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Low occurrence of molar use in black-tufted capuchin monkeys: Should adaptation to seed ingestion be inferred from molars in primates?

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Abstract

From squirrels to peccaries, seed predators are found in several mammalian orders. To access protected kernels, they use either their incisors or canines to remove seed shells but can also use their premolars and molars to break seed shells. Both behaviors can result in dental adaptations, such as a thicker enamel or round cusps. However, a large part of the literature focuses on molars, which is based on the basic assumption that seed predators commonly chew hard food or use their molars to break hard seed shells. In this study, we investigated the occurrence of molar seed breaking in a seed predator, the black-tufted capuchin monkey *Sapajus apella*. We conducted 65 feeding trials on captive specimens (N = 11) at the Guangzhou Zoo using soft shell (peanut) and hard shell seeds (walnut).

Molars biting represented 5.5% of the whole feeding repertoire. We did not find clear evidence of a difference in molar biting between peanuts and walnuts. This low occurrence of molar use suggests a preference for the use of anterior teeth when monkeys are ingesting challenging food. The occurrence of all ingesting behavior, including molar biting, was lower in males which was attributed to their larger size, stronger arms and jaw muscles. Molar shell breaking is therefore

interpreted as a costly behavior, only performed when other behaviors cannot be used to open the shells. While captivity could have affected feeding behavior, the low occurrence observed in this study questions the choice of *S. apella* as a preferred model of seed shell breaker in paleoecological studies. Morphological traits which allow *S. apella* to break hard shells using its molars could have been co-opted along adaptations to chew abrasive foods.

Keywords: animal model; diet; paleoecology; *Sapajus apella*; seed predation.

1. Introduction

1.1 Seed predation in extant and extinct mammals

Apart from non-physical protection such as mast-fruiting or toxic compounds, seed protection comes in many mechanical forms, from the hard shell of hazelnuts to the tough pods of tamarind fruit (Yamashita et al., 2012). Protective husks can sometimes be very thick, which requires longer food preparation in order to ingest, for example, the pyxidium of *Lecythis idatimon* fruit consumed by saki monkeys (*Chiropotes satanas* and *Pithecia pithecia*) from Amazonia (Norconk and Veres, 2011). The most challenging protections are both hard and tough at the same time, for example, the woody shell of *Sacoglottis gabonensis* consumed by mangabeys (*Cercocebus atys*) from Western Africa (McGraw et al., 2011).

Seeds and other physically challenging food items are expected to exert a strong selection, since individuals not adapted to their consumption may sustain considerable dental damage (Cuozzo and Sauter, 2012) or starve and suffer from under-nutrition (King et al., 2005). Consequently, the staple reliance on seeds (either as preferred or fallback food) is expected to result in adaptations to seed consumption and such individuals have a better chance to survive competition or episodes of food scarcity in the long term. Such dental adaptations can be used to infer the ability, or rather the aptitude sensu Gould and Vrba (1982) to consume seeds in extinct mammals.

The fossil record presents evidence of seed predation events by rodents dating back to the Eocene (Collinson and Hooker, 2000). Indeed, rodents are major seed predators but potentially, other extinct mammalian orders rank highly as strong seed predators, for example, artiodactyls (Bradham et al., 2008) or non-human primates (Teaford et al., 1996; Merceron et al., 2006;

Ramdarshan et al., 2010; Thiery et al., 2017). There are also likely seed predators in extinct metatherians (Sanchez-Villagra and Kay, 1997).

1.2 Role of molars in seed consumption

Hiiemäe and Ardran (1968) and many authors since then (e.g. Lucas, 2004) distinguished between food ingestion (defined as the process by which food is taken into the mouth) and chewing (defined as the food mechanical breakdown that takes place in the mouth before swallowing). Although this dichotomy had been described under other terms (e.g., harvesting and processing: Rosenberger, 1992), the general idea is that food consumption takes place at two separate levels: before mastication and during mastication.

On the one hand, every tooth class may participate in seed consumption at the pre-mastication level, even though some orders rely on a single tooth class. For instance, rodents almost exclusively use their incisors to gnaw holes into seed shells (Collinson and Hooker, 2000) while peccaries use their molars to crush both seeds and seed shells (Kiltie, 1981). Primates are flexible and seem to use both their anterior teeth (incisors and canines) to bite, scrap, tear and pry husks and shells open, and their posterior teeth (molars and premolars) to break seed shells (Rosenberger, 1992; McGraw et al., 2011; Norconk and Veres, 2011). On the other hand, chewing involves almost exclusively post-canine teeth i.e., premolars and molars.

Among other adaptations, the molars of seed consumers are usually characterized by blunter dental elements, an increase in occlusal complexity and a thicker enamel (Kay, 1981; Martin et al., 2003; Evans et al., 2007; Ledogar et al., 2013). Mammals are thought to have evolved molars concurrently with chewing, as molars interlock better than sub-molariform teeth during dental occlusion, which extends the contact between dental elements and thus, improves food

75 comminution (Butler, 1952). However, hard seed protection is barely masticated and is usually
76 discarded (e.g., McGraw et al., 2011) or swallowed whole (Kiltie, 1981). While seed shell
77 fragments might be difficult to spit out after the outer casing has been broken, and thus are likely
78 to cause dental microwear (Teaford et al., 2020), those pieces may not be subject to the same
79 peak forces as those used to break the shell. The seed kernel itself undergoes chewing, but it is
80 considerably softer than most seed protective shells and is easily fragmented (Table 1; Walker et
81 al., this issue). Therefore, ingesting behaviors are also expected to have a strong influence on
82 molar adaptations to hard food consumption, especially in primates.

83 ***1.3 The case of tufted capuchin monkeys***

84 Capuchin monkeys, which include platyrrhines from the genera *Cebus* (non-tufted capuchins)
85 and *Sapajus* (tufted capuchins), are opportunistic omnivores. They are known for their use of
86 tools (Izawa and Mizuno, 1977; Fragaszy et al., 2004; Luncz et al., 2016) and their sometimes-
87 destructive foraging behavior (Brocardo et al., 2010). More importantly, capuchin monkeys and
88 especially the black-tufted capuchin *Sapajus apella* have been reported to ingest a wide range of
89 physically challenging foods, including crabs (Port-Cavalho et al., 2003), oysters (Fernandes,
90 1991) and hard-shell seeds (Peres, 1991; Galetti and Pedroni, 1994). Since Terborgh (1983)
91 black-tufted capuchins have been viewed as a classic example of primates which use their molars
92 and premolars to exert bite force to cause catastrophic failure of seed shells. As a result, they
93 have often been used as a model of hard-shell breakers when inferring the diet of extinct primates,
94 including fossil hominins (Kinzey, 1974; Kay, 1981; Ungar et al., 2008; Ungar et al., 2010; Wood
95 and Schroer, 2012; Pampush et al., 2013). Yet, the occurrence of molar use when tufted capuchins
96 are confronted with the challenge of processing protected foods has not been evaluated. Filling

this gape is especially important since other ingesting behaviors, but also tool use could mitigate the effect of hard food consumption on their molar form.

1.4 Objectives

This paper aims to investigate the occurrence of molar use during seed ingestion in the black-tufted capuchin monkey *Sapajus apella*. Through feeding experiments performed on captive animals, we aimed to answer the following questions: (i), what are the seed ingesting behaviors observed in *S. apella*, and (ii), does age, sex or food hardness have an effect on the choice to break seed shells using molars. If breaking hard shells using molars presents a form of mechanical advantage for *S. apella*, we would expect the monkeys to use their molars significantly more while ingesting the hardest foods, especially younger animals which have yet to reach their full adult strength. Furthermore, if *S. apella* is indeed adapted to break hard shells using its molars, we would expect no difference in the frequency of molar biting between males and females during ingestion.

2. Methods

2.1 Feeding experiment

This protocol complies with the principles for the ethical treatment of non-human primates of the International Primatological Society. From May to June 2018, we performed feeding experiments on a group of 12 captive tufted capuchin monkeys (*S. apella*) living in the same enclosure at Guangzhou Zoo. The study group composed of 3 adult males, 2 adult females, 3 juvenile males, 3 juvenile females and 1 infant. Were considered as juvenile, individuals which did not reach their adult size with likely consequences for their dentition, but also for their gape

and their physical strength. We excluded the infant from the study as it was not yet weaned and presented a higher risk of dental injury.

Monkeys were fed every morning between 9:00 and 10:00 AM.. This time of the day was chosen for the study because it precedes the first meal of the monkeys, ensuring that satiety would not be a confounding factor for the experiments. Monkeys were fed with two kinds of food items representing two levels of protective shell hardness. We choose walnuts in the shell to represent a challenging hard food item and peanuts in the shell to represent a non-challenging soft food item. This choice was justified by the difference in shell hardness between the two fruits, but also by their reasonable amount of hardness which minimized the risk of dental injuries. Food hardness was controlled using a HP-500 durometer from Handpi Instruments. We used a flat head to compress food samples and estimated the stiffness (in N.mm-1) from the initial slope of the stress/displacement curve and the strength (in Kg) from the maximal force required to break the shell (Table 1).

[Insert Table 1 here]

Table 1. Stiffness, rupture force and strength of peanuts and walnuts used in feeding experiments

Food		Stiffness (N.mm-1)	Rupture force (N)	Strength (kg)
1. Peanut (<i>Arachis hypogaea</i>)	shell:	37.5 ± 8.6	59.7 ± 8.0	6.0 ± 0.8
	seam:	26.0 ± 11.6	32.8 ± 14.9	3.3 ± 1.5
2. Walnut (<i>Juglans regia l.</i>)	shell:	154.9 ± 37.2	175.0 ± 47.4	17.5 ± 4.7
	seam:	112.9 ± 17.5	161.8 ± 19.9	16.2 ± 2.0

A total of 65 feeding trials were conducted by giving a single food item to a selected monkey. In order to avoid interference due to food preference, only one kind of food was provided to the monkeys during the same day. Ingesting behavior was observed using focal animal sampling with no time record (Altman, 1974), and all occurrences were counted and scored using an ethogram

(Table 2) until the monkey stopped feeding either because there was nothing to feed on anymore, or because the food was dropped.

[Insert Table 2 here]

Table 2. Ethogram of oral ingesting behaviors performed by *S. apella*.

Ingesting behavior	Operational definition
Incisor biting	The monkey holds the food before its mouth using one or two hands, then bites it one to several times using its incisors. Only the strength of the jaws is used (no arms). A bout starts with the first bite and ends when the monkey pauses to manipulate the food or starts performing another behavior.
Canine biting	Similar to incisor biting, but the monkey holds the food on one side and uses its canines to puncture the food protective layer.
Molar biting	Similar to incisor biting, but the monkey holds the food on one side and uses its molars or premolars to crush the food protective layer.
Scraping	The monkey holds the food against the teeth using one or two hands, then pushes its teeth forward to remove the food or its protective layer from the substrate. Instead of the jaws, it is the strength of the neck and the arms that is used. A bout starts when the monkey starts pushing and ends when it succeeded in obtaining the food, removed the protective layer, or starts performing another behavior.
Tearing	The monkey holds the food with the teeth, then pulls it away using one or two arms. Only the strength of the arm(s) is used to remove the protective layer. A bout starts when the monkey starts to pull and ends when it pauses to manipulate the food, removed the protective layer, or starts performing another behavior.
Non ingesting behavior	
Hitting	The monkey holds the food in one hand and hits it repeatedly on a solid substrate, such as a rock or tree branches. The bout starts from the second hit, indicating that the food is being actively hit, and ends when the monkey starts performing another behavior.
Chewing	The monkey takes a bit of food, then starts opening and closing its jaws in a chewing motion. A chewing bout starts after two or more chewing motions and ends when the monkey swallows or starts performing another behavior.

Based on Ungar (1994) and Yamashita (2003). We consider stripping as a special occurrence of tearing, where the food consists in leaflets on a branch, and crushing a special occurrence of biting, where the tooth does not go through the food.

2.2 Data analysis

The analysis was performed in R 3.6.0 (R Core team 2019). Three factors were considered: food hardness (peanut: N = 38 vs. walnut: N = 27), age (adult: N = 35 vs. juvenile: N = 30) and sex (females: N = 35 vs. males: N = 30). For each feeding behavior, two variables were investigated: (i) count per trial, calculated as the count of events involving this behavior per feeding trial; and (ii) contribution to the entire feeding repertoire, calculated as the total percentage of events where the behavior was observed. In order to take into account non-independence of data due to animals being involved in multiple trials, the effect of food type, sex and age on count per trial was estimated from generalized linear mixed models built using the ‘lme4’ package, with a Poisson distribution and individuals as a random effect (Bates et al., 2015). We used two-tailed tests with statistical significance set at $p \leq 0.05$.

3. Results

3.1 Seed ingestion behaviors

The black-tufted capuchin monkeys in our study showed all the expected ingesting behaviors described in the ethogram (Table 2). Observations from a total of 65 feeding trials showed that molar biting represented only 5.5% of the observed behaviors. Tearing was the most performed behavior (30.4%) followed by incisor biting (23.5%), scraping (21.9%) and canine biting (18.7%). While the contribution of each behavior to the repertoire of monkeys depended on food hardness (Fig. 1A) as well as age and sex (Fig. 1B), molar biting was consistently the least performed behavior.

Capuchin monkeys also engaged in non-oral food preparation behaviors, most commonly, repeatedly hitting the food item on a substrate surface (usually tree branches or man-made wooden structures). This “hitting behavior” was particularly frequent during feeding bouts

166 involving walnuts. Hitting was not recorded, as it never resulted in the shell being opened, but it
167 might have weakened the shell before oral processing behaviors, which eventually resulted in the
168 kernel being accessible. It was also performed while the monkeys were eating other non-
169 challenging foods e.g., cut apples provided by the caretakers.

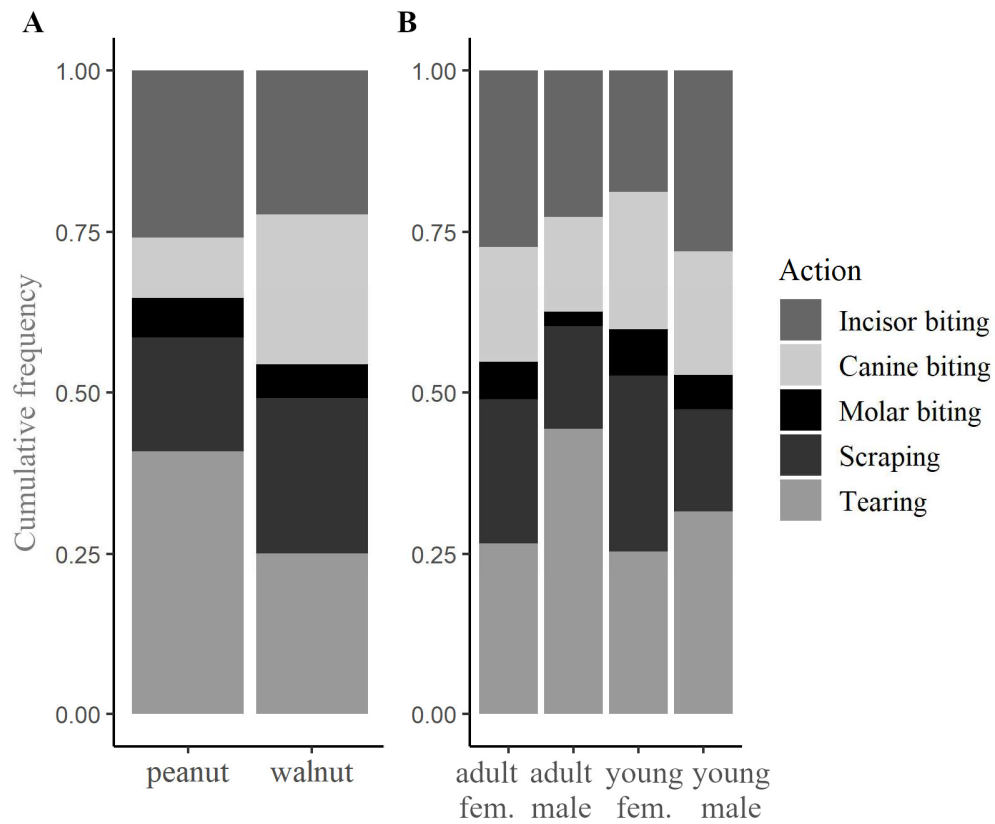


Figure 1. Relative contribution of ingesting behaviors to the entire feeding repertoire, as the proportion of events corresponding to each of the five behaviors, with (A) food hardness and (B) age*sex cohorts as factors. [2-column fitting image]

3.2 *Effect of food hardness, age and sex*

When the monkeys processed walnut shells, count per trial was higher for scraping as well as incisor, canine and molar biting (Fig. 2A). Ingestion of hard food resulted in a significantly higher count per trial for all four behaviors (Table 3). However, the width of the confidence interval of food effect for molar biting (0.85 ± 0.83) means it could have been overestimated. In addition, scraping and canine biting were performed significantly less than incisor biting while ingesting peanuts. One young female individual was exceptionally good at scraping peanuts, removing all the husk with a swift rotating move against her teeth, but other monkeys reserved scraping for walnuts, which is reflected by a higher standard deviation of the random effect for scraping count ~ food type (0.44). The effect of food hardness on tearing count was low, but significant.

Count per trial was higher in females for scraping as well as incisor, canine and molar biting (Fig. 2B). Again, ingestion by females resulted in a significantly higher count per trial for all four behaviors (Table 3). However, the width of the confidence interval of sex effect for both incisor biting (-0.47 ± 0.41) and molar biting (-1.18 ± 0.99) does not support the observed effect for both incisor and molar biting. In contrast, there was no visible effect of age on count per trial for any of the ingesting actions either on the diagrams (Fig. 2C) or from the GLMM (Table 3)

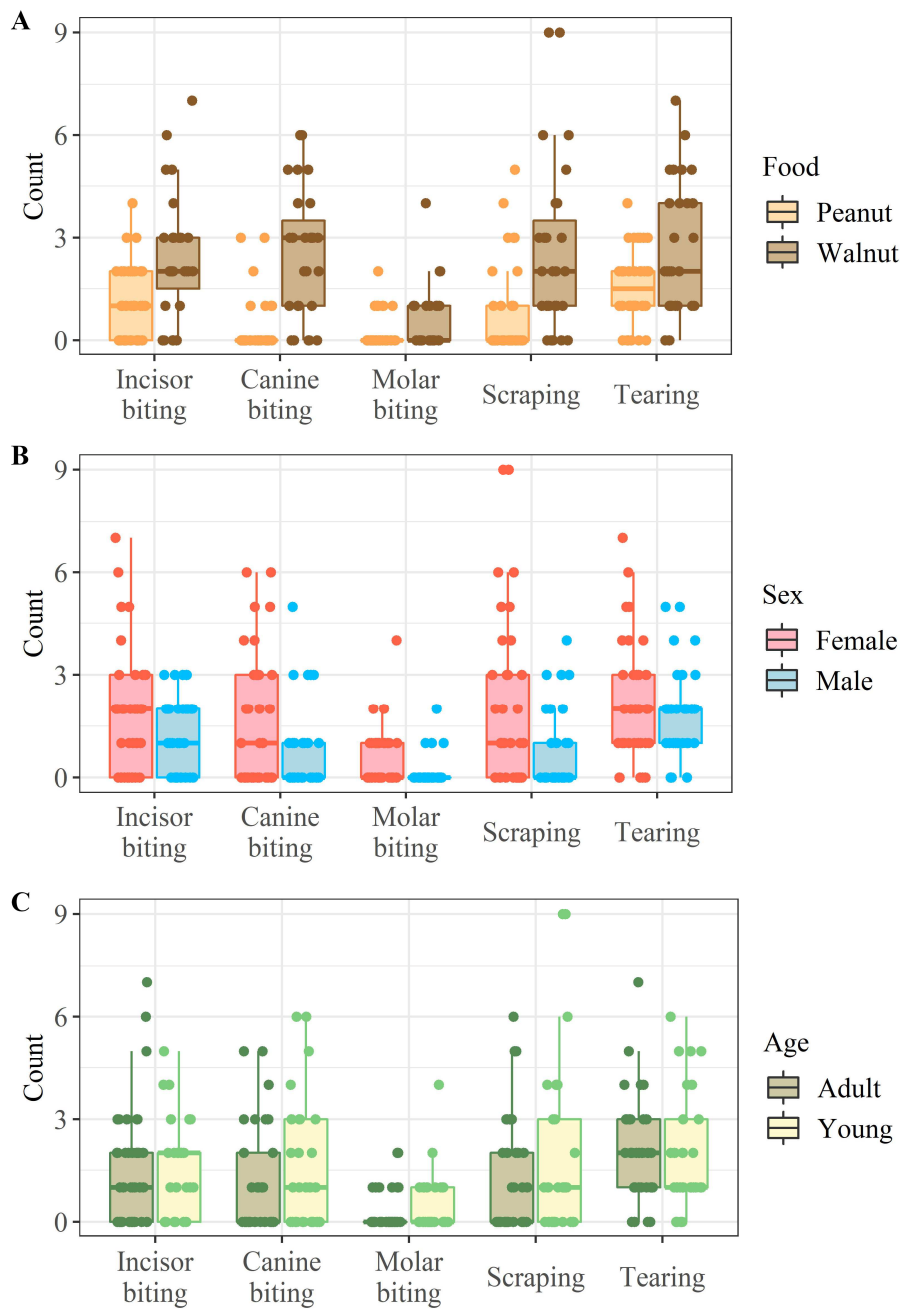


Figure 2. Count per trial for each of the five ingesting behaviors, with (A) food hardness, (B) age and (C) sex as factors. Middle lines correspond to the median, boxes to the first and third quartiles, and whiskers to the first and ninth deciles. [2-column fitting image]

[Insert Table 3 here]

Table 3. Generalized linear mixed models (GLMM) of count per trials for each ingesting behavior, with food type, sex and age as fixed effects and individuals as random effect.

formula	AIC	BIC	logLik	Fixed Effect Estimate	Fixed Effect CI	Random Effect SD	z	P-value
Scraping ~ Food + (1 ID)	225.5	232.0	-109.8	1.28	±0.46	0.44	5.43	<0.001***
Tearing ~ Food + (1 ID)	226.7	233.2	-110.3	0.54	±0.34	0.00	3.09	<0.01**
IncisorBiting ~ Food + (1 ID)	213.5	220.0	-103.7	0.88	±0.4	0.00	4.30	<0.001***
CanineBiting ~ Food + (1 ID)	179.2	185.8	-86.6	1.92	±0.58	0.10	6.53	<0.001***
MolarBiting ~ Food + (1 ID)	108.1	114.6	-51.0	0.85	±0.83	0.16	2.00	<0.05*
Scraping ~ Sex + (1 ID)	249.6	256.1	-121.8	-1.04	±0.59	0.28	-3.45	<0.01**
Tearing ~ Sex + (1 ID)	235.7	242.2	-114.8	-0.13	±0.34	0.00	-0.76	0.446
IncisorBiting ~ Sex + (1 ID)	227.6	234.1	-110.8	-0.47	±0.41	0.00	-2.26	<0.05*
CanineBiting ~ Sex + (1 ID)	229.1	235.6	-111.5	-0.73	±0.48	0.00	-3.00	<0.01**
MolarBiting ~ Sex + (1 ID)	105.6	112.2	-49.8	-1.18	±0.99	0.00	-2.35	<0.05*
Scraping ~ Age + (1 ID)	257.7	264.2	-125.8	0.32	±0.79	0.54	0.80	0.422
Tearing ~ Age + (1 ID)	236.1	242.6	-115.1	-0.07	±0.34	0.00	-0.41	0.683
IncisorBiting ~ Age + (1 ID)	232.7	239.2	-113.3	-0.04	±0.42	0.12	-0.17	0.868
CanineBiting ~ Age + (1 ID)	235.4	241.9	-114.7	0.37	±0.54	0.25	1.36	0.174
MolarBiting ~ Age + (1 ID)	110.5	117.0	-52.3	0.55	±0.81	0.00	1.33	0.182

AIC, Akaike information criterion; BIC, Bayesian information criterion; logLik, log-likelihood of the model; CI, confidence interval; SD, standard deviation; z, Wald's z-value of the model. The ‘*’ refer to the level of statistical significance. Molar biting highlighted in gray.

4. Discussion

4.1 Effect of food material properties

The ingestion of walnuts, compared to peanuts, took the monkeys a greater number of actions, except tearing for which the difference is negligible. For molar biting, the effect of food hardness might have been overestimated, likely because of the small number of reported events. Nonetheless, consuming hard food took monkeys more ingesting actions, which likely took them more time. This is consistent with results reported for another seed predator, the sooty mangabey *Cercocebus atys* (McGraw et al., 2011).

Even so, the fact that molar biting represented less than 5% of all observed behavior when confronted to walnuts contradicts our expectation that monkeys would take advantage of their molar's hard-food breaking adaptations. The use of distal teeth, which are closer to the joint than incisors or canines, requires a larger gape (Fig. 3). This could explain why capuchin monkeys tended to use anterior teeth more when confronted with the challenge of processing walnuts. However, two lines of evidence contradict this interpretation.. Firstly, being the largest individuals but also because their jaw muscle architecture does not compromise their jaw gape (Taylor and Vinyards, 2009), adult males have the widest gape and are therefore expected to perform molar biting more easily on walnuts. Still, adult males seem to be characterized by the lowest frequency of molar biting (Fig. 1B). Secondly, walnut dimensions fall within the size range of food items consumed by wild *S. apella* in French Guiana (Norconk et al., 2011). Furthermore, Terborgh (1983) reports capuchin monkeys breaking hard palm nuts of ~4cm of diameter using their molars. While these observations do not entirely preclude an effect of food size on the monkeys' decision to perform molar biting, the low occurrence of this behavior cannot be explained by food size alone.



Figure 3. A young male black-tufted capuchin monkey, performing molar biting to break a walnut shell. (A) The walnut is positioned into the mouth; (B) it is then pushed inside the mouth, between the premolars; (C) the monkey searches for an adequate position and then exerts a strong bite on the shell; (D) once the shell has broken, the monkey takes the walnut out for further examination. [single-column fitting image]

4.2 Effect of sex-related differences in physical strength

Similar to food hardness, sex had a strong impact on the average count per trial, as females performed significantly more ingesting actions in order to process the food, regardless of their age (Fig. 2B; 2C). Sex-related difference in strength is known to affect foraging behavior in the white-faced capuchin *Cebus capucinus* (Rose, 1994). In *S. apella*, there is a strong influence of ontogeny on the ability to forage hard food, which requires not only more physical strength but also better manipulative abilities (e.g., Gunst et al., 2010). Sexual dimorphism of the masticatory

apparatus is also greater in *S. apella* than in other capuchin monkeys, which is thought to be a consequence of dietary behavior (Masterson, 1997). In accordance with Masterson's hypothesis, our data suggest that males are more efficient at ingesting protected foods than females.

In addition, molar biting and to some extent canine biting were less common in adult males (Fig. 1B). If *S. apella* was adapted to break hard shells using its molars, we would expect no difference between males or females. Alternatively, given the differences in strength between males and females, one would expect adult male monkeys to perform better at molar seed-shell breaking. Yet, males and especially adult males used their incisors more frequently.

One possible explanation is that molar biting is used by capuchin monkeys as an alternative strategy when the use of incisors is not sufficient to get through the seed's defenses. Ross et al. (2016) showed that oral food processing with anterior teeth exerted more strain on the tufted capuchin's jaw than post-canine use. Furthermore, monkeys almost always engaged in incisor tearing (Fig. 3B), which requires strong arms and jaws to effectively tear shell fragments apart. While adult males would usually succeed at removing seed shells with their incisors, female and young male capuchin monkeys may struggle and eventually resort to molar biting. As biting force at the molars is significantly stronger than biting force at the incisors or canines (Wright 2005), molar biting could therefore facilitate ingesting by making primary cracks into the shell or even catastrophic shell failure, as observed by Terborgh (1983). As a matter of fact, molar biting has been reported in several primates that consumed seeds otherwise considered too challenging for them, including thin-enameled folivorous monkeys such as *Alouatta caraya*, as a fallback strategy when preferred foods were low (Oliveira-Filho and Galetti, 1996). However, using molars to bite hard seeds comes with a risk of tooth fracture even for thick-enameled primates, which might explain why *S. apella* tended to use their anterior teeth instead.

4.3 Are black-tufted capuchin molars adapted to breaking seeds?

According to the results reported in this study, the anterior teeth of *S. apella* may be more adapted to hard seed-breaking than its molars. This hypothesis is consistent with the patterns of cranial and dental morphology observed in *S. apella*. Daegling (1992) suggest that the mandibular morphology of *S. apella* better resisted high stresses during anterior dental use or powerful/frequent mastication, the latter being more advantageous for chewing tough foods than breaking hard shells. A comparison of mechanical advantage showed that *S. apella* has improved leverage of the masseter and temporalis muscles compared to other capuchin monkeys, which notably increases force production at the anterior dentition (Wright, 2005). The incisors of tufted capuchins are large and broad, and their canines are larger than what would be expected from their social structure and level of agonistic behavior, suggesting an influence of diet and especially hard foods (Plavcan and van Schaik, 1992).

In contrast, black-tufted capuchins as well as other capuchin monkeys have reduced third molars, despite a position which submits them to the highest potential load (Wright et al., 2005). This contrasts with other seed-breaking primates such as mangabeys. However, it could be the byproduct of capuchins' smaller size, since breaking walnut-sized seed shells with third molars may require a larger gape (Taylor and Vinyard, 2009). While black-tufted capuchins' enlarged fourth premolar, first molar and second molar are used as a tool for breaking seed casings on some occasions (Terborgh, 1983; Wright, 2005), they are also used to masticate a wide range of foods including exceedingly tough foods (Wright et al., 2009) to which their blunt, low-relief molars would not seem adapted. Meanwhile, capuchin's thick enamel is thought to be a primitive feature (Wright, 2005; Delgado et al., 2015) and could have been selected because of capuchins' long life expectancy combined with the reliance on abrasive foods such as palms and palm nuts

(Rabenold and Pearson, 2011). In this context, their thick-enameled, blunt, low-relief molars which are core features of their aptitude to break hard-shelled food with molars could have been co-opted from adaptation to chew abrasive foods (Gould and Vrba, 1982).

Putting the influence of abrasive foods aside, would the reported low occurrence of hard-shell breaking using molars be insufficient to drive dental adaptation? Hard foods that are only consumed seasonally as fallback foods can exert a strong selective pressure on animals in the wild, eventually leading to the emergence of (dental) adaptations (Lambert et al., 2004). While fallback foods are expected to apply more selection on processing than on ingesting adaptations (Marshall and Wrangham, 2007), the necessity to ingest some foods using molars to break their protective shell could have played a central role in the evolution of tufted capuchins' molar morphology. It should also be noted that studies of black-tufted capuchin's dental microwear have shown on multiple occasions that it does use its molars to process hard food (e.g., Teaford, 1985; Daegling et al., 2011; Scott et al., 2012). In fact, its average microwear complexity (Asfc) is very close to that of *C. atys* (Daegling et al., 2011), although Asfc shows more dispersion in *S. apella* (Ungar et al., 2017). This may reflect the recent expansion of the black-tufted capuchin monkey's distribution during the Pleistocene which could have broadened its dietary range, introducing more hard foods in its diet (Delgado et al., 2015). Still, it suggests that the occurrence of molar seed breaking could be higher in the wild. The feeding experiments described in this paper were conducted in captivity and the monkeys could not freely choose food items available to wild conspecifics that could have required more molar processing. Conditions in captivity could also have led to a higher prevalence of dental and oral diseases, preventing them from using their molars to break seed shells (Fecchio et al., 2019).

5. Conclusions

Our results seem to indicate that black-tufted capuchin monkeys prefer to remove seed shells using their anterior teeth rather than their posterior teeth. Monkeys would only resort to molar biting occasionally, most likely when they lacked the physical strength to ingest seeds using only their incisors. This is supported by the effect of sex on molar biting count, which was significantly higher in females. Adaptations of *S. apella* to break hard shells using molars, including a thick enamel and blunt, low-relief molars, could have been selected from such occasional molar use, for instance when breaking hard shells of fallback foods. Still, our results imply that their molar morphology could have been selected by other dietary behaviors than seed shell breaking, for instance the chewing of abrasive foods. This hypothesis requires further investigation, from (1) the observation of extant wild animals and (2) the dental microwear analysis of extinct animals.

To conclude, this study questions the choice of tufted capuchins for inferring molar adaptation to hard-food breaking in extinct mammals, including fossil hominins. Instead, incisors and canines of tufted capuchins would better suit the inference of hard-food ingesting adaptations. The analysis of molar and premolar dental microwear is still expected to carry some signal because of shell fragments ingested by mistake, but other estimates such as enamel thickness or dental topography could be misleading without the input of anterior teeth.

Data availability

Numeric data and R code will be made available on Researchgate (https://www.researchgate.net/publication/338067653_Low_occurrence_of_molars_use_in_capuchins_code_and_raw_data). Annotated movies of each feeding behavior can be provided on demand.

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