n = 50)	100% (n = 62)	100% (n = 44)
	Conflicting	0% (n = 0)	0% (n = 0)	0% (n = 0)
	Blonde capuchin:Pacific	NO	NO	100% (n = 44)
	Conflicting	NO	NO	0% (n = 0)
Respondents perceptions of where to find the monkeys				
Where do you see monkeys? (region 3 = 44 respondents)(respondents could say more than one place)	Guaribas Reserve	NA	NA	59.1% (n = 26)
	Gargaú Private Reserve	NA	NA	100% (n = 44)
	Sugarcane plantation	NA	NA	59.1% (n = 26)
	Orchards	NA	NA	0% (n = 0)
	Backyards	NA	NA	50% (n = 22)
	Roads	NA	NA	6.8% (n = 3)

Table 1 (continued)

Questions	Responses	Percentages of responses		
		Region 1 (Caatinga)	Region 2 (Caatinga/ Cerrado)	Region 3 (Atlantic forest)
Where do you see caatinga howler monkeys? (number of respondents: region 1 = 50; region 2 = 62)	Forest	100% (n = 50)	100% (n = 62)	NO
	Plantations	36% (n = 18)	65% (n = 40)	NO
	Urban areas (e.g., roads, backyards)	0% (n = 0)	0% (n = 0)	NO
	Captive (e.g., houses)	0% (n = 0)	5% (n = 3)	NO
Where do you see bearded capuchins? (number of respondents: region 1 = 50; region 2 = 62)	Forest	100% (n = 50)	100% (n = 62)	NO
	Plantations	100% (n = 50)	100% (n = 62)	NO
	Urban areas (e.g., roads, backyards)	0% (n = 0)	0% (n = 0)	NO
	Captive (e.g., houses)	20% (n = 10)	0% (n = 0)	NO
Where do you see common marmosets? (number of respondents: region 1 = 50; region 2 = 62; region 3 = 44)(respondents could say more than one place)	Forest	100% (n = 50)	100% (n = 62)	9.1% (n = 4)
	Sugarcane plantations	0% (n = 0)	0% (n = 0)	0% (n = 0)
	Urban areas (e.g., roads, backyards)	76% (n = 38)	70% (n = 43)	6.8% (n = 3)
	Captive (e.g., houses)	20% (n = 10)	32% (n = 20)	50% (n = 22)
	I don't know	0% (n = 0)	0% (n = 0)	34.1% (n = 15)
Where do you see red-handed howler monkeys? (region 3 = 44 respondents)	Forest	NO	NO	68.2% (n = 30)
	Plantations	NO	NO	0% (n = 0)
	Urban areas (e.g., roads, backyards)	NO	NO	0% (n = 0)
	Captive (e.g., houses)	NO	NO	0% (n = 0)
	I don't know	NO	NO	31.8% (n = 14)
Where do you see blonde capuchin? (region 3 = 44 respondents) (respondents could say more than one place)	Forest	NO	NO	100% (n = 44)
	Sugarcane plantations	NO	NO	59.1% (n = 26)
	Urban areas (e.g., roads, backyards)	NO	NO	0% (n = 0)
	Captive (e.g., houses)	NO	NO	0% (n = 0)
	I don't know	NO	NO	0% (n = 0)

NA non-applicable for the study region (e.g., when questions were specific to one region and not the others), *NO* no occurrence in the study region (e.g., when a species does not occur in the region)

(e.g., what were or are monkeys hunted for?) and whether primates were among the hunted animals (e.g., which monkeys are poached or killed?). We would then ask whether people ate the meat of monkeys in the region. We recorded interviewees' answers and comments in field diaries, after which we transferred the information to spreadsheets to compute the frequency and percentages of responses, considering the number of respondents for each question. In northeastern Brazil, hunting is restricted to men (Souza and Alves 2014). Also, in Brazil, upon turning 18, a man is considered an adult and tends to perform outdoor activities (e.g., taking care of cattle and crops) (Souza and Alves 2014). For this reason we chose men over 18 years of age for interviews in regions 1, 2, and 3.

In both regions 1 and 2, the researcher RFF and a local field assistant conducted semi-structured interviews in Portuguese, and each interview lasted on average 20 min. We targeted men aged 18 years and older (ranging from 18 to 80 years) who lived near areas with natural vegetation and were more likely to be found on the road. Thus, the researcher approached people on roads near areas with natural vegetation. The researcher RFF and a local field assistant drove approximately 650 km in region 1 in August 2016 and 700 km in region 2 in January 2017. Each field expedition lasted 10 days, resulting in 50 interviews conducted in region 1 and 62 interviews conducted in region 2. Interviews initially also took the shape of an informal conversation about the local fauna so that we could perceive the overall interviewee's knowledge of the animals found in the region. For instance, we asked questions about specific species of mammals that we knew to occur in the region, and then we asked about the primate species living in the area.

In region 3, we interviewed two rural communities between April and July 2015. One community was located at a village adjacent to the Guaribas Biological Reserve, and the other was adjacent to the Engenho Gargaú Private Natural Heritage Reserve. The researcher CSSC conducted 44 semi-structured interviews in Portuguese in region 3, and each interview lasted on average 50 min. CSSC conducted the interviews at the respondents' homes. We also

targeted men between 18 and 80 years of age (farmers, ranchers, fisherman, and hunters).

We understand that it is challenging to as certain locals' impressions of hunting, mainly because they are often aware that there are penalties for killing wildlife in Brazil. Since researchers were going to ask questions regarding hunting wildlife, the interview took the form of an informal conversation so that the respondents did not feel intimidated or provide inaccurate information. Also, the researchers who interviewed the locals are native to the geographical areas where the interviews were conducted. They also never used any official government uniforms that could indicate they were conducting monitoring and inspections of the areas. The researchers' appearance and local accents potentially helped the interviewees to feel more relaxed about providing the requested information. Even though data must be treated with caution, the features mentioned above minimised potential biases in the responses to the interviews.

Analysis

We used descriptive statistics to show the information obtained from the interviews (Table 1). To evaluate whether the socioeconomic profiles of regions 1, 2, and 3 influenced the use of primates by humans in the areas, we compared the gross domestic product (GDP) of the regions using averaged data from 2010 to 2015, which were the years immediately preceding the data collection in all studied sites. We also compared the urbanisation of public roads (%), essential sanitation services (%), the municipal human development index (MHDI), human population density, and the human population size of the municipalities to profile regions 1, 2, and 3 for the year 2010. We obtained these data from the Brazilian Institute of Geography and Statistics (https://cidades.ibge.gov.br/), and we have detailed them in Table 2. To compare the three regions, we conducted Kruskal–Wallis tests followed by Dunn's post hoc comparisons. Significance was attained when $p < 0.05$.

Table 2 Socioeconomic aspects of the municipalities in the three studied regions

Regions	Municipality	Urbanization of public roads (%)	Essential sanitation services (%)	Municipal human development index (MHDI) ($)	Human population density (habitant/km^2)	Human population size
Region 1	Morinhos	0	21.4	1010.242	49.81	20,700
	Santana do Acaraú	5.6	33.3	1059.41	30.89	29,946
	Massapê	1.2	37.7	987.819	62.11	35,191
	Uruoca	5.1	23.1	1203.029	18.49	12,883
	Viçosa do Ceará	4.1	9	1090.189	41.90	54,955
	Tianguá	4.2	39.4	2048.89	75.80	68,892
	Ubajara	10.2	7.2	1713.652	75.50	12,883
	Ibiapina	2	17.4	1350.603	57.38	23,808
	Graça	0.7	5.8	969.9914	53.39	15,049
	Guaraciaba do Norte	5.5	7.6	1548.513	61.78	37,775
	Ipú	5.5	7.2	1362.923	64.03	40,296
Region 2	Castelo do Piauí	0.6	17	1302.878	9.01	18,336
	São Miguel do Tapuio	0.7	19.3	1012.264	3.48	18,134
	Pimenteiras	0	5.5	1016.736	2.57	11,733
	Valença do Piauí	1.9	5.3	1551.502	15.23	20,326
	Aroazes	0	1.4	1200.785	7.03	5779
	Buriti dos Montes	0	42.7	982.521	3.01	7974
	Santa Cruz dos Milagres	0.3	3.4	1271.371	3.87	3794
	Lagoa do Sítio	0	8.2	1092.997	6.03	4850
Region 3	Rio Tinto	14.5	26.6	42,057.65	49.42	22,976
	Mamanguape	3.9	8.3	93,526.67	124.23	42,303
	Santa Rita	3.6	21.1	391,013.7	165.52	120,310
	Bayeux	16.9	45.9	211,641.7	3,118.76	99,716
	Lucena	5.8	29.7	29,892.29	131.88	11,703
	Marcação	0	23.2	12,452.44	61.91	7609
	Baia da Traição	5.7	11.6	12,637.95	78.27	8012
	Mataraca	0	4.1	36,925.14	40.19	7407

Results

Primate use

We obtained reports from the local people about the occurrence of primate hunting in all three studied regions (region 1: 47%; region 2: 43%; and region 3: 90.9%) where primates are either used as pets (region 1: 52%; region 2: 63%; and region 3: 37.5%) or for meat consumption (region 1: 16%; region 2: 16%; region 3: 13.5%) (Table 1). During the informal conversation, the respondents also mentioned medicinal use in region 2, where three respondents said that people drink water using the Caatinga howler's hyoid bone as a cup to cure respiratory diseases. In region 3, answers related to hunting (90.9%) referred to the past (32 respondents) and the present (8 respondents). Thirty-two respondents said monkeys were eaten in the past, and five respondents said they are eaten currently (92.5% of the answers—Table 1). Twelve respondents reported that hunting is less frequent today than in the past. Thirteen respondents stated that hunting was performed for subsistence in the past, whereas 22 respondents said that hunting is currently performed for leisure purposes so that the primate meat is consumed as a snack.

The interviewees stated that bearded capuchins, Caatinga howler monkeys, and common marmosets are used as pets. In regions 1 and 2, 100% of respondents indicated that common marmosets and bearded capuchin are used as pets (Table 1), because they are funny and small (the latter related to marmosets only), gracious animals that behave like humans, and are seen as "family members". In region 3, 53.4% of respondents said that common marmosets are kept as pets, and 50% said that they see marmosets in captivity, such as in locals' houses (Table 1). Nine respondents said that common marmosets are kept at home as pets because they have a small body and would not be worth consuming due to the tiny amount of flesh.

In regions 1 and 2, all respondents mentioned that Caatinga howlers were disappearing from the forests (Table 1). Region 1 and 2, 80% and 92% of interviewees, respectively, said that hunting is a threat to the monkeys (Table 1). In region 3, people mentioned that the number of red-handed howler (16% of interviewees) and blonde capuchin (25% of interviewees) had decreased. They pointed out deforestation (61.4% of interviewees) and hunting (38.6% of interviewees) as reasons for the decrease. On the other hand, some interviewees indicated an increase in the number of red-handed howlers (31.9% of interviewees) and pointed out the creation of the Guaribas Reserve (13.6% of interviewees) and Gargaú Private Reserve (9% of interviewees) as well as hunting surveillance (20.5% of interviewees) as reasons for the increase (Table 1).

In both regions 1 and 2, bearded capuchins were also victims of retaliation by local communities. For example, 94% of respondents in region 1 and 96% in region 2 stated that bearded capuchins are chased away or killed when they approach crop fields (i.e., "conflicting interaction"). Furthermore, interviewees reported that bearded capuchins damage crops and waste the crop fruits when they arrive in large groups. In addition, 100% of respondents in regions 1 and 2 indicated pacific interactions with Caatinga howler monkeys and common marmosets (Table1).

Primate species were seen by respondents in several places in region 3, including people's backyards, sugar cane plantations, roads, and protected areas (also locally known as reserves). We found that 100% of the respondents reported having pacific interactions with blond capuchins and common marmosets (Table 1). We also found that 59.1% of the respondents reported that blonde capuchin monkeys visit sugar cane plantations. In addition, 6.8% of the respondents reported the presence of common marmosets in backyards, but they did not mention any damage caused by the marmosets in these places (Table 1).

Socioeconomic profiles of the three study regions

Human population density differed among the three regions (Kruskal–Wallis test: $H = 13.64$, $p < 0.05$). Based on post hoc tests, region 1 presented a higher human population density than region 2 (Dunn's post hoc test: $z = 3.12$, $p < 0.05$). Region 3 also had a higher human population density than region 2 (Dunn's post hoc test: $z = 3.33$, $p < 0.05$). We found no differences in the human population density between regions 3 and 1 (Dunn's post hoc test: $z = 0.46$, $p > 0.05$).

Resident population size differed among the three regions (Kruskal–Wallis test: $H = 7.79$, $p < 0.05$). Region 1 had higher resident population than region 2 (Dunn's post hoc test: $z = 2.76$, $p < 0.05$). There were no differences between regions 2 and 3 (Dunn's post hoc test: $z = 1.77$, $p > 0.05$) or between regions 1 and 3 (Dunn's post hoc test: $z = 0.85$, $p > 0.05$).

GDP varied among the three studied regions (Kruskal–Wallis test: $H = 16.40$, $p < 0.05$). Based on post hoc tests, the GDP of region 3 differed from that of regions 1 (Dunn's post hoc test: $z = 3.51$, $p < 0.05$) and 2 (Dunn's post hoc test: $z = 3.59$, $p < 0.05$), but regions 1 and 2 did not differ (Dunn's post hoc test: $z = 0.35$, $p > 0.05$).

We found differences between the urbanization of public roads among the studied regions (Kruskal–Wallis test: $H = 8.73$, $p < 0.05$). According to post hoc tests, both region 1 (Dunn's post hoc test: $z = 2.58$, $p < 0.05$) and region 3 (Dunn's post hoc test: $z = 2.59$, $p < 0.05$) had greater urbanization of public roads (%) than region 2. There was no difference between regions 1 and 3 (Dunn's post hoc test: $z = 0.21$, $p > 0.05$).

We found no significant differences in basic sanitation services (Kruskal–Wallis test: $H = 3.46$, $p = 0.1770$) or MHDI (Kruskal–Wallis test: $H = 3.38$, $p = 0.1842$) amongst the three study regions.

Discussion

Humans used primates in all three study sites in northeast Brazil for several purposes, including as a food source (subsistence and/or recreational snacks), for medicine, and as pets. As we predicted, the medium-sized *S. libidinosus*, *S. flavius*, *A. belzebul*, and *A. ululata* were targeted for meat by hunters in all three regions, potentially due to their larger body mass, which may represent a higher energy reward per hunted specimen (Peres 1990; Cullen et al. 2001; Rosin and Swamy 2013; da Silva Neto et al. 2017). In addition, the small-bodied common marmosets were targeted as pets in all three regions. Our second prediction, however, was refuted because we did not observe substantial differences in primate use between the studied regions despite presenting distinct socioeconomic profiles.

The behaviours of capuchin and howler monkeys in the wild may facilitate detectability by hunters. Bearded and blonde capuchins live in large groups ranging from 6 to 35 individuals (Bicca-Marques et al. 2006) and from 30 to over 160 individuals (Valença-Montenegro 2011; Andrade et al. 2020), respectively. Peres (1990) reported that large primates that live in large groups could have a high percentage of the total group members eliminated in a single encounter with hunters. On the other hand, the Caatinga and red-handed howler monkeys live in groups ranging from 7 to 10 individuals (Pinto and Roberto 2011) and from 6 to 16 individuals (Bonvicino 1989), respectively, but they produce very loud vocalisations that can be detected miles away. Such a powerful vocal feature could facilitate the localisation of howler monkey groups by hunters.

At the three study regions, local men reported that hunting of the four medium-sized primates occurred in the areas. Alves et al. (2016a) draw attention to population decline and local extinction of many medium-sized and large mammal species in northeastern Brazil due to hunting and habitat loss. Humans have hunted blonde capuchins in Brazil since the colonial period, as recorded in paintings dating from 1520 (Masseti and Veracini 2010). Thus, several populations may have already disappeared. Hunting also seems to be the main factor contributing to the local historical extinction of the Caatinga howler monkeys in many areas of Ceará (Freire Filho et al. 2018) and the red-handed howler monkey population at Paraiba (MMA/IBAMA 2003). When the Guaribas Biological Reserve was created in 1990 in region 3, the red-handed howler monkey population was locally extinct due to extensive habitat loss and hunting (MMA/IBAMA 2003). Four individuals were initially translocated to the reserve in 2000 (Porfirio 2005). In the 18 years of research and management actions carried out by the National Center for Primate Research and Conservation (CPB/ICMBio), 28 individuals (18 females and 10 males) were introduced to the reserve, and the estimated population was between 40 and 50 individuals (Valença-Montenegro et al. 2018).

In regions 1 and 2, the common marmoset and the bearded capuchin were reported as pets, whereas in region 3, only the common marmoset was reported as a pet. We suspect that smaller and diet generalist species are easier to keep in captivity than larger primates with a more restricted diet. Common marmosets were not hunted for feeding purposes in the studied sites, as we predicted. Interviewees reported that they are small animals, and thus the food reward for people is low. Nevertheless, in an Atlantic Forest patch about 60 km from region 3, Souza and Alves (2014) reported the use of common marmosets as a food source and pets. Common marmosets are frequently seen as pets in houses and markets in regions 1 and 2 (20% and 32% of 50 and 62 respondents, respectively) and kept at home as pets in region 3 (50% of 44 respondents). Marmosets were illegally trafficked in large numbers in the 1980s and 1990s, potentially due to their small size and charisma (Zanon 2020). Marmosets were also legally traded between 2006 and 2012, with several being exported to other countries between 1977 and 2013 (Fialho et al. 2016; Oliveira 2019). Marmosets are also often found in great numbers in government rescue centres in northeast Brazil due to the illegal pet trade (Nascimento et al. 2013). Even though the IUCN categorise common marmosets as a least-concern species (Valença-Montenegro et al. 2021a, b, c), the historical use of the species as pets and in biomedical studies warrants our attention to the need for preserving populations in areas of natural occurrence. Common marmosets were once endemic to northeast Brazil but were introduced in other areas of the country, such as Rio de Janeiro, negatively affecting local primates (Ruiz-Miranda et al. 2006).

Respondents reported no conflict with blonde capuchins in region 3, but they reported bearded capuchins as pests in regions 1 and 2. Even though such difference could be related to the different survey approaches (i.e., residence vs road interviews) and the presence of protected areas in region 3 but not in regions 1 and 2, we believe the different types of crops surrounding the three regions may play a major role in determining the conflicting interactions. The extent of primate crop-raiding is influenced by the primate species, type of plantation, planting patterns, and farming tradition (Hill 2018). Also, crop damage by primates depends on whether it happens on subsistence plantations or commercial plantations. Damage was perceived as economically higher and more conflicting in commercial plantations than in subsistence plantations in another area in northeast Brazil (Spagnoletti et al. 2016). In regions 1 and 2, crops

were usually small (a few hectares) and belonged to local farmers, whereas in region 3, the sugar cane plantations are large and belong to large companies. Bearded capuchins arrive at the crop fields in large groups, wasting most of the collected fruits and destroying the plantation. On the other hand, interviewees reported that the damage caused by blonde capuchins to sugar cane plantations was minimal. This feeling seems to be shared by landowners, who also reported minimal impact caused by the blonde capuchins in their plantations (Castro, personal communication). Blonde capuchins use the border of the plantations to collect only a few sugar cane stalks (da Silva 2019). Thus, the manner in which blonde capuchins feed on sugar cane does not damage the plantations or cause any significant economic impact.

The use of the Caatinga howler's hyoid bone to treat respiratory diseases was the only record for the use of primates as traditional medicine. Similar records were previously documented for other species of howler monkeys in a different part of northeast Brazil (Pinto and Roberto 2011; Alves et al. 2013, 2016a). However, Alves et al. (2016a) reported that the hyoid bone of howler monkeys is used in magic rituals to heal whooping cough. Although this sounds like a similar use of the hyoid bone (i.e., traditional medicine), the reports we obtained related to curing respiratory diseases without an apparent connection with magic rituals.

Despite legal restrictions imposed by the Brazilian government to prevent hunting, we learned from our interviews that locals hunt primates recreationally for snacks, for subsistence consumption, for medicine and pets, and to avoid crop-raiding in the northeast. Violation of the hunting restrictions results in fines ranging from R$500 (US$78) to R$5000 (US$780) (Article 29 of Federal Law 9605/98—Law of Environmental Crimes). Communities located around protected areas are often aware of the law but do not recognise the role of such areas in biodiversity protection and maintenance (Castro and Casanova 2018). We suggest that future environmental education actions in the studied areas should focus on (i) raising awareness among local people regarding the ecological importance of primates, (ii) providing alternatives to hunting whenever possible, and (iii) minimising conflicts. The involvement of locals may help in implementing effective conservation programs (Danielsen et al. 2010). A good example is Jane Goodall's successful program, which supports environmental awareness education campaigns connected to the local communities so that local people can benefit from preserving wildlife and maintaining a harmonious relationship with the ecosystem. The Brazilian National Center for Primate Research and Conservation (CPB/ICMBio), CSSC (Projeto Primatas do Litoral Norte), and BMB (Projeto Galego) carry out awareness actions in region 3, whereas RFF (Projeto Guariba) carries out environmental education actions in regions 1 and 2. Future awareness and environmental education actions could be developed together with the locals to increase outreach in the study regions.

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Declarations

Conflict of interest None.

Ethical standards This study agrees with the ethical code developed by the British Sociological Association for the conduct of interviews (https://www.britsoc.co.uk/media/24310/bsa_ statement_of_ethical_practice.pdf). The studies in region 1 and region 2 were endorsed by the MSc Programme in Conservation Biology, Faculty of Sciences, Lisbon University, Portugal. The study in region 3 was authorised by the Brazilian Environmental Agency (SISBIO/ICMBio:47436) and the Ethics Committee of the Federal University of Paraíba (1.531.237).

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