



OPEN The basal area explains the abundance of stone tool sites reused by blonde capuchin monkeys

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Behavioural adaptability in primates is widely known. However, the role of local landscape metrics on the use of stone tool sites 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 3078 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.

Keywords Adaptability, Behavioural ecology, Caatinga, Local landscape metrics, *Sapajus flavius*

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^{1–4}. This set of information is fundamental to the formulation of functional measures for the preservation of biodiversity^{5–8} 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 pattern and their impacts on them⁹. 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 adaptability 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 adaptability is crucial to regulate foraging, resource exploitation, displacement, and communication strategies^{10–13}. On a regional scale, forest cover has had a positive influence on the diet and behaviour of the spider monkey (*Ateles geoffroyi*) in Mexico¹⁴. 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 areas¹⁵. On the local scale, primates exhibit a range of behavioural patterns^{16–18}. 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 area¹⁹. Furthermore, movement strategies of five primate species were found to vary according to the availability of resources¹⁷. 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 area²⁰. 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 tools²¹. It is therefore imperative to study behavioural adaptability at all scales and in all behaviours, in order to gain insight into the role of habitat effects on primates.

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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^{21,24–34}. This behaviour plays a pivotal role in the maintenance and survival of species^{21,35,36}, as it is cultural and transmitted from generation to generation^{37–40}. The transmission of this behaviour appears to be more pronounced when the frequency of use and reuse of stone tool sites is high^{41–44}. From an archaeological perspective, the frequency of reuse of stone tool sites can be linked to their archaeological signature⁴⁵. 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^{46,47}, contributing to the understanding of the ecological and behavioural dynamics of primates^{48,49}.

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.⁵⁰ 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 chimpanzees⁵¹. 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^{52–55}. Furthermore, in such an arid environment, the presence and proximity to water sources may influence the foraging strategy employed by *S. libidinosus*^{56,57}, 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 event²⁹, the sites were mapped, the stone tools were characterised, a list of plant species consumed was presented, and the most exploited foods were identified⁵⁸. There is a scarcity of studies on the blonde capuchin monkey in the Caatinga. Currently, the following studies have been published: Ferreira et al.⁵⁹ and Martins et al.⁶⁰ on distribution; Garcia et al.⁶¹ on traces of tool use; Lima et al.²⁹ on the use of stone as a tool; and Lins et al.⁶² 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^{43,44}. However, the abundance of stone tool use sites 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.

Results

Characterisation 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* (n=122), followed by *Mimosa* sp. 1 (n=44), and *Cnidocolus 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).

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).



Fig. 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 0.19.36 plugin from QGIS version 3.32.3 (<https://qgis.org>).

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

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. Significant values are in bold.

Local landscape metrics

A total of 53 edible nuts were recorded as available on the ground throughout the study period. The transect analysis revealed that the mean number of edible nuts on the ground was $4 \pm \text{SD } 7$ (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 a mean of $307 \pm \text{SD } 172$ (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 $181.6 \pm \text{SD } 161.1$ m (range: 15.7–514.64 m).

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).

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 plant species in the area. Furthermore, the study area is characterised by the presence of trees that are, on mean, 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 size⁶³. A high concentration of available food resources on a given site tends to attract a larger number of primates⁶⁴. 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 group⁴⁵. 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^{65,66}. Furthermore, this dynamic is crucial for the perpetuation of the cultural tradition of tool use among younger individuals⁶⁷ 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^{43,68–70} 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 area⁷¹. In areas of high tree density, it is possible to predict that a particular tree species will have grouped distribution⁷². 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*⁵⁸, 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 area⁷³. 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 time⁷⁴, 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. Additionally, the preservation

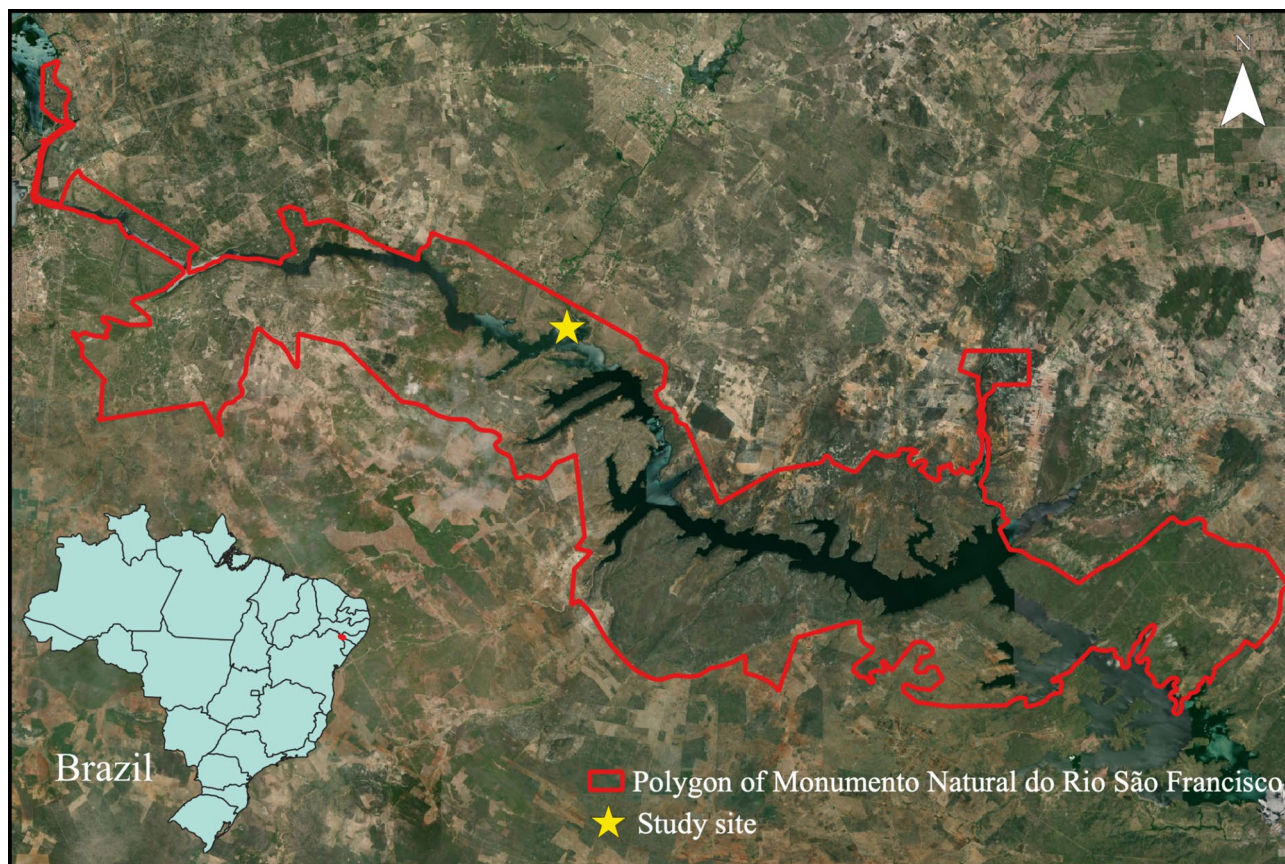


Fig. 2. Location of the study site in the limit of the Monumento Natural do Rio São Francisco, northeastern Brazil. This figure was created using the QuickMapServices version 0.19.36 plugin from QGIS version 3.32.3 (<https://qgis.org>).

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 monkeys⁷⁵. Archaeological sites utilised by capuchin monkeys have already been documented, thus underscoring the necessity for further exploration of this approach.

Methods

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 (9° 27' 35" S, 38° 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 km²) due to the expansion of cattle ranching activities, while the Caatinga vegetation occupies 27.2% (approximately 221 km²)⁷⁶. 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 mm⁷⁷. 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 months⁷⁸.

The blonde capuchin monkey group monitored was composed of up to 21 individuals with varied sex-age classes⁷⁹. The male–female ratio is 1.3:1, and adult:juvenile ratio is 1:1.2⁸⁰. 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.

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 methods⁸¹ (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 them⁸². In this study, only inorganic anvils and hammerstones were considered. We established a 50-m transect for each area that covered the sites. A fixed point was established at 10-m 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 m ($n=60$). 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.

Characterisation 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-m intervals using the nearest-neighbour method⁷¹. 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.⁸³ 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 individually⁸³. 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, respectively⁶³, to ascertain their impact on the abundance of reused stone tool sites.

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 m. Given that the number of edible nuts on the ground is subject to change on a monthly basis⁸⁴, 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 m 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 ($337 \text{ g} \pm \text{SD } 483$; see³⁶). 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.

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 m 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.

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 Brasil⁸⁵.

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 root⁸⁶. We evaluated the multicollinearity of predictor variables in each model to identify those with a variance inflation factor (VIF) > 2 as correlated⁸⁷. 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 samples⁸⁸, 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 excluded⁸⁹. 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+⁹⁰. 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.

Ethical statement

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).

Data availability

The datasets used and/or analysed during the current study available from the corresponding author on reasonable request.

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Author contributions

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.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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