

Vertebrate predation and tool-aided capture of preys by savannah wild capuchin monkeys (*Sapajus libidinosus*)

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Research Article

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Abstract

Vertebrate predation was a vital behavior during human evolution. Some non-human primates, such as baboons and chimpanzees, frequently hunt and consume vertebrate prey. Capuchin monkeys (*Cebus* and *Sapajus*) are omnivorous neotropical primates, and although vertebrate prey is not their primary food source, they hunt and consume those opportunistically. Bearded capuchin monkeys (*Sapajus libidinosus*) living in semi-arid savannah environments use stone tools to obtain food resources. Still, only one population at Serra da Capivara National Park is known to use stick probes to enhance predation. I present here data collected for two years on vertebrate predation and consumption by two groups of capuchins in this population. Sampling all observed vertebrate predation events, I observed 72 events of predation, with an overall rate of 4.6 events/100h. The most frequent preys were lizards and snakes, followed by birds and rodents, including larger ones like adult rocky cavies (*Kerodon rupestris*). Although rare, bats were also observed being preyed on by these monkeys. The predation of vertebrate prey, even larger ones (compared to their body size), the use of tools to aid predation, and the high terrestriality degree in the savannah environment, make robust capuchins a suitable model of hominid behavior to understand human evolution, as well as a good comparison with the Afro-Eurasian primate models.

Introduction

Predation on large vertebrate prey was an important behavior present during human evolution (Butynski 1982; Thompson et al. 2019). Hunting for the meat of larger animals gave an energetic input that allowed the maintenance of larger brains, enhanced cooperation, prolonged childhood, and shorter female interbirth intervals, among other human characteristics that were only possible by the energy obtained from consuming meat (Thompson et al. 2019; however, see Barr et al. 2022 for a critical view of carnivory link to human evolution). Other primates also hunt and consume vertebrates opportunistically. Olive baboons (*Papio anubis*) prey upon at least 3 species of primates, 10 ungulates, 4 rodents, 3 hares, 1 bat, 4 herpetofauna and 6 species of bird (Strum 1975; Sommer et al. 2016). Hamadryas baboons (*P. hamadryas*) can present a vertebrate predation rate of 2.8/100 hours of observation, preying on dik dik (*Madoqua kirki*), hares, Guinea fowl, among other preys (Schreier et al. 2019). Yellow baboons (*P. cynocephalus*) hunt lizards, birds, and gazelles (Hausfater 1976; Rhine 1986). The environment can be an important factor in the amount of predation by primates. Baboons living in close forests present a much lower predation rate than those on open savannahs (Sommer et al. 2016).

Chimpanzees (*Pan troglodytes*) also prey on vertebrates, such as colobus monkeys and duikers (Hosaka et al. 2002; Hobaiter et al. 2017). Although predation does not seem essential for chimpanzees, they prey at a relatively high frequency (4.65 kills/100h), and those hunts provide a high protein input (Wrangham and Riss 1990). Chimpanzees at Fongoli use wooden tools as “spears” to hunt for galagos at their hiding places (Pruetz and Bertolani 2007; Pruetz et al. 2015). These chimpanzees were thought until recently to be the only known non-human population that systematically hunts vertebrate prey with tools (Pruetz et al. 2015).

Sometimes, there are sexual and age differences in the frequency and success of predation (e.g., male chimpanzees usually hunt more frequently and successfully than females, Watts and Mitani 2002; Gilby et al. 2010). In gracile capuchins (*Cebus capucinus*), the frequency and success of squirrel hunting by males and females differed across two sites in Costa Rica. In the site with fewer sex differences, simultaneous hunts of multiple squirrels were more frequent, maybe allowing females to have a higher success (Rose et al. 2003). Sex differences in hunting can be due to distinct energetic balances. Female mammals may need more stable food sources to increase their energetic intake during pregnancy and lactation (McCabe and Fedigan 2007), being averse to the more unreliable sources (e.g., hunt). On the other hand, bigger males in highly sexually dimorphic species can have more energetic costs and be more resilient to energetic intake oscillation than females and may seek challenging to catch prey more often (Key and Ross 1999).

Afro-Eurasian primates are regularly used as models to understand the evolution of human behavior regarding several behaviors, including predation and tool use, as they are phylogenetically closer to humans than Neotropical monkeys (Rose 1978). Neotropical monkeys are separated by 40 Myr of evolution from the human lineage (Lima et al. 2018). Still, one group of Neotropical monkeys presents several characteristics similar to those present during hominid evolution and could be used as an alternative model. Capuchin monkeys (*Sapajus* and *Cebus*) are omnivorous primates, consuming plants, arthropods, and vertebrate prey (Izawa 1978; Fragaszy et al. 2004). Although primarily arboreal, some Savannah populations of robust capuchin monkeys (genus *Sapajus*) are highly terrestrial (Wright et al. 2019), and the same populations are also the ones presenting frequent and, sometimes, highly variable tool use behavior (Ottoni and Izar 2008; Spagnoletti et al. 2011; Falótico and Ottoni 2016; Falótico et al. 2018a).

In dry forests, white-faced capuchins (*C. capucinus*) hunt several vertebrates preys, such as lizards, frogs, birds, squirrels, coatis, anteaters, and bats (Fedigan 1990; Rose 1997; Rose et al. 2003). Brown tufted capuchins (*Sapajus apella*) in the Amazonian forest have been reported to prey on small vertebrates (Izawa 1978), and a *Sapajus* group in an urban park in São Paulo (Brazil) was also observed to hunt for birds and share the meat (Ferreira et al. 2002). Although vertebrate prey is a small part of the capuchin diet, it consists of high-quality food rich in protein and fat (Fedigan 1990).

Those results, however, are primarily for gracile capuchins (*Cebus*) and groups living in dry forests. Vertebrate predation data for robust capuchins (*Sapajus*) living in savannah environments are lacking to date; there is only a case report of predation of an adult rock cavié, *Kerodon rupestris* (Filho et al. 2021), and data on snake predation (Falótico et al. 2018b; Silva et al. 2019). In other primates, groups living in closed forest environments presented lower predation rates than ones living in open savannahs (Sommer et al. 2016). If the same is true for capuchins, it is expected that the capuchins from dry environments present higher predation rates than forest capuchins.

Another interest in Savannah robust capuchins is that they have several wild populations that customarily use tools (Ottoni and Izar 2008) and present a high degree of terrestriality (Visalberghi et al. 2005;

Falótico 2011; Wright et al. 2019), making them an alternative model to Afro-Eurasian primates to understand vertebrate predation in a similar environment present during human evolution. Moreover, the population of bearded capuchin monkeys (*S. libidinosus*) from Serra da Capivara National Park (SCNP) studied here is known to use stick probes to enhance predation of lizards, carpenter bees, and other prey (Falótico and Ottoni 2014), a behavior only known to be customary, so far, in this population, and that can be of interest to understand the use of such tools for hunting. The probes at SCNP have an average length of 27.9 cm and are made of tree branches and sticks. Although some probes can be used without modification, most of them (64%) are modified by the capuchins before or during the use (Falótico and Ottoni 2014). The rate of probe tool use in SCNP is 0.27 event/h, and the use is almost only performed by males (97%, Falótico and Ottoni 2014).

I present here data collected for 2 years on vertebrate predation and consumption by two groups of capuchin monkeys in a dry Savannah environment (*Caatinga*) in Brazil. This paper aims to describe the targets and frequency of predation observed in those groups and explore possible differences between sex and age classes. Adult males are the most common sex-age class observed preying vertebrates in several primate species, including capuchin and other primates (Butynski 1982; Rose 1997). Adult male capuchins are larger than females, thus having more possibilities to predate larger vertebrate prey. Also, females are expected to seek for more stable food sources to cope with reproductive costs fluctuations, being, in theory, less prone to look for unpredictable food sources such as vertebrate prey. Thus, I expect this age-sex pattern in predation also to happen here.

Methods

Study site

We collected data on two bearded capuchin monkey (*S. libidinosus*) neighboring groups living at Serra da Capivara National Park (SCNP, 8°50'S, 42°33'W) from September/2007 to July/2009 for Pedra Furada (PF) group, and from February/2008 to February/2009 for Bocão (BC) group (Suppressed references for double-blind manuscript).

During the collection period, the PF group ranged from 30 to 45 individuals (15–29 adults, adults sex ratio M/F = 0.75–0.93), and the BC group ranged from 25 to 28 monkeys (13–15 adults, adults sex ratio M/F = 0.8-1).

The climate in the area is semi-arid, with dry bush vegetation (*Caatinga* biome) and a long annual dry season from May to October/November (Falótico and Ottoni, 2013). The annual rainfall average is 689 mm (Pessis 1994). The SCNP has a range of potential vertebrate prey that fall inside the capuchin diet, including small lizards (e.g., *Tropidurus*, *Cnemidophorus*, *Glaucomastix*), snakes (e.g., *Philodryas*, *Oxybelis*), frogs (e.g., *Leptodactylus*), turtles (*Phrynops*), rodents (e.g., *Dasyprocta*, *Kerodon rupestris*, *Galea spixii*, *Trichomys*, *Oryzomys*), bats (e.g., *Molossus*, *Phyllostomus*), marmosets (*Callithrix jacchus*),

and birds, such as species from family Columbidae (e.g., *Zenaida auriculata*, *Columbina*, *Leptotila*) and Psittacidae (e.g., *Amazona*, *Aratinga*), among others (Araujo *et al.* 1998).

Data collection

The researcher and one field assistant followed the capuchin groups from contact (usually in the early morning, near where the monkeys stopped the day before) to dusk, or until they lost contact with the group. All observed vertebrate predation was registered, both when the catch of the prey was observed or inferred (individual was seen eating a still alive or fresh dead prey). We tried to register all occurrences of predation in the group, but as the group was large and not all individuals were observed all the time, we treated the sampling as *ad libitum*.

For each event, we recorded: time and day, subject (and/or age and sex), type of prey (visually identifying species when possible), if a tool was used, if catching was observed, consumption of the prey, and sharing with group members. For this work, the individuals were classified as adults (> 5 years) or immatures (< 5-year juveniles and infants).

Results

Contact time with both groups summed to 1711 hours (PF 1288h, BC 423h). We observed 78 predation events (Table 1 and Table S1), including 24 inferred by consumption of fresh whole prey.

The overall rate of predation was 4.6 events/100h. PF group's rate was 4.9 events/100h, and BC group 3.5 events/100h. The predation events do not appear to be seasonal, recorded during most months of the year, but there was insufficient data to statistically test seasonality (Table S1).

Table 1
– Events of predation

Prey	N events	% observed catching (N)	% Probe use
Lizard	54	70 (38)	7 (4)
Snake	7	43 (3)	0
Bird	8	75 (6)	0
Rock cavy (<i>Kerodon rupestris</i>)	2	50 (1)	0
Other rodents	4	100 (4)	0
Bat	3	67 (2)	0
TOTAL	78	69 (54)	5 (4)

We observed 72 predation events that had the individual sex and age recognized (in six events it was not possible to identify the juvenile sex), and 23 individual monkeys were identified in 49 of those events (Table S1). Most events were by adult males, followed by immature males (Table 2).

Table 2
 – Frequency of predation events by sex and age class.
 N = 72

Age / Sex	% Male (N)	% Female (N)
% Adult/Subadult (N)	47 (34)	19 (14)
% Immature (N)	31 (22)	3 (2)

We observed passive sharing (when an individual holding the food item allows others to pick up part of it) and scrounging of the carcass in 12% of the events. The scroungers were mostly males (90% of the cases), immatures and adults (5 events each).

Lizards, including snakes, were the most common prey (54 events, 69%). The genus *Tropidurus* was one of the most frequent targets (Fig. 1a), and at least one endemic species from the SCNP region, *T. helenae*, was also preyed on. Part of the lizard predation events (5%) were done using probe tools to expel the prey from rock crevices (Falótico and Ottoni, 2014). Snake predation (7 events, 9%) was on non-dangerous snakes, mostly Colubridae. In contrast, the monkeys avoided dangerous poisonous and constrictor snakes (for detailed results and discussion on the topic of capuchin-snake interaction, see Falótico et al., 2018b).

Birds were the second most frequently preyed on vertebrate (8 events). An adult white-tipped dove (*Leptotila verreauxi*) and adult blue-fronted parrots (*Amazona aestiva*) were preyed on by the capuchins.

Rodents were the third most preyed class (6 events). Although most rodents were small prey, we observed a predation of an adult rock cavy (*Kerodon rupestris*), that weight around 1000g (Lacher 1979). In this case, capture was not observed, but the prey was still alive when noticed by the researcher. The rock cavy was held, killed, and at least partially consumed by an adult male capuchin (Fig. 1c and Video S1).

Finally, we observed 3 events of consumption of bats (Fig. 1b). All events took place near caves or shelter entrances (< 20m), and the bats were still alive when first seen being held by the monkeys. In two events, the first individual seen holding the prey consumed the bats. In the third event, an adult female examined the bat for approximately 4 minutes and dropped it. A juvenile male closely observing the female caught the discarded and still live prey and sprinted outside the r.

Discussion

The results show that vertebrate predation is common in the studied capuchin monkey groups living in a dry Savannah ecosystem. Compared to vertebrate predation rates in dry forest living *C. capucinus* (3.66 events/100h, Rose, 1997; 4.7 events/100h, Fedigan 1990), the *S. libidinosus* living in Savanah had a similar rate (4.6 events/100h). Although living in a drier environment, the *Sapajus* population did not present a higher absolute vertebrate predation rate than *Cebus* living in a forest environment. This could

be expected if the drier environment provides less prey availability. However, as we do not know prey availability in each environment, we still cannot thoroughly compare those rates.

Adult males were the most common sex-age class observed preying on vertebrates, a result that is similar to other studies both in capuchin and other primates (Butynski 1982; Rose 1997), although other groups of gracile capuchins present no difference between males and females frequency of hunting for some vertebrate prey (Rose et al. 2003). The *ad libitum* sampling may have affected this result as the sampling of predation was not controlled by individuals or sex; however, the large number of events decreased this effect. Adult male capuchins are 60% larger (or more) than females (Fragaszy et al. 2016). This may be one factor allowing males to pursue and capture larger vertebrates better, as they would be capable of subduing larger animals than females. However, body size differences would probably not influence their hunting of small vertebrates, such as the lizards, the main prey captured by capuchins in this study. Another explanation would be an energetic balance - although vertebrate prey is high-quality food, it is an inconsistent source - females would not hunt as much as males, as females need more stable food sources to increase their food intake during lactation (McCabe and Fedigan 2007). Still, in highly sexually dimorphic primates (> 60% difference), males can present more energetic costs than females (Key and Ross 1999). Capuchins are around this limit of dimorphism, so capuchin males could be hunting more because it is a high-energy food source.

The prey types were consistent with other *Sapajus* studies (Fragaszy et al. 2004; Canale et al. 2013), showing that small lizards are common prey, usually captured on the ground when the monkeys are foraging in the leaf litter. The studied capuchins were also observed catching bats, a rare behavior among primates (Tapanes et al. 2016). This is likely an opportunistic prey, as the study groups live in valleys full of rock shelters and shallow caves that can increase the chance of encounters with bats.

The use of probe tools to aid the predation by capuchin monkeys, dislodging the prey from their hiding place is a behavior observed, so far, only in this population (Ottoni and Izar 2008; Falótico and Ottoni 2014). The probe tool use can supposedly enhance the chances of capturing prey, as it extends the reach of the capuchin monkey to places where they cannot get with their hands, increasing, in theory, the success of capturing a hidden prey. Most of the probe tool-use observed in predation events or attempts were aimed at small prey, such as lizards, carpenter bees, and scorpions (Falótico and Ottoni 2014). However, the monkeys have been observed using longer probes (maybe better described as spears, > 60cm in length), trying to dislodge larger prey, such as rock cavies (*K. rupestris*) from hiding places, although no success in capturing the prey was observed in those cases (see Video S2).

This behavior is similar to the Fongoli chimpanzees using wooden spears to maim galagos in trunk hollows and capture them (Pruetz and Bertolani 2007; Pruetz et al. 2015). Another interesting parallel is that, like Fongoli chimpanzees, capuchin monkeys from SCNP also live on a dry Savannah and are the only capuchin population known to hunt vertebrates with the aid of tools customarily. Those similarities could be related to the environment, which could be a necessary factor for the behavior to develop. However, the fact that it is so common in this population of capuchins but not others also presents a

case of a behavioral tradition in these groups (Haslam *et al.* 2019), as several studied populations inhabiting similar environments have not been seen performing this behavior (Ottoni and Izar 2008; Falótico *et al.* 2018a). Tool use by capuchin monkeys is typical behavior, although only stone tool to process encased resources is habitual in Brazilian capuchin living in the savannah biome. Stone tool use repertoire has variations regarding the food targets and the processing style by populations and even neighboring groups (Falótico and Ottoni 2013; Sirianni and Visalberghi 2013; Falótico *et al.* 2018a). This variation is most likely due to behavioral traditions maintained by social learning of tool use (Ottoni, 2021). Probe tool use traditions in capuchin monkeys are much rarer than stone tool use. Although it has been occasionally or anecdotally reported in capuchin groups (Souto *et al.* 2011) and individuals (Haslam and Falótico 2016), the capuchin males at SCNP are the only known population to customarily use probes. This behavior has a learning sex bias probably caused by a distinctive sex motivation to observe the probe manipulation (Falótico *et al.* 2021).

The predation of larger vertebrate prey (compared to their body size) with the occasional use of tools to aid predation makes robust capuchin, particularly this population, a suitable neotropical monkey model of hominid behavior to understand human evolution, as well as a good comparison with the Afro-Eurasian primate models. Moreover, this and other savannah environment capuchin populations also present a high terrestriality degree (Fragaszy *et al.* 2005; Falótico 2011) and stone tool use behavior (Ottoni and Izar 2008; Falótico and Ottoni 2016), adding to this suitability. Hunting using tools was crucial in human evolution (although the accepted evidence of increased carnivory after the appearance of *Homo erectus* has been recently questioned, see Barr *et al.* 2022), and studying primates that present similar traits evolved independently is a promising way to understand better the evolutionary factors involved.

Declarations

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Ethics approval and consent to participate

The research was only observational and complied with protocols approved by the Animal Research Ethical Committee of the Institute of Psychology, University of São Paulo, and fully adhered to Brazilian law under authorizations IBAMA/ICMBio 037/2007 and 14825-1.

Consent for publication

The author consents to publication

Availability of data and material

Data is available as supplementary material

Competing interests

The author declares no competing interests

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Authors' contributions

Not applicable. Single author.

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Figures



Figure 1

Capuchin monkeys (*Sapajus libidinosus*) preying on vertebrates. Predation of lizard (a), bat (b) – both events with juveniles observing –, and adult rock cavy (*Kerodon rupestris*) by an adult male capuchin (c, d). Serra da Capivara National Park, Brazil. Photographs by the author, taken on nov/2008 (a) and fev/2008 (b, c, d).

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