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MARIA GABRIELLA RUFINO MADRUGA

USO DE SÍTIO DE QUEBRA PELO MACACO-PREGO-GALEGO (*Sapajus flavius*) NA CAATINGA

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de mestre(a) em Biologia Animal.

Orientador(a): Prof. João Pedro Souza-Alves

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RESUMO

O macaco-prego-galego (*Sapajus flavius*) é uma espécie Ameaçada e endêmica do Nordeste do Brasil. Embora sua distribuição inicialmente estivesse restrita à Mata Atlântica, atualmente sabe-se da ocorrência de populações também na Caatinga, onde exibem o comportamento de uso de pedra como ferramenta. Esta dissertação teve como objetivo investigar o padrão de uso dessas ferramentas pelo macaco-prego-galego na Caatinga alagoana e compreender como características da paisagem local influenciam o reuso dos sítios de quebra. Durante dez meses de trabalho de campo, duas trilhas foram percorridas, resultando no mapeamento e quantificação de 215 bigornas e 247 martelos utilizados pelo macaco-prego-galego. Em média, as bigornas apresentaram um comprimento de 470 (± 57 cm) cm e largura de 600 (± 500 cm). Já os martelos, o comprimento médio foi de 91 (± 36 mm) cm, largura média 66 (±36 mm), espessura 41 (± 52 mm), e peso média de 337 (± 483 g). As bigornas foram significativamente mais compridas que os martelos, todavia não houve diferença significativa para a largura. A maioria dos restos de alimento utilizados pelo macaco-prego-galego encontrados nas bigornas foram classificados como antigos (91%); e as espécies mais comuns foram *Cnidoscolus quercifolius* (77,3%) e *Terminalia catappa* (22,7%). Os martelos utilizados para quebrar *T. catappa* apresentaram largura, espessura e peso significativamente maiores do que os usados para *C. quercifolius*. Para compreender o reuso dos sítios, foram delimitadas áreas de amostragem ao redor dos sítios a partir de 10 transectos medindo 50 m. Nestes, foram registradas a densidade de árvores (793,33 indivíduos/ha), área basal (20,54 m^2/ha), disponibilidade de frutos comestíveis no solo (média = 4 ± 7), pedras disponíveis no solo (média = 307 ± 172 un.) e distância de fontes de água (média = 181,6 ± 161,1 m). A abundância total de sítios reutilizados foi 72, com média de 2,05 ± 1,74 por área amostrada. Modelos Lineares Generalizados (GLM) revelaram que a área basal das árvores correlacionou positivamente com a abundância de sítios reutilizados. Portanto, áreas com árvores que apresentam uma alta quantidade de alimento disponível favorecem a abundância de sítios reutilizados pelo macaco-prego-galego. Esses resultados evidenciam que a estrutura da vegetação influencia diretamente o comportamento. Esse estudo fornece subsídios importantes para estratégias de conservação, destacando a relevância da estrutura da vegetação e da disponibilidade de recursos na manutenção do comportamento de uso de ferramentas pelo grupo de macaco-prego-galego na Caatinga.

ABSTRACT

The blonde capuchin monkey (*Sapajus flavius*) is an endangered species endemic to northeastern Brazil. Although its distribution was initially restricted to the Atlantic Forest, populations are now known to occur in the Caatinga as well, where they exhibit stone tool use behavior. This dissertation aimed to investigate the pattern of tool use by the blonde capuchin in the Caatinga of Alagoas and to understand how local landscape features influence the reuse of stone tool sites. Over ten months of fieldwork, two trails were surveyed, resulting in the mapping and quantification of 215 anvils and 247 hammers used by the blonde capuchin. On average, the anvils measured 470 (± 57 cm) in length and 600 (± 500 cm) in width. The hammers had an average length of 91 (± 36 mm), width of 66 (± 36 mm), thickness of 41 (± 52 mm), and weight of 337 (± 483 g). Anvils were significantly longer than hammers, although no significant difference was found in width. Most of the food remains found on anvils were classified as old (91%), with the most common species being *Cnidoscolus quercifolius* (77.3%) and *Terminalia catappa* (22.7%). Hammers used to crack *T. catappa* were significantly wider, thicker, and heavier than those used for *C. quercifolius*. To understand site reuse, sampling areas were established around the tool-use sites using ten 50-meter transects. Within these, the following were recorded: tree density (793.33 individuals/ha), basal area (20.54 m^2/ha), availability of edible fruits on the ground (mean = 4 ± 7), number of loose stones on the ground (mean = 307 ± 172 units), and distance to water sources (mean = 181.6 ± 161.1 m). The total number of reused sites was 72, with an average of 2.05 ± 1.74 per sampled area. Generalized Linear Models (GLMs) revealed that tree basal area was positively correlated with the abundance of reused sites. Therefore, areas with trees that offer a greater amount of available food favor a higher abundance of tool-use site reuse by the blonde capuchin. These results highlight that vegetation structure directly influences behavior. This study provides valuable insights for conservation strategies, emphasizing the importance of vegetation structure and resource availability in maintaining stone tool use behavior in blonde capuchin groups inhabiting the Caatinga.

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INTRODUÇÃO GERAL

A definição de comportamento abrange todos os movimentos realizados pelo animal em estado natural, desde ações evidentes até atividades sutis (Souto, 2003; Del-Claro, 2004). Trata-se de um conceito amplo, que pode ser analisado em diferentes níveis, desde indivíduos até populações, e em variados contextos, como ambientes naturais ou de cativeiro (Teixeira et al., 2018). Estudos comportamentais possibilitam a compreensão da adaptabilidade das espécies frente a mudanças ambientais, identificando fatores que influenciam seus padrões comportamentais e os possíveis impactos decorrentes dessas alterações (Thatcher et al., 2020).

Esse conceito de comportamento se estende ao uso de ferramentas, um exemplo notável de como a espécie se ajusta ao ambiente. Shumaker et al. (2011) descrevem a evolução da definição de uso de ferramentas, inicialmente visto como a utilização de um objeto externo para atingir um objetivo imediato, desde que manipulado. Com o tempo, a definição foi ampliada para incluir a manipulação de objetos inanimados visando modificar outros objetos, sendo consolidada para abranger tanto objetos fixos quanto não fixos, desde que manipuláveis. O uso de ferramentas envolve interações entre o indivíduo e o ambiente, com foco na capacidade do animal de ajustar e usar a ferramenta de forma eficaz para alcançar um objetivo.

A diversidade no uso de ferramentas entre espécies reflete as variações em suas necessidades e comportamentos, observadas em diversos grupos taxonômicos e em diferentes localidades. Na Austrália, golfinhos localizados na Baía Shark utilizam esponjas marinhas para forragear (Mann et al., 2008; Seed & Byrne, 2010). Entre as aves, o uso e a fabricação de ferramentas mais complexas são realizados por corvos da Nova Caledônia, que utilizam ferramentas feitas de galhos ou caules de folhas para auxiliar em seu forrageio (Bluff et al., 2010; Wimpenny et al., 2011). Além disso, invertebrados, como os polvos, também têm comportamentos que envolvem o uso de ferramentas. Como estratégia de defesa, o polvo listrado (*Amphioctopus marginatus*) pode usar cascas de coco como abrigo frente a ameaças (Finn et al., 2009). Entre os insetos, as fêmeas das vespas *Ammophila urnaria* e *Ammophila aberti*, ao capturar uma presa e enterrá-la no solo, usam uma pedra com o auxílio de suas mandíbulas para fechar o buraco (Brockmann, 1985).

Em primatas não humanos, em determinadas situações, soluções comportamentais flexíveis são necessárias, sendo o uso de ferramentas uma estratégia recorrente para a obtenção de objetivos específicos, incluindo contextos de alimentação e de interações sociais.

Em contextos alimentares, algumas espécies utilizam ferramentas para acessar recursos de difícil obtenção como, por exemplo, o uso de pedras para quebrar alimentos de casca dura, como sementes e frutos encapsulados, e o emprego de gravetos para sondar cavidades ou extrair presas ocultas, como insetos ou pequenos invertebrados (Valença et al., 2024; Gumert et al., 2009; Mannu & Ottoni, 2009; Mendes et al., 2015; Fragaszy et al., 2004; Sanz et al., 2004; Garber et al., 2012). Já em interações sociais, fêmeas em período proceptivo foram observadas arremessando pedras em direção a machos, comportamento que parece integrar seu repertório de sinalização sexual (Falótico & Ottoni, 2013). A escolha e aplicação dessas ferramentas variam conforme as condições ecológicas e os aspectos socioculturais de cada população, e essa variação, por sua vez, demonstra a diversidade funcional do uso de ferramentas e reforça seu papel adaptativo no comportamento de primatas. Além disso, a aprendizagem social constitui um fator crucial, pois permite que os indivíduos observem e reproduzam os comportamentos de outros membros do grupo, facilitando a transmissão de conhecimentos e habilidades entre gerações (Ottoni & Izar, 2008; Coelho et al., 2015).

No Brasil, exemplos de uso de pedra como ferramentas por macacos são frequentemente observados em ambientes semiáridos, como a Caatinga, onde a adaptação ao clima e à escassez de recursos é essencial para a sobrevivência (Rufino et al., 2025). A Caatinga é um bioma exclusivo do Brasil, caracterizado pelo clima semiárido e pela predominância de florestas secas e vegetação arbustiva (Tabarelli & Silva, 2003; Prado, 2003). A Caatinga enfrenta uma estação seca prolongada, com chuvas escassas e irregulares. Sua cobertura vegetal é formada por florestas de pequeno porte, com dossel descontínuo e folhagem decídua durante a seca. A flora e fauna possuem diversas estratégias adaptativas, como a perda de folhas para reduzir a evaporação, a conversão de folhas em espinhos e, para algumas espécies animais, a redução das atividades energéticas (Coe & Souza, 2014; Moura, 2004; De la Fuente et al., 2014). As principais famílias botânicas dominantes são Fabaceae, Euphorbiaceae, Malvaceae, Asteraceae e Cactaceae (Coe & Souza, 2014; Leal et al., 2005). Anteriormente vista como um bioma de baixa riqueza de espécies e endemismo, a Caatinga é hoje reconhecida por sua rica biodiversidade, incluindo diversas espécies endêmicas (Leal et al., 2005).

Diante dessas condições ecológicas, algumas espécies de primatas na Caatinga recorrem ao uso de pedras (e gravetos) como ferramentas como estratégias funcionais para superar limitações impostas pelo ambiente, facilitando a obtenção de recursos e contribuindo para sua sobrevivência. Apesar dos registros de uso de ferramentas por macacos-prego, ainda é pouco compreendido de que forma fatores ambientais se correlacionam com esse comportamento. Nesse contexto, partimos da hipótese de que o reuso de ferramentas por macacos-prego-galego (*Sapajus flavius*) não ocorre de maneira aleatória, mas é influenciado por características da paisagem que favorecem a recorrência desses eventos. Assim, este estudo busca compreender o padrão de uso e reuso de ferramentas nessa população, contribuindo para o avanço do conhecimento em ecologia comportamental, além de oferecer subsídios para a conservação de uma espécie criticamente ameaçada e do bioma em que está inserida.

OBJETIVOS

2.1 GERAL

Descrever o padrão de uso de ferramentas e investigar como as variáveis da paisagem influenciam no comportamento de reuso de ferramentas em um grupo de macacos-prego-galego em uma área da Caatinga alagoana.

2.2 ESPECÍFICOS

a. Investigar se as dimensões das ferramentas (martelos e bigornas) variam em relação ao uso pelos macacos-prego-galego;

b. Identificar os alimentos consumidos através do uso de pedra;

c. Caracterizar a área de estudo quando a sua composição florística e estrutura da vegetação;

d. Investigar a influência das variáveis da paisagem local (disponibilidade de frutos e pedras, estrutura da vegetação e proximidade de fontes d'água) na abundância de sítios de quebra reutilizados.

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CAPÍTULO 1: Where and how: stone tool sites of the Endangered *Sapajus flavius* in a Caatinga environment in northeastern Brazil

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Short title: Identifying and characterizing stone tool use sites

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Abstract

The blonde capuchin monkey (*Sapajus flavius*) was, until a few years ago, an endemic primate of the Atlantic Forest. Today, populations inhabit the Caatinga dry forest and these have been documented using stone tools to access encased foods. It is important to know the distribution of these sites and the characteristics of the stone tools to inform conservation actions for this primate in the Caatinga. To this end, we identified and characterized stone tool sites used by a group of blonde capuchin monkeys in the Caatinga dry forest of northeastern Brazil. For eight months, we walked two pre-existing trails to georeference the stone tool use sites, to measure the dimensions and weight of the anvils and hammerstones, and to identify the food items processed at the sites. A total of 215 anvils and 247 hammerstones were mapped. The anvils were significantly longer than the hammerstones, while there was no difference in width. Most food remains found on the anvils were old (*n*= 101; 91%). *Cnidoscolus quercifolius* (*n*= 85; 77.3%) and *Terminalia catappa* (*n*= 25; 22.7%) were most common among the plant species found on the anvils. The width, thickness, and weight of hammerstones used to crack fruits of *T. catappa* were significantly greater than those used to crack *C. quercifolius*. These results should be used as a baseline for the development of conservation actions for the species and habitat.

Keywords: Blonde capuchin monkey, percussive tool, processing sites, Caatinga

4.1 Introduction

Some animals use tools to search for and access food (Emery & Clayton, 2009; Mann & Patterson, 2012; Seed & Byrne, 2010). Non-human primates stand out as using a wide variety of tools across a variety of environments (Souto et al. 2011; Malaivijitnond et al. 2007; Sanz & Morgan, 2007). Stones or branches are mainly used to crack encased foods and plant probes are used to access invertebrate nests (Gumert et al. 2009; Mannu & Ottoni, 2009; Mendes et al. 2015; Fragaszy et al. 2004; Sanz et al. 2004; Ohashi, 2015). Although not exhibited by the majority of species, diverse species of primates use stone tools to access resources, from arid to coastal environments (Malaivijitnond et al. 2007; Barrett et al. 2018; Falótico et al. 2017; Spagnoletti et al. 2011; Valença et al. 2024; Luncz et al. 2020).

The sites where percussive stone tool use occurs, known as "tool use sites" or "processing sites," are identified by the presence of larger stones or logs (anvils) on the ground and smaller stones (hammers) (Visalberghi et al. 2007). Anvils can be identified by the presence of stones potentially used as hammers and food items processed on or near them, and sometimes by use wear such as pitting, from the cracking process with stones (Visalberghi et al. 2007; Ferreira et al. 2010). Tool use is habitual in some populations of bearded capuchin monkeys (*Sapajus libidinosus*) and individual blonde capuchin monkeys (*Sapajus flavius*) (Ottoni & Izar, 2008; Moura & Lee, 2004; Mannu & Ottoni, 2009; Souto et al. 2011). Within these species, the use of stones and probes has been documented for cracking encased food, digging tubers, flushing prey, and collecting termites (Ottoni & Izar, 2008; Moura & Lee, 2004; Mannu & Ottoni, 2009; Santos et al., 2010; Souto et al. 2011). The use of stones was documented mostly widely among bearded capuchin monkeys in the arid and semi-arid Caatinga and Cerrado-Caatinga ecotone (Moura & Lee, 2004; Mendes et al. 2015). While bearded capuchins are widely known for using stone as a tool to access encased food (Fragaszy et al. 2004; Ottoni & Izar, 2008; Falótico et al. 2024; Valença et al. 2024); blonde capuchin monkeys have been reported to do so in fewer published studies to date (Ferreira et al. 2010; Garcia et al. 2020; Lima et al. 2024).

The blonde capuchin monkey was rediscovered 18 years ago and was quickly included among the 25 most endangered primates of the world (Oliveira & Langguth, 2006; Mittermeier et al. 2012). Today, this primate is listed as Endangered on the IUCN Red List, mainly due to the reduction of forest cover (Valença-Montenegro et al. 2021). The distribution range of blonde capuchin monkeys was thought to be limited to the Atlantic Forest fragment located in the Pernambuco Endemism Center (Fialho et al. 2014). In this region, ecological and behavioral aspects of the species (Bezerra et al. 2014; Bastos et al. 2018; Lins & Ferreira 2019; Medeiros et al. 2019; Andrade et al. 2020) as well as its habitat (Guedes et al. 2023) are known. However, recent studies have documented the presence of blond capuchin monkeys in the Caatinga environment (Ferreira et al. 2010; Garcia et al. 2020; Martins et al. 2023). To date, data related to the population of blonde capuchin monkeys inhabiting the Caatinga are linked to the potential and use of stone tools (see Ferreira et al. 2010; Garcia et al. 2020; Lima et al. 2024), distribution range (Ferreira et al. 2010), and influence of size and protection of native forest on the local occupancy (Lins et al. 2022). Mapping and characterizing the stone tools and processing sites used by blonde capuchin monkeys are the first steps to know the pattern of this behavior for the species.

This study identified and surveyed the stone tool sites used by blond capuchin monkeys, *S. flavius*, in a Caatinga environment in northeastern Brazil. Specifically, we 1) described the dimensions of hammers and anvils used by blonde capuchin monkeys, and 2) compared the weight, thickness, length, and width of hammerstones used by blonde capuchin monkeys to crack, the two most commonly exploited foods found on the anvils. Finally, we compiled an initial list of plant species exploited by blonde capuchin monkeys with and without percussive tools. This study provides the first baseline for systematic behavioral studies of the species in the Caatinga environment, thus contributing to the goals of the National Action Plan for the Conservation of Northeastern Brazil.

4.2 Material and Methods

4.2.1 Study area

This study was conducted in an environment of Caatinga contained within of the Monumento Natural do Rio São Francisco - MNRF. This protected area is located in five municipalities - Piranhas, Olho D'água do Casado, Delmiro Gouveia, Paulo Afonso, Canindé de São Francisco - in the northeast of Brazil. The MNRF was created in July 2019 to conserve natural ecosystems of great ecological importance and scenic beauty, allowing scientific research and the development of environmental education activities, recreation in contact with nature and ecological tourism. This protected area includes approximately 27,000 hectares of Caatinga terrain along the São Francisco River. Within this protected area, pasture occupies 39.3% (equivalent to 320 km^2) due to the expansion of cattle ranching activities, while Caatinga terrain occupies 27.2% (approximately 221 km^2) (Lima et al. 2019). The region experiences a rainy season from May to June, with precipitation occurring primarily in May. Annual rainfall ranges between 500 and 700 mm (RADAMBRASIL, 1983). Local temperatures show minimal variations, with an annual average of 25°C, rising to over 27°C during the hottest months and falling to 20°C during the coldest months (INPE, 2001).

4.2.2 Data collection

The data were collected in an area located in the municipality of Delmiro Gouveia (9º 27' 35" S, 38º 01' 48" W). To map the stone tool use sites used by blond capuchin monkeys, we walked two pre-existing trails in the study area from November 2023 to May 2024. We spent six days each month on the ground examining lithic processing sites (see Falótico et al. 2024). These processing sites are identified by the presence of a flat surface used as a substrate for the processed encased food, referred to as "anvils," a stone with traces of use - such as marks or food remains attached - on the anvil, referred to as "hammers," and remains of the processed encased food on or near the anvil (Falótico et al. 2018). In this study, we only considered the food resources found on the anvils.

When a processing site was identified, we collected the geographic location using a handheld GPS (GPS Garmin Etrex), anvil size (length and width), hammer size (maximum length, width, and thickness), and weight (see Falótico & Ottoni, 2016), processed encased food, and its approximate age (fresh or old, based on color and integrity). We used two scales (model Pesola© 1,000 g and 5,000 g) to measure weight, calipers (to the nearest 0.1 mm) to measure length, and measuring tapes to measure length and distance greater than 15 cm.

We compiled a list of plant species used by blond capuchin monkeys with and without stone tools during the study period. To do this, we used the three sampling protocols. In the first protocol, we identified the food remains found at the processing sites. In the second, we used passive monitoring through camera traps. Thus, we randomly installed 16 camera traps (model Suntek HC-801A) to obtain behavioral, ecological, and ancillary data related to stone tool use by blonde capuchin monkeys. We installed the camera traps on the trunks of the trees, 30-40 cm above the forest floor. We programmed the traps to take photos (one photo) and videos (60 seconds) at 30-second intervals. The photos were taken at a resolution of 24MP, while the videos had a resolution of 1080 pixels. The sampling effort comprised a total of 3360 camera trap days where each day corresponded to 24 hours. Finally, in the third protocol, we used the ad libitum procedure (Altmann, 1974) in the presence of the blonde capuchin monkeys. We totalized 210 hours of fieldwork activities (walking on the trails and monitoring the anvil sites). In the final, we obtained ad libitum samples during 170 minutes of direct observation (7.41% of total time). We tried to identify food items that we saw monkeys eating. The processed and exploited foods were collected and identified by a local field assistant. When possible, fertile branches were collected for identification and deposited in the Geraldo Mariz Herbarium of the Universidade Federal de Pernambuco.

4.2.3 Data analysis

We considered each processing site as a sampling unit in our analysis. For the list of plant species exploited by blonde capuchin monkeys in the study area, we identified the food item exploited. We calculated descriptive statistics (mean and standard deviation) of anvil size (length and width), hammerstone size (length, width, and thickness), and weight for all anvils and hammerstones, and separately for those with remains of the two most commonly processed foods. To test the variation in the size of anvils and hammerstones, we used a generalized linear model (GLM) with the independent variables being tool type (anvil or hammer) and the dependent variables being stone length and width. To test whether the characteristics of hammers and anvils differed according to the two most commonly processed foods, we used GLMs to test the effect of the independent variables (encased-food type) on the dependent variables (hammer-stone tool dimensions). A gamma distribution for the dependent variable with a log link function was used for all of the above GLM tests. The assumptions of normal distribution and homogeneity of variance of the model residuals were verified using the DHARMa package (Hartig, 2022). Moreover, the coefficient of determination (McFadden's R-squared) was calculated for each model using the ISLR package (James et al. 2022).

Ethical notes

All contributors declared that the studies adhered to the legal requirements of Brazil, where we conducted the fieldwork. The study complied with the ethical requirements of the institutions and government concerned. The study adhered to the Code of Best Practices for Field Primatology of the American Society of Primatologists (https://www.asp.org/society/resolutions/EthicalTreatmentOfNonHumanPrimates.cfm) and of the International Primatological Society (www.asp.org/resources/docs/Code%20of_Best_Practices%20Oct%202014.pdf).

4.3 Results

During 42 days of fieldwork (November 2023 - May 2024), we walked 1.514 km along two pre-existing trails at MNRF (Figure 1). We identified 215 processing sites and 247 hammers (Figures 1 and 2, and Table 1). In overall terms of hammerstone dimensions, the mean values found were: width - 66 mm (± *SD* 36), length - 91 mm (± *SD* 36), thickness – 41 mm (± *SD* 52), and weight 337 g (± *SD* 483) (Table 1). Regarding the number of hammers found on the anvils, most of the processing sites presented only one hammer (n= 185; 86%), followed by two hammers (n= 24; 11.2%) and three hammers (n= 6; 2.8%). Generally, the anvils presented a mean length of 470 cm (± *SD* 57) and a mean width of 600 cm (± *SD* 500) (Table 1). When compared the dimensions between hammers and anvils using the GLM, we found variation in length (GLM: Chi-square = 47.0, df= 455, $p < 0.001$, $R^2 = 0.18$); however, we found no difference in width (GLM: Chi-square = 0.46, df= 455, $p = 0.443$, $R^2 = 0.002$).

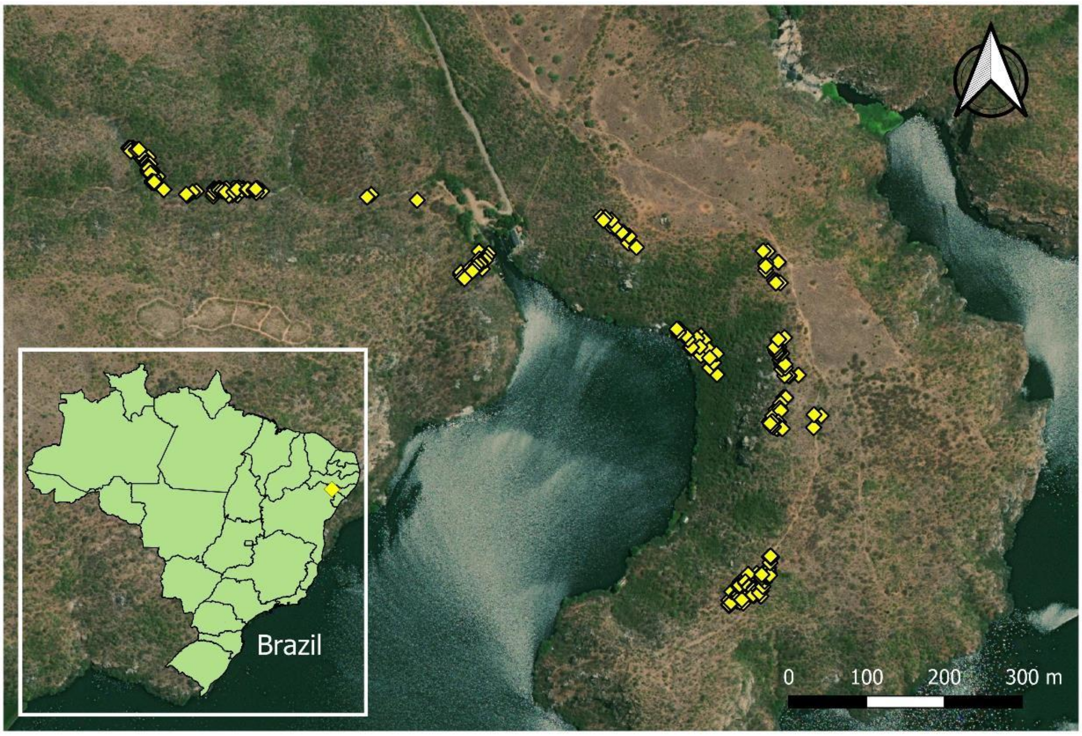

Figure 1. Map demonstring the locations of the processing sites (yellow) used by the blond capuchin monkeys.

Figure 2. Plate presenting photos related to (A) Fruit of *Cnidosculus quercifolius*, (B) Young individual of blond capuchin monkey using a stone tool to crack *C. quercifolius* fruit, (C) Processing site and hammerstone marked, (D) Processing site and hammerstone with the presence of flesh food remain of *C. quercifolius*, (E) Processing site and hammerstone with the presence of old food remain of *T. catappa*, (F) Young individual of blond capuchin monkey using a stone.

Table 1. Dimensions of anvils (i.e processing sites) and hammers used by blonde capuchin monkeys at Monumento Natural do Rio São Francisco. Mean ± standard deviation (maximum and minimum).

	Weight (g)	Length	Width	Thickness
Anvil (*N*= 215)	-	470 cm ± *SD* 570 (2.07 - 483)	600 cm ± *SD* 500 (6 - 64)	-
Hammer (*N*= 247)	337 ± *SD* 483 (20 - 4.300)	91 mm ± *SD* 36 (101 - 190)	66 mm ± *SD* 63 (21.3 - 130)	41 mm ± *SD* 52 (11 - 90)

To date, we have identified nine plant species utilized by blond capuchin monkeys (Table 2) using three sampling protocols. Four plants were exclusively recorded using camera traps, one exclusively for the *ad libitum* protocol, and one exclusively for food remains. Three plant species were recorded using at least two protocols (Table 2).

Five plant species were used exclusively with stone tools (Table 2). A total of 137 processing sites with the presence of food remains were recorded. Of these, 118 food remains (86.1%) were identified. Processing sites with only one type of food remains represented 90.5% (n= 124), while those with two or more types of food remains represented 9.5% (n= 13). We recorded 111 processing sites with the presence of only one type of food remains identified. Of these, 6.3% (n= 7) had only fresh food remains, 91% (n= 101) had only old food remains, and 2.7% (n= 3) had both fresh and old food remains. Among the plant species exploited with stone tools, fruits of *Cnidoscolus quercifolius* (faveleira, n= 85; 77.3%) and fruits of exotic *Terminalia catappa* (almonds, n= 25; 22.7%) had the highest number of food remains.

Table 2. List of plant species exploited by blonde capuchin monkeys at Monumento Natural do Rio São Francisco.

Family	Species	Native/Exotic	Part of fruit exploited	Exploited with stone tool
Euphorbiaceae	*Cnidoscolus quercifolius* Pohl	Native	Seed	Yes
Rosaceae	*Terminalia catappa* L.	Exotic	Seed	Yes
Malpighiaceae	*Malpighia emarginata* DC.	Exotic	Pulp	No
Bromeliaceae	*Bromelia laciniosa* Mart. ex Schult. & Schult.f.	Native	Leaf	No
	Neoglaziovia variegata (Arruda) Mez	Native	Leaf	No
Fabaceae	*Prosopis juliflora* (Sw.) DC.	Exotic	Pulp	No

	Cenostigma pyramidale (Tul.) Gagnon & G.P.Lewis	Native	Seed	Yes
Anacardiaceae	*Mangifera indica* L.	Exotic	Pulp	Yes
Cactaceae	*Tacinga inamoena* (K.Schum.) N.P.Taylor & Stuppy	Native	Pulp	Yes

The mean values for the dimensions (weight, length, width, and thickness, respectively) of hammerstones used to process *Terminalia catappa* fruits were 467 g (± *SD* 311), 116 mm (± *SD* 20), 77 mm (± *SD* 23), and 50 mm (± *SD* 16). In the case of *C. quercifolius,* the mean values of the dimensions recorded were 231 g (± *SD* 154), 97 mm (± *SD* 47), 62 mm (± *SD* 18), and 36 mm (± *SD* 10). In regards to anvils, the mean width and length of those utilized for processing *P. dulcis* were 91 cm (± *SD* 49) and 125 cm (± *SD* 126), respectively. For *C. quercifolius*, the mean width and length of the anvils were 64 cm (± *SD* 53) and 51 cm (± *SD* 37), respectively. The GLMs comparing the dimensions of the hammerstones used to crack the two most exploited encased foods demonstrated a significant effect on weight, width, and thickness. Thus, the hammerstones used to process *T. catappa* fruits were significantly larger than those used for *C. quercifolius* (Table 3 and Figure 3).

Table 3. GLM results for comparison of hammer dimensions across encased foods. Hammers were sampled at tool-use sites in Monumento Natural do Rio São Francisco. **p-values* in bold represent significant differences.

Dependent variable	Effect	Estimate	Chi-square	*df*	*p-value*
Weight	Intercept	0.004	11.393	73	0.001
	Encased-food	-0.002	-4.354		**0.001**
Length	Intercept	0.0102	18.863		0.001
	Encased-food	-0.0015	-1.599		0.114

Width	Intercept	0.0160	26.383	0.001
	Encased-food	-0.0031	-3.053	**0.003**
Thickness	Intercept	0.0276	25.020	0.001
	Encased-food	-0.0074	-4.309	**0.001**

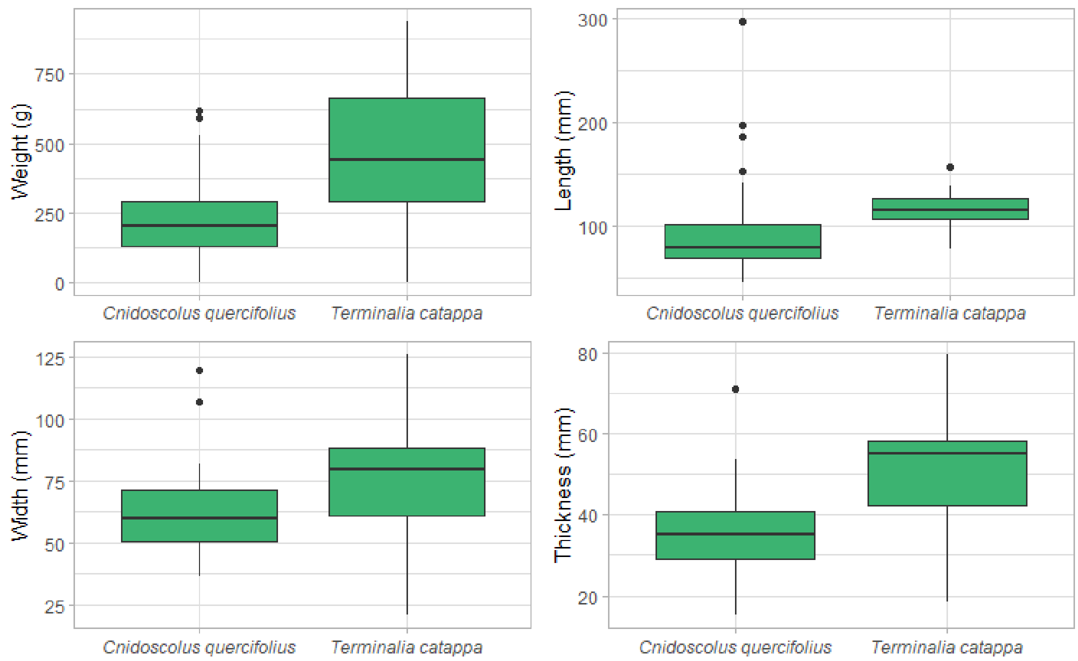

Figure 3 Box-plot represents the comparison between the dimensions (length, width, thickness) and weight of the hammerstone to crack *C. quercifolius* and *T. catappa*. The top and bottom lines of the box-plot represent the third and first quartile, respectively, and the central line inside indicates the median.

4.4 Discussion

Our study identified the stone tool use sites of blond capuchins in a Caatinga environment in northeastern Brazil and provided the first systematic database of this behavior for this threatened primate species. Most of the food remains found at the processing sites were old, and only two plant species – *T. catappa* and *C. quercifolius* - had encased food that was frequently cracked. Finally, the dimensions (width and thickness) and weight of the hammerstone used to crack *T. catappa* -encased food were greater than those of C. quercifolius. Unfortunately, it is not possible to compare our results with other studies of blond capuchin monkeys in both the Atlantic Forest and the Caatinga. However, a robust and reliable comparison can be made with studies focusing on the congeneric species, the bearded capuchin monkeys.

The dimensions of the anvils utilized by the blonde capuchin monkeys in the study area exhibited a comparable length to those observed in other species. However, the width of the anvils was found to be greater (Supplemental Material I). The weight of the hammerstones is consistent with the range observed in other species. For example, the bearded capuchin population at Serra da Capivara National Park utilized hammers with a mean mass of 202 g. Conversely, in the Chapada dos Veadeiros National Park, the hammerstones employed by bearded capuchin monkeys had a mean mass of 1672 g (Supplemental material I). With regard to the dimensions of the remaining hammerstones (length, width, thickness), the mean values recorded in the study area fall within the range observed for the genus as a whole. The characteristics of the anvils and hammerstones utilized by these primates are intrinsic aspects of each study area. The type of encased food processed, hardness, presence or absence of irritating stings, geomorphology of the region, and study period (rich or lean period of food availability) can exert a significant influence on this variable. Consequently, it is essential to conduct further research and analysis in other areas, specifically those that differ from the study area, to enhance the accuracy and precision of the mean values recorded in this study.

Following the typical pattern of stone tool use sites in capuchin monkeys (see Falótico et al. 2024), blond capuchin monkey tool sites were characterized by the presence of a hammerstone on the broad anvils. This kind of site persists in the environment, thus affording opportunities for practice and learning for naive individuals, in line with the niche theory (Laland et al. 2000). Stable anvil sites probably contribute to the maintenance of using stone hammers as a tradition in this group of blonde capuchin monkeys.

We noticed a difference in the majority (customary) of plant species identified and exploited by blond capuchin monkeys at the processing sites compared to other studies. Even with a wide distribution range of *C. quercifolius* throughout the Caatinga in northeastern Brazil (Maya-Lastra et al. 2024), it was only highly exploited by the blonde capuchins at this site. Similarly, the exotic *T. catappa* fruits were only cracked and ingested in this study. Although both blonde and bearded capuchin monkeys live in the Caatinga, the floristic and fruit diversity available at the sites appears to be a factor in the usual cracking in these areas. For example, bearded capuchin monkeys in Serra da Capivara showed a preference for Anacardium sp. nuts and Hymenaea sp. fruits (Falótico & Ottoni, 2016). In the Caatinga-Cerrado ecotone at Fazenda Boa Vista, Visalberghi et al. (2008, 2016) verified that the habitual consumption of Attalea barreirensis and Anacardium sp. was common. Also, Mendes et al. (2015) recorded the highest number of *Syagrus oleracea* cracked by bearded capuchin monkeys at Fazenda São Judas Tadeu, in the northern region of Goiás. Finally, Falótico et al. (2024) found that individuals of bearded capuchin monkeys inhabiting the Parque Nacional de Ubajara habitually cracked and exploited nuts from *Acrocomia aculeat*a and *Attalea speciosa*. Our study area is characterized as a Caatinga scrubland, with a low number and spacing of trees (unconnected canopy), a high density of shrubs, and without the presence of palm trees (i.e. *Syagrus* and *Attalea*) (J.P. Souza-Alves, pers. comm.). Thus, it is likely that habitat-specific conditions, such as floristic composition, are a driver of what capuchins must crack and exploit in these areas.

Exotic plant species are characterized by bearing fruit throughout the year to facilitate seed dispersal and avoid competition with native species (Wolkovich & Cleland, 2011). The consumption of exotic plant species by primates has been widely documented in the literature (see Oliveira-Silva et al. 2017; Medeiros et al. 2019; Wimberger et al. 2017; Eppley et al. 2017). To date, only the exotic cashew nut (Falótico et al. 2017; Visalberghi et al. 2021) has been cracked by bearded capuchin monkeys (Falótico et al. 2022). Exotic plants play a key role in the diet of native and exotic primate species (Oliveira-Silva et al. 2017; Lins & Ferreira, 2019; Medeiros et al. 2019). In this study, the consumption of *T. catappa* fruits usually occurred during the dry season. The seeds of this plant species are considered to be of high quality due to the high concentration of proteins, minerals, and vitamins (Tomishima et al. 2022). Although a systematic and seasonal evaluation is needed, the consumption of *T. catappa* fruits seems to favor energy acquisition during the driest and hottest period for blond capuchin monkeys.

Several studies have demonstrated differences in the stone tools used to crack encased foods. For example, the stones used to crack *A. aculeata* nuts were longer than those used for *A. speciosa* (Falótico et al. 2024). According to Ferreira et al. (2010), hammers used to crack Attalea nuts are almost twice as heavy as those used for *Syagrus*, and hammers used for Manihot are lighter than those used for the other two resources. In this study, we verified that the stones used to crack the *T. catappa* fruits were larger and heavier than those used to crack the *C. quercifolius* fruits. The main hypothesis to explain this difference is the hardness of the nuts. Heavier hammerstones were usually used to crack harder nuts (Spagnoletti et al. 2011;

Visalberghi et al. 2007, 2008). We do not yet have data on the resistance to fracture of the two species of fruits cracked most often by the monkeys in this study. Future studies related to the relationship between hammerstone weight and fruit resistance are in development.

It is not yet possible to suggest that the survival of the blonde capuchin monkeys in the Caatinga is associated with the use of stone tools to access encased foods. In Atlantic Forest fragments, groups of blonde capuchin monkeys exploit a variety of food resources, including fleshy fruits, leaves, seeds, invertebrates, and vertebrates (Lins & Ferreira, 2019; Medeiros et al. 2019). Additionally, bearded capuchin monkeys have ingested encased food throughout the use of stone tools, as well as other food items that do not require processing (dos Santos, 2015). Therefore, it is feasible that the blonde capuchin monkey group can exploit other foods to maintain the group. However, the high frequency of consumption of exotic almonds (*T. catappa*) by the studied blonde capuchin monkeys can support the nutritional capacity of the species during a drought period.

4.5 Conclusion

This study provides the first comprehensive data on cracking sites and type, and condition of the food items cracked by the Endangered blond capuchin monkeys inhabiting an area of the Caatinga. Here it was possible to understand that the behavioral pattern observed for the species is similar to another capuchin species, even though the study area is located at 532 km of distance (Lima et al. 2024). Similar to other populations of *Sapajus*, the observed pattern of processing sites should contribute to the maintenance of stone tool use in this primate. A novel aspect appears to be the strong influence of habitat characteristics on the plant species cracked by blond capuchins. Habitat analysis as well as niche and habitat modeling of these plant species need to be implemented in these studies to understand the distribution pattern of these species in the Caatinga biome and their potential driver on the cracked food. Furthermore, we presented a preliminary list of plant species ingested with and without stone tools, highlighting the high rate of the exotic *T. catappa*. In addition to the previous knowledge of the plant species used by this primate, such a record should contribute to specific actions for the conservation of these plant species aimed at reducing the potential negative effects on the diet of blond capuchin monkeys. Finally, our study presents a baseline for the development of conservation actions for the species, habitat, and behavior through monitoring of these sites for the manager of the protected area, reducing the logging of plant species cracked, and carrying out environmental activities with the local community to demonstrate the importance of this cycle (primate - habitat - culture).

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4.7 Supplemental Material

Table I. Comparison between blonde capuchin monkeys studied at the Monumental Natural Rio São Francisco and capuchin monkey populations studied in different sites and biomes concerning dimensions of the tool utilized to process encased foods. *Numbers presented only for the weight of the hammers and the area of the anvil

				Stone tool average (mean ± *SD*)						
				Anvil		Hammer				
Site	Study duration	Biome	Species	Width (cm)	Length (cm)	Weight (g)	Length (mm)	Width (mm)	Thickness (mm)	Source
Monumento Natural Rio São Francisco	**10 months**	**Caatinga**	***S. flavius***	**470 ± 570**	**600 ± 500**	**337 ± 483**	**91 ± 36**	**66 ± 63**	**41 ± 52**	**Present study**
Alagoas*	7 months	Caatinga	*S. flavius*	**-**	**-**	475 ± 142	**-**	**-**	**-**	Lima et al. (2024)
Ubajara	12 months	Caatinga	*S. libidinosus*	378 ± 224	643 ± 364	1142 ± 718	141 ± 87	94 ± 25	61 ± 18	Falótico et al. (2024)
Serra da Capivara	>10 years	Caatinga	*S. libidinosus*	-	-	202 ± 209	740 ± 280	470 ± 170	350 ± 110	Falótico & Ottoni (2016); Mannu & Ottoni (2009)
Serra Talhada*	15 months	Caatinga	*S. libidinosus*	-	-	396 ± 559	-	-	-	Moraes et al. (2014)
Serra das Confusões	2 years	Caatinga/Cerrado	*S. libidinosus*	309 ± 183	449 ± 256	316 ± 254	96 ± 30	56 ± 15	33 ± 11	Falótico et al. (2018)
Chapada dos Veadeiros	5 months	Cerrado	*S. libidinosus*	315 ± 176	499 ± 270	1672 ± 1051	152 ± 41	102 ± 26	74 ± 63	Falótico et al. (2022)
Fazenda Boa Vista*	>10 years	Cerrado-Caatinga ecotone	*S. libidinosus*	-	-	1168 ± 489	-	-	-	Visalberghi et al. (2007)

CAPÍTULO 2: The basal area of the tree explains the abundance of stone tool sites reused by blond capuchin monkeys in a seasonally tropical dry forest in Brazil

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Abstract

Behaviour flexibility in primates is widely known. However, the role of local landscape metrics on the use of stone tools remains poorly understood. Therefore, we tested whether the distance from water sources, the availability of edible nuts and stones on the ground, and the density and basal area of the trees can influence the abundance of stone tool sites reused by blonde capuchin monkeys. A total of 238 trees were measured in the area. The area exhibited a density of 793.33 individuals/ha and a base area of 20.54 m²/ha. A total of 53 edible nuts (4 ± 7) and 3,078 stones (307 ± 172) were recorded as available on the ground during the study period. The total number of reused sites was 72 (2.05 ± 1.74). Distances to water sources were measured on 35 occasions (181.6 ± 161.1 m). GLM revealed a positive correlation between the basal area of the trees and the abundance of stone tool sites reused by blonde capuchin monkeys within the study area. In this sense, understanding of the manner in which habitat has shaped the behavioural pattern of a species is essential for the implementation of functional measures aiming at the conservation of the species.

Key words: Adaptability, behavioural ecology, Caatinga, local landscape metrics, *Sapajus flavius*

5.1 Introduction

A comprehensive understanding of animal behaviour is a prerequisite for the development of effective conservation strategies for species. Behavioural studies offer valuable insights into a number of key areas, including demography, life history, activity patterns (such as food and habitat preferences), and social interactions[1,2,3,4]. This set of information is fundamental to the formulation of functional measures for the preservation of biodiversity[5,6,7,8] mainly when associated with modification in the environment. By examining how species adapt and respond to changes in their environment, it is possible to identify and comprehend the factors that influence their behavioural patterns and their impacts on them[9]. This knowledge is crucial for providing data for short-medium (e.g., creation of protected areas) and long-term (e.g., fostering the database of action plans) actions aimed at ensuring the protection of species populations in their natural habitats.

The behavioural flexibility of certain species can be observed in their responses to alterations in the surrounding environment at varying scales. For non-human primates (hereafter primates), for example, this flexibility is crucial to regulate foraging, resource exploitation, displacement, and communication strategies[10,11,12,13]. On a regional scale, forest cover has had a positive influence on the diet and behaviour of the spider monkey (*Ateles geoffroyi*) in Mexico[14]. Furthermore, cuxiús (*Chiropotes sagulatus*), which inhabit small forest fragments in the Brazilian Amazon, have been found to exhibit a restrictive diet due to the limited number of plant species present in these areas[15]. On the local scale, primates exhibit a range of behavioural patterns[16,17,18]. For instance, the selection of habitat by a group of squirrel monkeys (*Saimiri*) was found to be contingent on the plant community in the study area[19]. Furthermore, movement strategies of five primate species were found to vary according to the availability of resources[17]. Finally, individuals of long-tailed macaques (*Macaca fascicularis aurea*) in the Ao Phang-Nga National Park utilised stone tools to crack oil palm nuts in response to anthropogenic change in the area[20]. Moreover, a population of common long-tailed macaques (*Macaca fascicularis fascicularis*) exhibited an adaptive response to food shortages, triggered by a decline in tourism, by utilising stone tools[21]. It is therefore imperative to study behavioural flexibility at all scales and in all behaviours, in order to gain insight into the role of habitat effects on primates.

It is established that certain primate species employ tools for a variety of behavioural purposes[22,23]. To date, the ability to use stone as a tool to access food resources has been observed in nine species of primates[24,25,26,27,28,29,30,31,32,33,34,35]. This behaviour plays a pivotal role in the maintenance and survival of species[36,37,21], as it is cultural and transmitted from generation to generation[38,39,40,41]. The transmission of this behaviour appears to be more pronounced when the frequency of use and reuse of stone tool sites is high[42,43,44,45]. From an archaeological perspective, the frequency of reuse of stone tool sites can be linked to their archaeological signature[46]. Consequently, the higher the frequency of use of a given site for activities that leave traces, the more pronounced and visible the signature becomes. Consequently, the frequency of reuse of these sites becomes more evident. In this context, the application of archaeological methods to study the stone tool use in primates allows for the exploration of how environmental variables shape this behaviour, for example, through the analysis of traces, such as use marks on stones (pitting, flakes, polishing, and percussion fractures), wear patterns, and food fragments. These traces can provide insights into the persistence, changes, and variations in technological behaviour over time[47,48], contributing to the understanding of the ecological and behavioural dynamics of primates[49,50].

There is a paucity of studies that consider local ecological conditions as an influencing factor in the reuse of stone tool sites by primates. For example, in a study conducted with chimpanzees (*Pan troglodytes verus*), Almeida-Warren et al.[51] found that the reuse of stone tool sites was attributed to the abundance of stones available on the ground and the proximity of nesting sites. Furthermore, the availability and distribution of food resources within the home range, and the presence of specific plant species, also appear to influence the reuse of sites by chimpanzees[52]. In the case of groups of bearded capuchin monkeys (*Sapajus libidinosus*) inhabiting arid environments in Brazil, such as seasonally tropical dry forest, also called Caatinga, the use of specific sites is linked to low altitudes, an abundance of forest cover, and proximity to food sources[53,54,55,56]. Furthermore, in such an arid environment, the presence and proximity to water sources may influence the foraging strategy employed by *S. libidinosus*[57,58], due to the necessity of hydration or thermoregulation. Consequently, the distribution of water sources can be a critical resource for the optimal movement and landscape use by capuchin monkeys.

The use of stone as a tool by Endangered blonde capuchin monkeys (*Sapajus flavius*) in the Caatinga dry forest has recently been documented. In addition to recording the event[30], the sites were mapped, the stone tools were characterised, a list of plant species consumed was presented, and the most exploited foods were identified[59]. There is a scarcity of studies on the blonde capuchin monkey in the Caatinga. Currently, the following studies have been published: Ferreira et al.[60] and Martins et al.[61] on distribution; Garcia et al.[62] on traces of tool use; Lima et al.[30] on the use of stone as a tool; and Lins et al.[63] on occupancy models. It is therefore necessary to gain a deeper understanding of the behavioural aspects of the species, including the influence of local ecological factors - local landscape metrics - on the pattern of use of stone tool sites.

As demonstrated in the preceding section, recent literature concerning the reutilisation of stone tool use sites by primates has considered the frequency (i.e. number of reutilisation events) as a predictor variable. It is imperative to verify the frequency of these events in view of the behavioural and ecological patterns that have been demonstrated, as well as the potential effect on the cultural transmission of behaviour among individuals within a given group[44,45]. However, the abundance of stone tool use sites reused by primates was not considered a significant predictor variable until today. The quantification of the abundance of these sites, in addition to their relationship with local environment parameters, is also expected to contribute to our understanding of behavioural and cultural transmission issues.

Therefore, in this paper, we aimed to study the abundance of stone tool sites reused by a group of blonde capuchin monkeys in an area of Caatinga dry forest in Alagoas, northeastern Brazil. In light of the aforementioned considerations, we will hypothesize that local landscape metrics, including distance to water sources, the availability of edible nuts and stones on the ground, tree density, and tree basal area, may exert an influence on the abundance of stone tool sites reused by blonde capuchin monkeys within the study area. We tested three predictions regarding the relationship between the abundance of reused stone tool sites and local landscape metrics, where i) the abundance of reused stone tool sites should be positively correlated with proximity to water sources, ii) the high availability of edible nuts and stones on the forest floor should positively affect the abundance of reused stone tool sites, and iii) the high density and basal area of trees should be positively correlated with the low abundance of reused stone tool sites.

5.2 Results

5.2.1 Characterization of the study area

A total of 238 trees were measured within the study area and were grouped into four families, nine genera, and 10 species. Fabaceae exhibited the highest richness (n = 4), followed by Cactaceae and Euphorbiaceae (both n = 2), and Combretaceae (n = 1). The highest number of tree species were observed within the study area for *Cenostigma nordestinum* Gagnon & G.P. Lewis (n = 122), followed by *Mimosa* sp. 1 (n = 44), and *Cnidoscolus quercifolius* (n = 26). The area exhibited a density of 793.33 individuals/ha and a basal area of 20.54 m²/ha. In each transect, the mean tree density was 10.0 ± SD 0.3 individuals/ha (range: 9.2–10.1), the mean basal area was 9.3 ± SD 3.3 m²/ha (range: 4.58–14.31), and the mean height was 4 ± SD 3 m (see Supplementary Table S1 for more details).

5.2.2 Abundance of reused stone tool sites

A total of 296 stone tool sites were recorded during the 10-month data collection period. Of these, 47 sites (15.9%) were identified as reused by blond capuchin monkeys in the study area (Fig. 1). It is worth noting that, although the number of reused sites was 47, the frequency of reuse varied, with some sites being reused more than once within the same month. This pattern resulted in a total of 72 reuse records over the course of the study (2.05 ± SD 1.74; range: 1–10).

Figure 1. Location of the stone tool sites – used and reused – by the blonde capuchin monkey group during the study period. This figure was created using the QuickMapServices version 0.19036 plugin from QGIS version 3.32.3 (https://qgis.org).

5.2.3 Local landscape metrics

A total of 53 edible nuts were recorded as available on the ground throughout the study period. A transect analysis revealed that the mean number of edible nuts on the ground was 4 ± SD 7 (range: 0 – 23). The availability of stones on the ground was evaluated by counting a total of 3,078 stones distributed along the transects, resulting in an average of 307 ± SD 172 (range: 58 – 547). Distances to water sources were measured on 35 occasions, according to the reuse of the sites. The mean distance within the transects was 181.6 ± SD 161.1 m (range: 15.7 m - 514.64 m).

5.2.4 Influence of local landscape metrics on the abundance of stone tool sites reused

The model that included the tree density and basal area of the trees was the best-fitted model based on the AICc (Supplementary material Table S2). The GLM demonstrated that an increase in the basal area of the trees observed in the transects was positively associated (R^2 = 0.16) with the abundance of stone tool sites reused by blonde capuchin monkeys within the study area (Table 1). The results of the model were corroborated by the differences observed for each metric (tree density: LRT: df = 33, deviance = 1.408, p = 0.235; tree basal area: LRT: df = 32, deviance = 4.3129, p = 0.037). The comparison of this model with the null model was significant (LRT: df = 2, deviance = 5.721, p = 0.057) (Supplementary material Table S3).

Table 1. GLM results for the relationship of local landscape metrics (predictor variables) and the abundance of the stone tool site reused by blonde capuchin monkeys. Std. Error = Standard Error, *df* = Degree of freedom. Intercept represents the abundance of stone tool use sites reused when the tree basal area is zero.

Predictor variables	Estimate	Std. Error	*df*	*p-value*
Intercept	-9.128	8.046	34	0.256
Tree density	0.918	0.797		0.249
Tree basal area	0.067	0.032		**0.037**

5.3 Discussion

This study presents the floristic and structural composition of a Caatinga dry forest in which the Endangered blonde capuchin monkey is present. Fabaceae were found to exhibit the greatest species richness, with *C. nordestinum* representing the most abundant species in the area. Furthermore, the study area is characterised by the presence of trees that are, on average, relatively short and thin, yet exhibit a high density. Furthermore, the number of stone tool sites reused within a given area was identified, representing approximately one-third of the total recorded. Additionally, the local landscape was characterised, in which the amount of edible nuts present on the ground throughout the study period was low, whereas the availability of stones on the ground for potential use as hammers was high. The distance between the reused stone tool sites and the nearest water source was less than 20 m. Finally, it was determined that the basal area of the trees is a positive influencing factor in the abundance of reused stone tool sites. Consequently, an increase in the availability of food in the canopy of the trees results in a corresponding increase in the number of sites reused by the blonde capuchin monkeys within the study area. Albeit the relationship found between the predictor and response variable is weak, our findings are significant and robust; however, it is essential to consider the role of habitat in the tool-using behaviour of blonde capuchin monkeys within the context of specific habitats.

The findings of our study indicated that the size of the basal area of the trees recorded throughout the study area had a positive effect on the abundance of anvils reused by blonde capuchin monkeys. Trees with a larger basal area are indicative of greater productivity and food availability due to their positive relationship with crown size[64]. A high concentration of available food resources on a given site tends to attract a larger number of primates[65]. This appears to result in an increase in the number of anvils used, which in turn may result in an increase in the number of traces (i.e. marks or food remains) left at the sites. In this sense, the creation of a favourable environment for the reuse of these anvils is facilitated, both by the same individual and by other members of the group. This increase in opportunities, due to the high abundance of anvils, occurs through the construction of a niche. In this niche, when individuals use the stone tool sites, they leave what may be termed “signatures”. These comprise the marks of use and, in some cases, the tools that were used, making the sites attractive to other individuals in the group[46]. Nevertheless, the reuse of the site may also be associated with the nature of organic anvils and the development of holes in the anvil that facilitate its use by capuchins[66,67]. Furthermore, this dynamic is crucial for the perpetuation of the cultural tradition of tool use among younger individuals[68] by fostering heightened social interactions within the group. It is also important to mention the importance of scrounging opportunities, observational learning, and individual exploratory behaviours in capuchin monkeys[44,69,70,71] in social learning in capuchins.

The observed lack of influence of the tree density and nut availability variables on the ground on the abundance of reused sites can be explained by the intrinsic characteristics of the study area and the behaviour of the primate in obtaining the resource. The tree density variable provides insight into the distribution of species within the study area[72]. In areas of high tree density, it is possible to predict that a particular tree species will have grouped distribution[73]. Consequently, the species in question exhibits a greater concentration of food sources in a given location. For the blonde capuchin monkey, a high density of trees within a site may act in a positive way with respect to the concentration of food, thus leading to a high abundance of sites. However, the two tree species most exploited by the primate, *C. quercifolius* and *Terminalia catappa*[59], exhibited low density values (see Supplementary Table S1) compared to other species. For example, within the study area, only three individuals of exotic *T. catappa* were recorded, in contrast to the high density of *C. nordestinum* present in all transects.

The presence of fallen nuts may be associated with the nut-gathering behaviour of the individuals within the studied group. This observation challenged the previous assumption that the nut was collected from the ground. The utilisation of camera traps to monitor mammals within the designated study area during the period of this study permitted the verification of the retrieval of nuts directly from the canopy trees by individuals of blonde capuchin monkeys, and their subsequent transportation to the anvils on the forest floor. This behaviour indicates a preference for fresh, intact nuts that have not yet fallen to the ground. In the case of the *S. libidinosus* groups studied in the Serra da Capivara and Ubajara National Parks in Brazil, the behaviour exhibited in obtaining the resource depends on its quality. For example, the macaúba nuts (*Acrocomia aculeata*) exploited by *S. libidinosus* when ripe were collected while still in the canopy; however, when dry, they were obtained from the ground (T. Falótico, personal communication). Furthermore, some plant species used as a food source by primates exhibit a ballochoric dispersal mode, whereby seeds are expelled from the endocarp. This mode of dispersal reduces the number of whole nuts available on the ground, thereby reducing the attractiveness of sites based on the low availability of whole nuts lying on the ground. Also, this behaviour forces individuals to venture into the canopy tree to access the food resource.

There is a paucity of studies that relate local landscape metrics and tool use in primates. However, an understanding of the manner in which the habitat has shaped the behavioural pattern of a species is essential for the implementation of functional measures aimed at its conservation. In light of the findings presented here, it seems reasonable to consider the implementation of enforcement measures aimed at reducing indiscriminate logging of trees in the region for the production of charcoal and use as firewood. Furthermore, the high abundance of goats and cattle can strongly contribute to mortality and the reduction of seedling survival in the area[74]. Maintaining the arboreal community, particularly those species exploited by blonde capuchin monkeys, will contribute to reproductive aspects (high birth rates and low mortality rates) and survival of individuals (high seed consumption, lipid-rich food) during the short rainy season (3–4 months). Furthermore, the utilisation of camera traps is proposed as a supplementary approach for the monitoring of site reuse. This method has been proven to be both efficient and non-invasive in the collection of behavioural data over time[75], owing to its continuous image capture capability. The revelation of patterns of site use and the provision of objective information regarding the frequency and dynamics of reuse are key advantages of this technique. Thus, a suitable and robust management in this area should mitigate the harmful effects of actions. Furthermore, the preservation of the habitat's characteristics ensures the maintenance of the cultural practice of stone tool utilisation. This consequently permits younger individuals to survive and remain in the area, while also maintaining the species' tool-using culture. The analysis of traces of tool use has been demonstrated to facilitate the preservation and comprehension of how stone tool-using animals adapt to ecological changes over time. This is of particular importance for threatened species, such as the blond capuchin monkeys[76]. Archaeological sites utilised by capuchin monkeys have already been documented, thus underscoring the necessity for further exploration of this approach.

5.4 Methods

5.4.1 Study Area and subjects

This study was carried out in a Caatinga environment inserted within the limits of the Monumento Natural do Rio São Francisco - MNRF (9º 27' 35" S, 38º 01' 48" W) (Fig. 2). This protected area is located in five municipalities - Piranhas, Olho D'água do Casado, Delmiro Gouveia, Paulo Afonso, Canindé de São Francisco - in the northeast of Brazil. The MNRF was created in July 2019 to conserve natural ecosystems of great ecological importance and scenic beauty, allowing scientific research and the development of environmental education activities, recreation in contact with nature and ecological tourism. This protected area includes approximately 27,000 ha of Caatinga along the São Francisco River. Within this protected area, the pasture area occupies 39.3% (equivalent to 320 km^2) due to the expansion of cattle ranching activities, while the Caatinga vegetation occupies 27.2% (approximately 221 km^2)[77]. The region experiences a rainy season of only two months (May to June) and a dry and hot season of 10 months. Annual rainfall ranges between 500 and 700 mm[78]. Local temperatures show minimal variations, with an annual average of 25°C, rising to more than 27° C during the hottest months and falling to 20° C during the coldest months[79].

The blonde capuchin monkey group monitored was composed of up to 21 individuals with varied sex-age classes[80]. The male-female ratio is 1.3:1, and adult:juvenile ratio is 1:1.2[81]. Unfortunately, until the present study we do not have a more detailed information on the monitored group. However, we have an excellent database to, in the future, present a new and singular information on the density, group composition and birth seasonality.

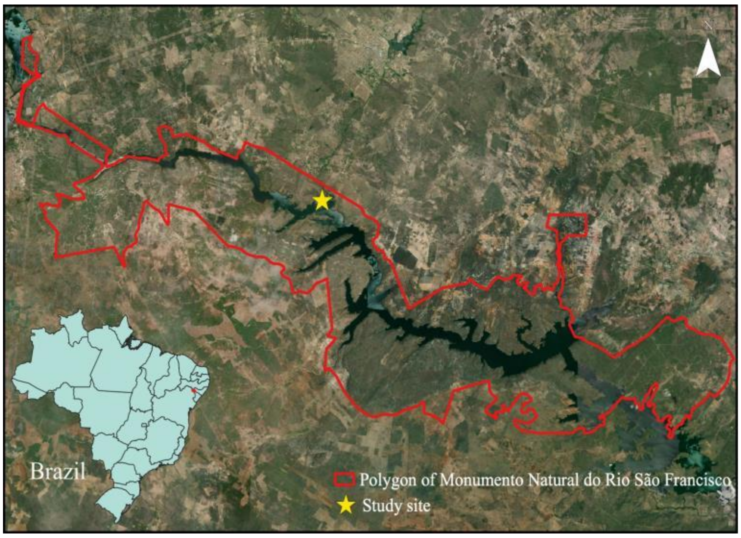

Figure 2. Location of the study site in the limit of the Monumento Natural do Rio São Francisco, northeastern Brazil. This figure was created using the QuickMapServices version 0.19.36 pluing from QGIS version 3.32.3 (https://qgis.org).

5.4.2 Data Collection

Data collection was carried out in a Caatinga area within the municipality of Delmiro Gouveia from November 2023 to August 2024, spanning a total of 10 months. During the course of this period, we conducted six-day fieldwork expeditions per month for active data collection, including visits to monitored sites and the recording of new sites, resulting in a total of 60 days of fieldwork. We employed a mixed approach for data collection, using the method of indirect observation of stone tool sites and an ecological approach with transect and quadrat methods[82] (Supplementary material Figure S1). The initial stage of the investigation involved an assessment of the presence of stone tool sites within the study area. The following three criteria were adopted for the purpose of qualifying a stone tool site: firstly, the presence of an anvil, which is typically a larger stone that is positioned on the ground; secondly, the presence of a hammerstone – a smaller stone – that is positioned on top of anvils; and thirdly, the presence of use marks on hammerstones that are caused by friction during use. Anvil and hammerstone sites must also be associated with processed food remains on or around them[83]. In this study, only inorganic anvils and hammerstones were considered. We established a 50-metres transect for each area that covered the sites. A fixed point was established at 10-metre intervals along each transect (n = 10), resulting in a total of six points. At each of these points, a quadrat was established with a radius of 3 metres (n = 60). Within each quadrant, data specific to the stone tool sites, as well as ecological and general vegetation data, were collected (see below for further details).

The geographical coordinates of the anvils were determined using a handheld GPS (Garmin Etrex GPS model). Furthermore, the anvils and hammers were marked with permanent chalk or pen to facilitate identification over time and prevent loss or duplication of information. Ecological data, including the availability of edible nuts and stones on the ground, was also collected. Furthermore, the geographical coordinates of each site were recorded and imported into QGIS version 3.32.3, where the minimum distance to the watercourses found each month was calculated.

5.4.2.1 Characterization of the Vegetation

To characterise the vegetation present across stone tool sites, a transect was established as a reference for sampling. At each fixed point, measurements were taken at 10-metre intervals using the nearest-neighbour method[72]. This procedure involved measuring the diameter at ground level (dgl) and visually estimating the height of the trees (only by JPS-A) at the shortest distance from the fixed point. The methodology proposed by Rodal et al.[84] was adapted, where we established a dgl <5 cm as inclusion criterion, and only live trees were considered. Given the distinctive characteristics of Caatinga vegetation, which exhibits nonlinear stems with numerous branches close to the ground, we employed the following approach for trunk: if a common base was identified, it was measured; otherwise, each trunk was measured individually[84]. At the end of the data collection process, it was feasible to obtain measurements for 238 trees (one of the quadrants was situated in an area without vegetation on one side, making it impossible to gather two samples). From these data, we were able to determine the floristic composition of the study area and the parameters associated with the structure of the vegetation, including relative abundance, relative density, relative dominance, and basal area. The density and basal area of the trees in each transect were employed as proxies for the distribution of food sources and food availability, respectively[64], to ascertain their impact on the abundance of reused stone tool sites.

5.4.2.2 Sampling of edible nuts and stones on the ground

To evaluate the accessibility of edible nuts and stones at ground level, quadrants were used at fixed points. We visually counted the number of edible nuts and stones on the ground within a radius of 3 metres. Given that the number of edible nuts on the ground is subject to change on a monthly basis[85], a monthly count was carried out throughout the study period (10 months). This was achieved by enumerating the nuts that were deemed to be in good condition (i.e., nuts able to be consumed) within a radius of 3 metres of each fixed point. To avoid jeopardising future availability, no resources were opened or manipulated. With regard to the stones on the ground, only those of an inorganic nature that possessed the potential to be utilised as hammers were considered. We counted all stones that met the previously established dimensions (337 g ± SD 483: see[37]). The counting was performed only in the first month (November 2023), under the assumption that the availability of stones in each area where stone tool sites are concentrated does not vary monthly.

5.4.2.3 Presence of water source

In this study, the term “water” is defined as any source of water - fixed, perennial, or ephemeral - located within or in the immediate vicinity of the study area. This included riverbanks, lakes, perennial and ephemeral ponds, and small reservoirs. During the study period, we recorded the geographical coordinates of the water sources using a handheld GPS. To avoid the inclusion of multiple instances of the same pond, we established a distance of 5 metres between each recorded water source, ensuring independence. To identify the riverbanks, we used satellite imagery from Google Earth within the QuickMapService tool in QGIS. We imported all the locations where the water source was present into QGIS, and the distance between these locations and the points of tool usage was subsequently extracted. We calculated the Euclidean distance using the Measure Line tool within the QGIS.

5.4.3 Data Analysis

The initial approach involved the consideration of each transect as a sampling unit (n = 10) to characterise the vegetation. The values for relative density, relative frequency, relative dominance, basal area, and importance value index were extracted for each transect using FitoCom version 1.7 (https://higuchip.shinyapps.io/FitoCom/). All plants were identified at the species or genus level, and their names were confirmed using Flora e Funga do Brasil[86].

To determine the impact of local landscape metrics on the abundance of reused stone tool sites, we defined a site as reused if it exhibited an indication of use (i.e., presence of food remains) in the months following its initial identification. Consequently, we conducted monthly visits to each site containing stone tool sites previously utilised by blonde capuchin monkeys. The inspection of all sites was conducted on a single occasion during the study period. In order to ensure the identification of reuse in the subsequent month, the sites (anvils and hammerstones) were marked and numbered with yellow crayons during each visit, and any food remains present were removed in order to avoid a biased sample on the sites reused. This facilitated the identification of any new traces (i.e., food remains) found, thereby determining the reuse in the following month. The abundance of stone tool use sites reused was based on the number of anvils reused each month during the study period. In the event of a site being reused on multiple occasions within a single month, it was counted only once. If reuse occurred in the subsequent month, it was recorded as a new reuse event. Only sites with a monthly reuse frequency of at least once were included in the subsequent analysis. In this context, the transect was considered the appropriate sampling unit.

We run Generalised Linear Models (GLM) with the Poisson distribution and the *log* link to examine the effects of predictor variables (number of edible nuts and stones on the ground, distance to water sources, tree density, and basal area) on the abundance of reused stone tool sites in each month (response variable). Due to their high values, the distance of the variables from the water source and the number of stones on the ground were transformed using the square root[87]. We evaluated the multicollinearity of predictor variables in each model to identify those with a variance inflation factor (VIF) > 2 as correlated[88]. Only the full model demonstrated multicollinearity among predictor variables (i.e., distance to water sources and number of stones on the ground). Thus, this model was not used for the interpretation of the result. In order to verify the correlates of the abundance of stone tool use sites reused with the predictor variables (see above), GLM models were run with all combinations possible of predictor variables. Model support was then assessed through their AICc (*Akaike's Information Criterion*) corrected for small samples[89], which is an indicator of the best model fit. We calculated the AICc for model comparisons using the *MuMIn* package, and focused our discussion on the model that yielded the lowest AICc. The data from the selected model was found to be normally distributed and homogeneous according to the KS, outliers, and dispersion tests ($p < 0.05$) (Supplementary material Figure S2). Furthermore, the model did not exhibit overdispersion or potential inflation by zeros within the response variable (Supplementary material Figure S3). We performed significance tests for each one of the models considered, as well as each predictor variable within the selected model. To assess the significance of the full models, we ran Likelihood Ratio Tests (LRT) using the *anova* function, which compared each model to a corresponding null model from which all fixed effects were excluded[90]. Also, the significance of each predictor variable within the selected model was assessed using the LRT test.

All statistical analyses were performed in RStudio version 2024.04.2-764, using R version 3.6.0+[91]. A statistically significant result was identified when the p-value < 0.05. For the statistical test, we used *DHARMa*, *lme4*, *ggplot2*, and *car* packages. We extracted descriptive statistics, including maximum and minimum values, mean, and standard deviation for each variable.

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5.7 Author Contribuitions

MGR and JPS-A: design the experiment and acquisition of data; JPS-A performed the statistical analysis; MGR wrote the initial draft of the manuscript. JPS-A supervised and revised the manuscript.

5.8 Supplemental Material

Table S1. List of plants (genera or species) and families identified and collected in the study area with the blonde capuchin monkey group at Delmiro Gouveia, northeastern Brazil, and data related to vegetation structure

Family/Species	# individual	Relative density	Relative dominance	Relative frequency
Cactaceae				
Cereus sp.	7	2.94	2.62	10.2
Pilosocereus pachycladus	7	2.94	0.81	10.2
Euphorbiaceae				
Cnidoscolus quercifolius	26	10.9	7.64	14.2
Jatropha sp.	18	7.56	1.73	14.2
Fabaceae				
Amburana cearensis	8	3.36	2.43	10.2
Bauhinia sp.	3	1.26	0.87	4.08
Cenostigma nordestinum	122	51.2	54.5	20.4

Mimosa sp. 1	44	18.4	5.4	10.2
Mimosa sp. 2	2	0.84	0.68	4.08
Combretaceae				
Terminalia catappa	1	0.42	23.3	2.04

Table S2. Results of the AICc-Based Model Selection of the GLM for the predictors of stone tool site reused by blonde capuchin monkeys.

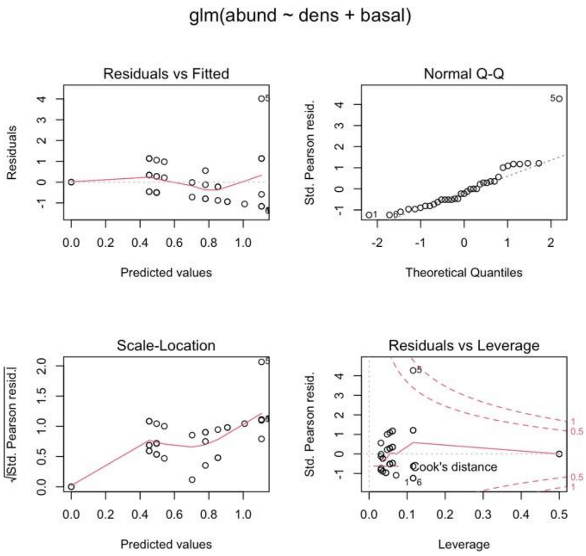
Model	df	AICc
~ dist + fruit + hammer + dens + basal	34	127.569
~ fruit + hammer + dens + basal	33	109.090
~ hammer + dens + basal	33	107.568
~ fruit + dens + basal	34	124.232
~ dens + basal	34	105.906

Table S3. Likelihood ratio test results of the Full-Null model comparisons of the site selection models.

Model	Resid. df	Resid. Dev	df	Deviance	p
~1 (Null model)	34	35.055			
dist + fruit + hammer + dens + basal	34	26.355	5	8.699	0.127
fruit + hammer + dens + basal	34	26.418	4	8.636	0.070
hammer + dens + basal	34	27.155	3	7.899	**0.048**
fruit + dens + basal	34	28.685	3	6.370	0.094
dens + basal	34	29.334	2	5.721	**0.057**

Figure S1. Map with the location of the transects across the study area.

Figure S2. Figures demonstrating the assumption of the selected model in relation to residuals.



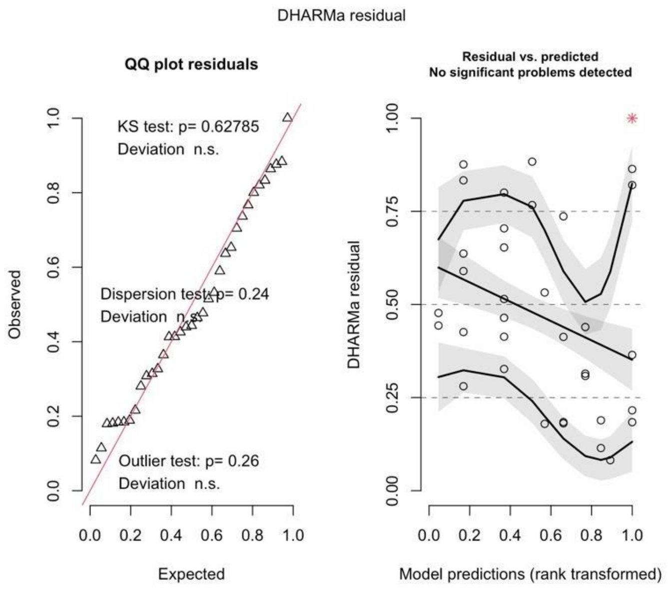


Figure S3. Figure demonstrating the assumption of the selected model in relation to overdispersion.

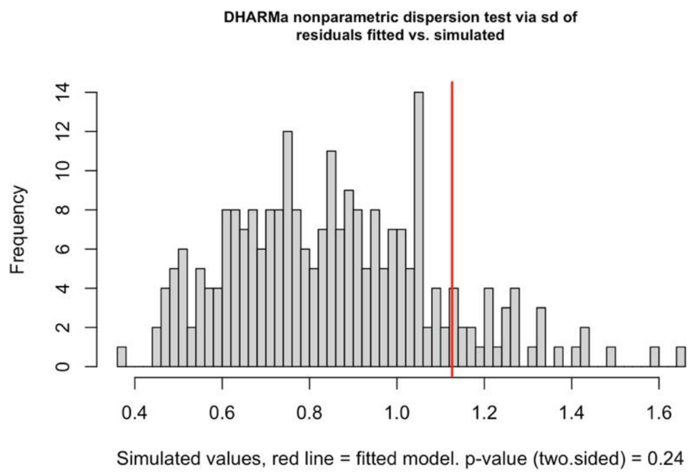


Table S4. Database used to obtain the results related to vegetation structure from the study area.

Site	Individual	Family	Genera	dgl	Height
SQ1	1	Fabaceae	Mimosa sp1	13.85	6
	2	Fabaceae	Mimosa sp1	6.21	4
	3	Fabaceae	Mimosa sp1	7.96	4
	4	Fabaceae	Mimosa sp1	14.8	7
	5	Fabaceae	Mimosa sp1	5.89	4.5
	6	Fabaceae	Mimosa sp1	8.28	5
	7	Fabaceae	Mimosa sp1	9.39	6
	8	Fabaceae	Mimosa sp1	16.4	6
	9	Fabaceae	Mimosa sp1	10.5	5
	10	Fabaceae	Mimosa sp1	5	4
	11	Fabaceae	Mimosa sp1	6.52	4
	12	Fabaceae	Mimosa sp1	5	3
	13	Fabaceae	Mimosa sp1	5.73	5
	14	Fabaceae	Mimosa sp1	11.78	5
	15	Fabaceae	Bauhinia	13.21	5
	16	Fabaceae	Mimosa sp1	11.62	5
	17	Fabaceae	Cenostigma	5.09	4
	18	Fabaceae	Bauhinia	21.33	7
	19	Fabaceae	Mimosa sp1	20.06	7
	20	Fabaceae	Cenostigma	10.82	7
	21	Fabaceae	Mimosa sp1	5.41	4
	22	Fabaceae	Mimosa sp1	7.64	6
	23	Fabaceae	Mimosa sp1	12.1	7
	24	Fabaceae	Cenostigma	12.1	7
SQ2	25	Fabaceae	Cenostigma	10.5	5
	26	Fabaceae	Cenostigma	10	4
	27	Fabaceae	Cenostigma	11.2	4
	28	Fabaceae	Cenostigma	9.5	3

	29	Fabaceae	Mimosa sp1	8.6	5
	30	Fabaceae	Cenostigma	9	4
	31	Fabaceae	Mimosa sp1	11.2	4.5
	32	Fabaceae	Mimosa sp1	9	5
	33	Fabaceae	Mimosa sp1	11.5	3
	34	Fabaceae	Mimosa sp1	7.5	3
	35	Fabaceae	Mimosa sp1	6.7	5
	36	Fabaceae	Mimosa sp1	10.7	4
	37	Fabaceae	Amburana	10	4
	38	Fabaceae	Mimosa sp1	7.9	5
	39	Cactaceae	Cereus	26.5	6
	40	Cactaceae	Cereus	10.5	5
	41	Fabaceae	Mimosa sp1	13	5
	42	Fabaceae	Mimosa sp1	6.9	5
	43	Fabaceae	Mimosa sp1	7.5	5
	44	Fabaceae	Mimosa sp1	7.8	5
	45	Rosaceae	Prunus	135	11
	46	Fabaceae	Cenostigma	19	3
SQ3	47	Fabaceae	Cenostigma	24	4
	48	Euphorbiaceae	Jatropha	6	4
	49	Fabaceae	Cenostigma	28.6	5
	50	Fabaceae	Bauhinia	7.5	5
	51	Fabaceae	Cenostigma	7	5
	52	Fabaceae	Cenostigma	30.4	5
	53	Fabaceae	Cenostigma	8.7	4
	54	Fabaceae	Cenostigma	55	3
	55	Fabaceae	Cenostigma	12.3	8
	56	Fabaceae	Mimosa sp1	6.3	5
	57	Fabaceae	Cenostigma	23.8	6
	58	Fabaceae	Mimosa sp1	9	5
	59	Fabaceae	Mimosa sp1	6.2	3
	60	Fabaceae	Cenostigma	19.2	5

	61	Fabaceae	Cenostigma	11.4	5
	62	Fabaceae	Cenostigma	10.8	6
	63	Fabaceae	Cenostigma	9.8	5
	64	Fabaceae	Mimosa sp1	15.3	5
	65	Fabaceae	Cenostigma	10.7	5
	66	Fabaceae	Cenostigma	6.2	4
	67	Fabaceae	Cenostigma	18	6
	68	Fabaceae	Cenostigma	6.6	5
	69	Fabaceae	Cenostigma	5	4
	70	Fabaceae	Mimosa sp1	9.2	5
SQ4	71	Fabaceae	Cenostigma	7	5
	72	Fabaceae	Cenostigma	8.5	4
	73	Fabaceae	Cenostigma	11.4	3
	74	Fabaceae	Cenostigma	7.9	4
	75	Fabaceae	Cenostigma	10.5	5
	76	Fabaceae	Cenostigma	18.5	5
	77	Fabaceae	Cenostigma	5.4	4
	78	Fabaceae	Cenostigma	21.2	5
	79	Fabaceae	Mimosa sp1	15.3	7
	80	Fabaceae	Mimosa sp1	9	6
	81	Fabaceae	Cenostigma	13	5
	82	Fabaceae	Cenostigma	6.8	4
	83	Fabaceae	Amburana	14.3	5
	84	Fabaceae	Mimosa sp1	5	6
	85	Fabaceae	Cenostigma	13.5	6
	86	Euphorbiaceae	Cnidoscolus	6.8	3
	87	Fabaceae	Cenostigma	20	5
	88	Fabaceae	Mimosa sp1	6.7	6
	89	Fabaceae	Cenostigma	9.5	6
	90	Fabaceae	Cenostigma	6.3	3
	91	Fabaceae	Cenostigma	8	5
	92	Cactaceae	Cereus	12	7

	93	Fabaceae	Mimosa sp1	9	8
	94	Fabaceae	Cenostigma	12.3	7
SQ5	95	Euphorbiaceae	Jatropha	14.1	4
	96	Euphorbiaceae	Jatropha	5.5	3
	97	Euphorbiaceae	Cnidoscolus	14.5	6
	98	Fabaceae	Cenostigma	5.9	2
	99	Fabaceae	Cenostigma	5.5	1.5
	100	Fabaceae	Cenostigma	6.5	2
	101	Fabaceae	Cenostigma	5.4	2.5
	102	Euphorbiaceae	Jatropha	7.9	3
	103	Fabaceae	Cenostigma	5.6	2
	104	Fabaceae	Amburana	8.1	4
	105	Fabaceae	Cenostigma	20	3
	106	Fabaceae	Mimosa sp1	6.4	3.5
	107	Cactaceae	Pilosocereus	13	1.5
	108	Euphorbiaceae	Cnidoscolus	10.2	5
	109	Fabaceae	Cenostigma	11.5	5
	110	Fabaceae	Mimosa sp1	7.1	5
	111	Fabaceae	Amburana	23.8	6
	112	Fabaceae	Cenostigma	25	3
	113	Fabaceae	Mimosa sp1	7.2	5
	114	Euphorbiaceae	Cnidoscolus	11.2	6
	115	Euphorbiaceae	Cnidoscolus	14	6
	116	Cactaceae	Cereus	11.7	4
	117	Fabaceae	Cenostigma	18	2.5
	118	Fabaceae	Cenostigma	15.9	1.5
SQ6	119	Euphorbiaceae	Jatropha	6.4	3
	120	Fabaceae	Cenostigma	23.1	3
	121	Fabaceae	Cenostigma	16.1	2
	122	Fabaceae	Cenostigma	34.1	2.5
	123	Euphorbiaceae	Jatropha	6.1	4
	124	Fabaceae	Cenostigma	35	5

	125	Fabaceae	Cenostigma	8.7	3
	126	Fabaceae	Cenostigma	10.5	5
	127	Euphorbiaceae	Cnidoscolus	5.1	3
	128	Fabaceae	Cenostigma	51.6	3
	129	Fabaceae	Cenostigma	30	3
	130	Fabaceae	Cenostigma	29.1	4
	131	Fabaceae	Cenostigma	10.3	2
	132	Fabaceae	Cenostigma	15.6	4
	133	Euphorbiaceae	Jatropha	9.7	3
	134	Euphorbiaceae	Jatropha	5.3	4
	135	Fabaceae	Cenostigma	8.5	2.5
	136	Fabaceae	Cenostigma	9.1	2
	137	Fabaceae	Cenostigma	14.4	4
	138	Fabaceae	Cenostigma	5.3	3
	139	Fabaceae	Cenostigma	13.2	2
	140	Fabaceae	Cenostigma	25.9	3
	141	Fabaceae	Cenostigma	21.5	3
	142	Fabaceae	Cenostigma	10	2
SQ7	143	Fabaceae	Cenostigma	7.3	2
	144	Fabaceae	Cenostigma	7	2
	145	Fabaceae	Cenostigma	7.5	2
	146	Euphorbiaceae	Jatropha	5	2
	147	Fabaceae	Cenostigma	13.5	3
	148	Cactaceae	Cereus	17.2	5
	149	Fabaceae	Mimosa sp2	15.4	5
	150	Fabaceae	Cenostigma	11	2
	151	Fabaceae	Amburana	20	3
	152	Fabaceae	Cenostigma	22.2	4
	153	Euphorbiaceae	Cnidoscolus	13.6	6
	154	Euphorbiaceae	Cnidoscolus	8	6
	155	Fabaceae	Cenostigma	7	2
	156	Fabaceae	Cenostigma	5.3	1.8

	157	Euphorbiaceae	Cnidoscolus	27	7
	158	Cactaceae	Pilosocereus	9	2
	159	Cactaceae	Cereus	15	5
	160	Euphorbiaceae	Cnidoscolus	7.7	4
	161	Fabaceae	Cenostigma	8	4
	162	Euphorbiaceae	Cnidoscolus	17.6	5
	163	Euphorbiaceae	Cnidoscolus	29.7	8
	164	Fabaceae	Cenostigma	21.7	5
	165	Fabaceae	Cenostigma	22.3	3
	166	Fabaceae	Cenostigma	7.2	5
SQ8	167	Euphorbiaceae	Cnidoscolus	15	5
	168	Fabaceae	Cenostigma	8.5	3
	169	Fabaceae	Cenostigma	11	3
	170	Euphorbiaceae	Cnidoscolus	13	5
	171	Cactaceae	Pilosocereus	9	1.5
	172	Fabaceae	Cenostigma	31.5	2
	173	Fabaceae	Cenostigma	32	5
	174	Euphorbiaceae	Cnidoscolus	9.5	6
	175	Euphorbiaceae	Cnidoscolus	17.3	6
	176	Euphorbiaceae	Cnidoscolus	16.5	6
	177	Fabaceae	Cenostigma	13.5	2
	178	Fabaceae	Cenostigma	16	2
	179	Cactaceae	Pilosocereus	10	1.5
	180	Fabaceae	Cenostigma	16.5	3
	181	Fabaceae	Cenostigma	5.5	2
	182	Fabaceae	Cenostigma	18.3	4
	183	Fabaceae	Mimosa sp2	17.3	5
	184	Cactaceae	Cereus	21	3
	185	Fabaceae	Cenostigma	29.5	3
	186	Cactaceae	Pilosocereus	10.2	1.5
	187	Euphorbiaceae	Cnidoscolus	6	3
	188	Euphorbiaceae	Cnidoscolus	13.6	5

	189	Euphorbiaceae	Jatropha	6.1	2
	190	Fabaceae	Cenostigma	19.5	2
SQ9	191	Fabaceae	Cenostigma	21.5	4
	192	Euphorbiaceae	Jatropha	8.5	4
	193	Fabaceae	Cenostigma	24.6	2
	194	Euphorbiaceae	Jatropha	9	3
	195	Euphorbiaceae	Cnidoscolus	14.3	6
	196	Fabaceae	Cenostigma	26.3	2.5
	197	Euphorbiaceae	Jatropha	8.4	3
	198	Euphorbiaceae	Jatropha	5.5	3
	199	Fabaceae	Amburana	19.5	7
	200	Fabaceae	Amburana	7.8	2
	201	Fabaceae	Cenostigma	15	2
	202	Fabaceae	Amburana	11.3	3
	203	Euphorbiaceae	Cnidoscolus	18.3	6
	204	Fabaceae	Cenostigma	19.2	3
	205	Fabaceae	Cenostigma	25.6	4.5
	206	Fabaceae	Cenostigma	13	3
	207	Fabaceae	Cenostigma	37	3
	208	Fabaceae	Cenostigma	18.5	2
	209	Euphorbiaceae	Jatropha	9.4	4
	210	Fabaceae	Cenostigma	19.2	4.5
	211	Fabaceae	Cenostigma	13.3	3
	212	Fabaceae	Cenostigma	12.7	4
	213	Euphorbiaceae	Jatropha	15	4
	214	Cactaceae	Pilosocereus	7.5	1
SQ10	215	Euphorbiaceae	Jatropha	12.5	2
	216	Fabaceae	Cenostigma	26.6	4
	217	Euphorbiaceae	Cnidoscolus	5.2	3
	218	Fabaceae	Cenostigma	24.5	5
	219	Fabaceae	Cenostigma	31	3
	220	Euphorbiaceae	Cnidoscolus	10.1	5

221	Fabaceae	Cenostigma	31.3	4
222	Fabaceae	Cenostigma	9.7	3
223	Euphorbiaceae	Cnidoscolus	19.5	4
224	Euphorbiaceae	Cnidoscolus	17	7
225	Fabaceae	Cenostigma	5.5	2
226	Fabaceae	Cenostigma	20.8	3
227	Fabaceae	Cenostigma	13	4
228	Fabaceae	Cenostigma	12	2
229	Fabaceae	Cenostigma	32.6	5
230	Fabaceae	Cenostigma	20.8	2
231	Euphorbiaceae	Jatropha	6.3	3
232	Fabaceae	Cenostigma	27.5	3
233	Cactaceae	Pilosocereus	6.5	1
234	Fabaceae	Cenostigma	21	1
235	Fabaceae	Cenostigma	15	2
236	Fabaceae	Cenostigma	22	1
237	Euphorbiaceae	Cnidoscolus	21.1	8
238	Fabaceae	Cenostigma	15.5	2.5

6 CONSIDERAÇÕES FINAIS

Este é o primeiro estudo que apresenta dados ecológicos e comportamentais do ameaçado macaco-prego-galego em uma área de Caatinga. Este estudo oferece uma contribuição relevante para o entendimento sobre o padrão de uso de ferramentas por um grupo de macaco-prego-galego, um comportamento recentemente descrito para essa espécie de primata. A coleta e análise dos dados permitiram preencher lacunas sobre a caracterização das ferramentas utilizadas, os recursos alimentares acessados e consumidos, e a influência de variáveis da paisagem local no comportamento de reuso dos sítios na espécie, oferecendo informações valiosas para a compreensão da interação entre os macacos-prego-galego e seu hábitat. Embora focado em uma população específica, os resultados ressaltam a importância de considerar aspectos ecológicos locais na análise de comportamentos complexos. Além disso, as contribuições deste trabalho são relevantes não apenas para o avanço do conhecimento científico sobre o uso de pedras como ferramentas por primatas, mas também para a orientação de futuras investigações e para a formulação de estratégias eficazes de conservação da espécie e manejo na área de Caatinga estudada. A continuidade de estudos que integrem aspectos comportamentais e ecológicos poderá aprofundar essa compreensão e ampliar as bases para ações sustentáveis de preservação da biodiversidade e dos ecossistemas que a sustentam. Ainda é necessário entender a dieta da espécie dentro de uma perspectiva geral e sazonal, bem como em associação com a disponibilidade de alimento. Embora o comportamento do uso de pedras como ferramentas foi estudado, se faz necessário compreender o padrão geral de atividade do grupo, tamanho e estratégia de uso da área de vida, parâmetros populacionais básicos (i.e., distribuição sexo-etária, padrão de nascimento de filhotes), e as interações com outros organismos. Além disso, é preciso pensar em verificar os aspectos abordados neste estudo em outras áreas com a presença do macaco-prego-galego bem como com o uso de ferramentas. Nesse contexto, permanecem questões em aberto, como a comparação das características das ferramentas de pedra entre diferentes grupos; o papel do habitat na distribuição dos sítios e no padrão de uso; e a similaridade entre os recursos explorados.