Capuchin monkeys use only proto-tools to crack jatobá hard-shelled fruits in an urban environment

Macacos-prego usam somente protoferramentas para quebrar frutos de jatobá em ambiente urbano

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Abstract

The goal of this study was to describe a nut-cracking behavior by six adult bearded capuchin monkeys of a group living on an urban protected area called Bosque Bougainville in the city of Goiânia, central Brazil. The nut-cracking events, occurring with jatobá (*Hymenaea stygonocarpa* Mart.), were recorded in digital video and classified in terms of behavioral categories of nut-cracking: proto-tool use and tool-use. The nut-cracking behavior was also quantified and analyzed by means of TOTE motor unit categories. All jatobá nut-cracking events records were of the proto-tool use category. The successful jatobá nut-cracking (complete TOTE motor units) occurred in most of the recorded events for all animals. The absence of tool-use records was explained by the ecological circumstances at the Bosque Bougainville and by the high level of efficacy of proto-tool used in jatobá nut-cracking.

Keywords: foraging, tools, motor control, animal cognition.

Resumo

O objetivo deste estudo foi descrever o comportamento de quebra de frutos por seis macacos-prego adultos de um grupo habitando uma área urbana de proteção ambiental denominada Bosque Bougainville, na cidade de Goiânia, Centro-oeste, Brasil. Os eventos de quebra de frutos, que ocorreram com jatobá (*Hymenaea stygonocarpa* Mart.), foram registrados em vídeo digital e classificados em termos de categorias comportamentais de quebra de frutos: protoferramenta e ferramenta. O comportamento de quebra de frutos também foi quantificado e analisado por meio de categorias de unidades motoras TOTE. Todos os eventos de quebra de fruto de jatobá registrados foram da categoria protoferramenta. A quebra bem-sucedida (unidades motoras TOTE completas) de frutos de jatobá ocorreu na maioria dos eventos registrados para todos os animais. A ausência de registros de uso de ferramentas é tentativamente explicada pelas circunstâncias ecológicas do Bosque Bougainville e pelo alto nível de eficácia do comportamento de quebra de fruto de jatobá por meio do uso de protoferramenta.

Palavras-chave: forrageio, ferramentas, controle motor, cognição animal.

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Introduction

Due to its great cognitive ability and behavioral flexibility, capuchin monkeys easily adapt to forest fragments in urban areas (Cunha *et al.*, 2006; Aguiar *et al.*, 2014). Thus, knowledge of the behavioral repertoire (use of space, diet and foraging strategies) of capuchin monkeys may contribute to the appropriate understanding of the cognitive bases of their adaptation to urban environments.

The motor control can be defined as the set of cognitive mechanisms underlying the regulation of body movement (Shumway-Cook and Wollacott, 2007; Schmidt and Lee, 2011). The TOTE model is a biomechanical and motor learning approach to the study of motor control skills (Miller *et al.*, 1960). The TOTE motor unit (acronym of the initials of the verbs "test", "operate", "test", "exit") was proposed by Miller *et al.* (1960) as a substitute for the basic unit of behavior based on the triple contingency instrumental learning paradigm. The cognitive conception of the TOTE model emphasizes perceptual-motor skills and assumes that plans or mental schemes could control motor behavior in the same way that a software could control the activities of computer hardware (Miller *et al.*, 1960; Shumway-Cook and Wollacott, 2007).

The perceptual-motor skill is considered an essential cognitive process for motor control (Miller *et al.*, 1960; Shumway-Cook and Wollacott, 2007; Schmidt and Lee, 2011). Therefore, the perceptual-motor skill has been seen as an important subject of research in the area of development of motor control in primates (Fragaszy and Cummins-Sebree, 2005; Nina-e-Silva *et al.*, 2015).

Tool-use to process hard-shelled fruits has been described as an important foraging strategy of capuchin monkeys (Antinucci and Visalberghi, 1986; Ottoni and Izard, 2008; Fragaszy, 2011; Spagnoletti *et al.*, 2011; Spagnoletti *et al.*, 2012; Fragaszy *et al.* 2013; Ventricelli *et al.,* 2013; Luncz *et al.*, 2016). Moreover, there is now evidence that capuchin monkeys seem to be able to select the tools depending on the maturation stage and properties of the fruits (Luncz *et al.*, 2016).

Several studies have reported the relation between tool-use and the capuchin monkey handedness and cognitive skills (Spinozzi *et al.*, 2004; Phillips and Thompson, 2013).

However, the tendency of capuchin monkeys to use one hand or the other to perform activities related to tool-use have been investigated in terms of motor control by very few studies (Resende *et al.*, 2008; Liu *et al.*, 2009; Nina-e-Silva *et al.*, 2015). Thus, the objective of this study was to describe the jatobá (*Hymenaea stygonocarpa* Mart.) nut-cracking behavior by adult bearded capuchin monkeys (*Sapajus libidinosus* Spix 1823).

Material and Methods

Area of Study

This study was carried out in an urban protected area called Bosque Bougainville (Goiânia, 1994) in the city of Goiânia, state of Goiás, in central Brazil (16°43'37"S, 49°13'19"W) from June to November 2014. The Bosque Bougainville is a highly human-disturbed area of 6.7 hectares of fragments of dry bush, which is typical of the Cerrado biome, being completely surrounded by houses. It has been used as a research field for previous ethological studies (Rocha, 2003; Nina-e-Silva, 2004; Cardoso, 2008; Nina-e-Silva *et al.*, 2015). Among the native edible fruit plants from the Brazilian Cerrado, which are widely distributed in the Bosque Bougainville, one that stands out in the foraging behavior and diet selection of capuchin monkeys is the jatobá (Rocha, 2003; Nina-e-Silva, 2004; Cardoso, 2008). Jatobá (*Hymenaea stygonocarpa* Mart.) is a cylindrical, oblong, and rough dark brown bark fruit of about 15 cm length (Lee and Langenheim, 1975). The jatobá seed is surrounded by a sweet farinaceous edible pulp that is consumed by capuchin monkeys in the Bosque Bougainville (Rocha, 2003; Nina-e-Silva, 2004; Cardoso, 2008). The jatobá nut-cracking behavior by capuchin monkeys has been frequently observed in the Bosque Bougainville (Rocha, 2003; Nina-e-Silva, 2004; Cardoso, 2008; Nina-e-Silva *et al.*, 2015).

Group of Study

According to previous studies, the group of capuchin monkeys in the Bougainville Wood has approximately 30 individuals (Rocha, 2003; Nina-e-Silva, 2004; Cardoso, 2008). We were able to identify 16 individuals, with six adults (two males and four females). In order to ensure the reliability of the records, we decided to include in the study sample only the six adult individuals whose identification was unambiguous for the two observers (91% of agreement between two observers).

Data Collection Procedures

We adopted the following behavioral categories of jatobá nut-cracking: (i) proto-tool use; (ii) tool-use. The proto-tool use category was defined as the use of a non-portable object or a fixed substrate in which a target object is manipulated by one hand or by both hands (Antinucci and Visalberghi, 1986). The tool-use category was defined as the use of any portable object that can be used by one hand or by both hands to modify the state or shape of another object, including the tool user itself (MacGrew and Marchant, 1997).

Data collection was developed in two phases: (i) unsystematic observation (from June to August 2014); and

(ii) systematic observation (from September to November 2014). During the unsystematic observation and habituation stage, the observers were trained to identify the individuals described in previous studies (Nina-e-Silva, 2004; Nina-e-Silva *et al.*, 2015). The observers also had to identify individuals that had not been previously described. The habituation period lasted only four weeks (June 2014) because the study site has a high degree of human impact. Animals were considered habituated to the presence of the observers when they stopped fleeing at sight or issuing terrestrial predator alarm vocalizations when followed by them.

During the systematic observation stage, we used the focal animal method (Altman, 1974). The jatobá nut-cracking categories (tool-use and proto-tool use) of a single animal at a time were recorded during a sample period of 20 minutes. The time interval between consecutive sampling periods was 10 minutes. The duration of each sampling period and the time interval between sampling periods was based on the procedure adopted in previous studies carried out in the Bosque Bougainville (Nina-e-Silva, 2004; Nina-e-Silva *et al.*, 2015). All sample periods for each animal were fully documented using a Nikon DSLR D3200 digital camera. Table 1 shows the number and the duration of focal records for each individual in the systematic observation stage.

We considered only the first event in a series to record the frequency of occurrence of each jatobá nut-cracking category. A new event was recorded only 30 seconds after the end of the previous series. For example, if an animal had pounded a jatobá fruit five times against a branch and then stopped, only one single event of the proto-tool use category was recorded in the protocol. The record of a new proto-tool use event would be done only 30 seconds after the end of the fifth and last strike of that series.

Procedure of Analysis

The following two categories of TOTE motor units based on the animal nut-cracking behavior outcome were established to assess motor control: (i) complete (if the nut-cracking behavior was successful, that is, if the jatobá hard shell was effectively broken); (ii) incomplete (in case of failure in the nut-cracking and/or withdrawal from the nut-cracking action by the monkey).

The motor control analysis involved quantification of the frequency of occurrence of TOTE motor unit categories in all independent jatobá nut-cracking events for each individual. The number of nut-cracking events was extracted from the digital video recordings.

The Ethowatcher© (Crispim-Júnior *et al.*, 2012) behavioral observation data transcription software was used to quantify the categories of TOTE motor units from the digital video recordings.

Results

All jatobá nut-cracking event records were of the proto-tool use category. The tool-use category was not recorded during the focal-animal sampling period, nor observed during the periods of habituation and unsystematic observation.

The regular pattern of jatobá nut-cracking performed by the monkeys was to pound the jatobá nut against tree trunks and branches. The most frequent form of proto-tool use observed was the monkey, perched on a thick and hard branch of jatobá tree, leaning on the semi-flexed hind legs and one hand, with its tail wrapped around the branch. The monkey kept the trunk parallel to the branch, holding a jatobá fruit with the free hand always perpendicular to the plane of the branch, and striking the fruit against the branch countless times until the nut breaks or the fruit escapes from the animal's hand.

Table 2 illustrates the efficacy of jatobá nut-cracking expressed in terms of number of complete and incomplete TOTE units extracted from the video recordings. The successful jatobá nut-cracking (complete TOTE motor units) occurred in most of the recorded events (91.83% on average) for all animals.

Table 1. Number and duration of focal records for each individual of capuchin monkey in the systematic observation stage.

Individual	Number of focal records	Duration of focal records
1(♂)	28	09h20min
2(♂)	27	09h00min
3(♀)	30	10h00min
4(♀)	30	10h00min
5(♀)	29	09h40min
6(♀)	28	09h20min
Total	172	56h20min

Table 2. Efficacy of jatobá nut-cracking by capuchin monkeys expressed in terms of percentage of complete and incomplete TOTE motor units.

Individual	Complete TOTE units (%)	Incomplete TOTE units (%)
1(♂)	90	10
2(♂)	92	08
3(♀)	90	10
4(♀)	93	07
5(♀)	92	08
6(♀)	94	06
$\bar{x}$	91.83	8.16

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Discussion

The absence of record of the tool-use category in our study does not agree with previous studies that have described customary tool-use by capuchin monkeys in urban forest fragments (Ottoni and Mannu, 2001; Aguiar *et al.*, 2014; Coelho *et al.*, 2015). Nevertheless, this behavior has been frequently observed in the Bosque Bougainville (Nina-e-Silva, 2004; Nina-e-Silva *et al.*, 2015). High levels of terrestriality, food provisioning and low predation risk are stronger predictors of nut-cracking tool-use than food scarcity (Ottoni and Izar, 2008). All these conditions are valid to the capuchin monkeys in the Bosque Bougainville; however, tools for nut-cracking have not yet been registered in this area.

Previous studies have described that the group of the Bosque Bougainville spends about 30% of its daily time budget on the ground (Rocha, 2003; Nina-e-Silva, 2004). This could be due to the absence of natural predators for this species in the area. The presence of stray dogs that may threaten the monkeys is controlled by the local police and by the Zoonosis Control Department patrols. Action of human hunters has never been reported in the area.

On a daily basis, the Municipal Environment Agency provides food to the monkeys of the Bosque Bougainville. Residents of the grove vicinity also often provide food to them. According to Rocha (2003), the capuchin monkeys of the Bosque Bougainville spent more than half of the total foraging time recorded with items provided by humans on the ground. The jatobá nut-cracking mainly occurs after the animals have fed on their supplemented food.

Capuchin monkeys took the fruits of jatobá directly from the tree and pounded them against the branches of the tree itself. Even when the animals took a jatobá fruit from the ground, they carried it to the branches of trees in order to crack it. So, the jatobá nut-cracking is carried out mainly in the branches of the trees, which could hinder the tool-use.

Ecological circumstances at the Bosque Bougainville may not favor the occurrence of tool-use. One of the possible reasons for the low incidence of tool-use records in forest areas would be the difficulty of finding, processing, and manipulating rigid and portable tools to crack hard-shelled fruits into the tree environment (Boesch and Boesch, 1994; Boesch *et al.*, 1994). This fact may explain the absence of tool-use in our records. There are few stones or concrete chunks that could serve as raw material for tools in the Bosque Bougainville. And even if those materials were available, considering that the jatobá nut-cracking mostly happens on the branches of trees, it would be difficult for the animals to carry rigid and eventually heavy materials up there. Moreover, the high level of efficacy of the proto-tool use in jatobá nut-cracking could also be a likely explanation for the absence of tool-use in our records. The present results indicated that all animals achieved successful jatobá nut-cracking rates over 90%

using proto-tool. Considering that the tool-use would be more cognitively and energetically demanding than that of proto-tool use (Antinucci and Visalberghi, 1986), if the animals are already successful in jatobá nut-cracking using proto-tool, tool-use would not be worth to the capuchin monkeys of the Bosque Bougainville in terms of ecological cost-benefit relationship.

Regarding motor control of jatobá nut-cracking behavior, our results were very similar to the average rates of nut-cracking proto-tool use efficacy described previously by studies developed at the same area (Nina-e-Silva, 2004; Nina-e-Silva *et al.*, 2015). Moreover, the average nut-cracking success rates recorded in this study were similar to the rates of success when the capuchin monkeys used stone tools to crack nuts (Otonni *et al.*, 2005; Visalberghi *et al.*, 2007; Visalberghi *et al.*, 2009; Spagnoletti *et al.*, 2011; Spagnoletti *et al.*, 2012). Thus, in accordance with the prediction of the TOTE model (Miller *et al.*, 1960; Shumway-Cook and Wollacott, 2007), placing the jatobá nut-cracking behavior under the control of a motor action plan constantly adjusted by the experience (haptic or visual perception) may have become relevant to the high rates of jatobá nut-cracking efficacy. This hypothetical motor action plan organizes the TOTE units running hierarchies, reducing errors, reducing system power consumption and the demands of concentrated attention by increasing the time allowed the assessment of the results of the action itself (Miller *et al.*, 1960; Shumway-Cook and Wollacott, 2007; Schmidt and Lee, 2011).

Regarding our methodology, the use of the TOTE model for the analysis of the perceptive-motor abilities of non-human primates seems to be a very fruitful theoretical-methodological approach, since it allows the quantitative analysis of the spatiotemporal dimensions of the animal movement. Due to its non-experimental nature, this study could privilege only the evaluation of the temporal dimension of the jatobá nut-cracking behavior. Because of this, we recommend conducting studies that determine habitat use and the use of vertical space by capuchin monkeys in the Bosque Bougainville.

Acknowledgments

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