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

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9 **Abstract**

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

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

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

29

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

31 **1. Introduction**

32 ***1.1 Seed predation in extant and extinct mammals***

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

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

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

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

55 ***1.2 Role of molars in seed consumption***

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

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

70 Among other adaptations, the molars of seed consumers are usually characterized by blunter
71 dental elements, an increase in occlusal complexity and a thicker enamel (Kay, 1981; Martin et
72 al., 2003; Evans et al., 2007; Ledogar et al., 2013). Mammals are thought to have evolved molars
73 concurrently with chewing, as molars interlock better than sub-molariform teeth during dental
74 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

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

99 **1.4 Objectives**

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

110 **2. Methods**

111 **2.1 Feeding experiment**

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

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

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

131 [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

132
 133
 134 A total of 65 feeding trials were conducted by giving a single food item to a selected monkey.
 135 In order to avoid interference due to food preference, only one kind of food was provided to the
 136 monkeys during the same day. Ingesting behavior was observed using focal animal sampling with
 137 no time record (Altman, 1974), and all occurrences were counted and scored using an ethogram

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

140 [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.

141

142

143 **2.2 Data analysis**

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

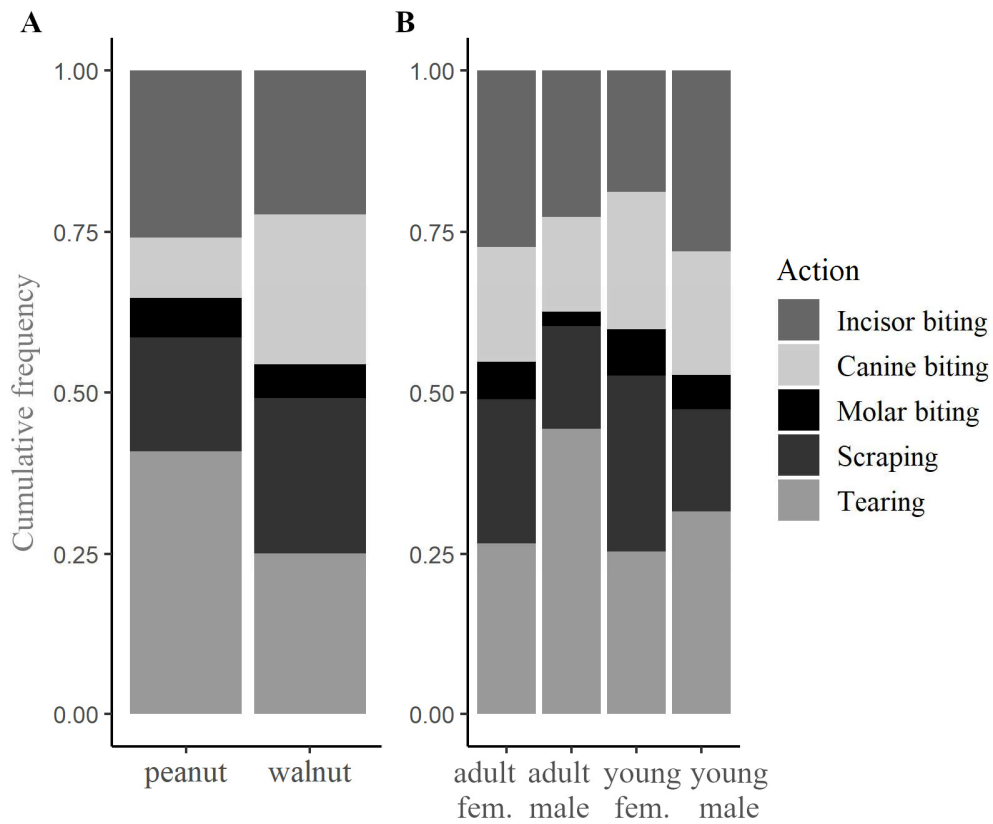
154 **3. Results**

155 **3.1 Seed ingestion behaviors**

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

163 Capuchin monkeys also engaged in non-oral food preparation behaviors, most commonly,
164 repeatedly hitting the food item on a substrate surface (usually tree branches or man-made
165 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.



170

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

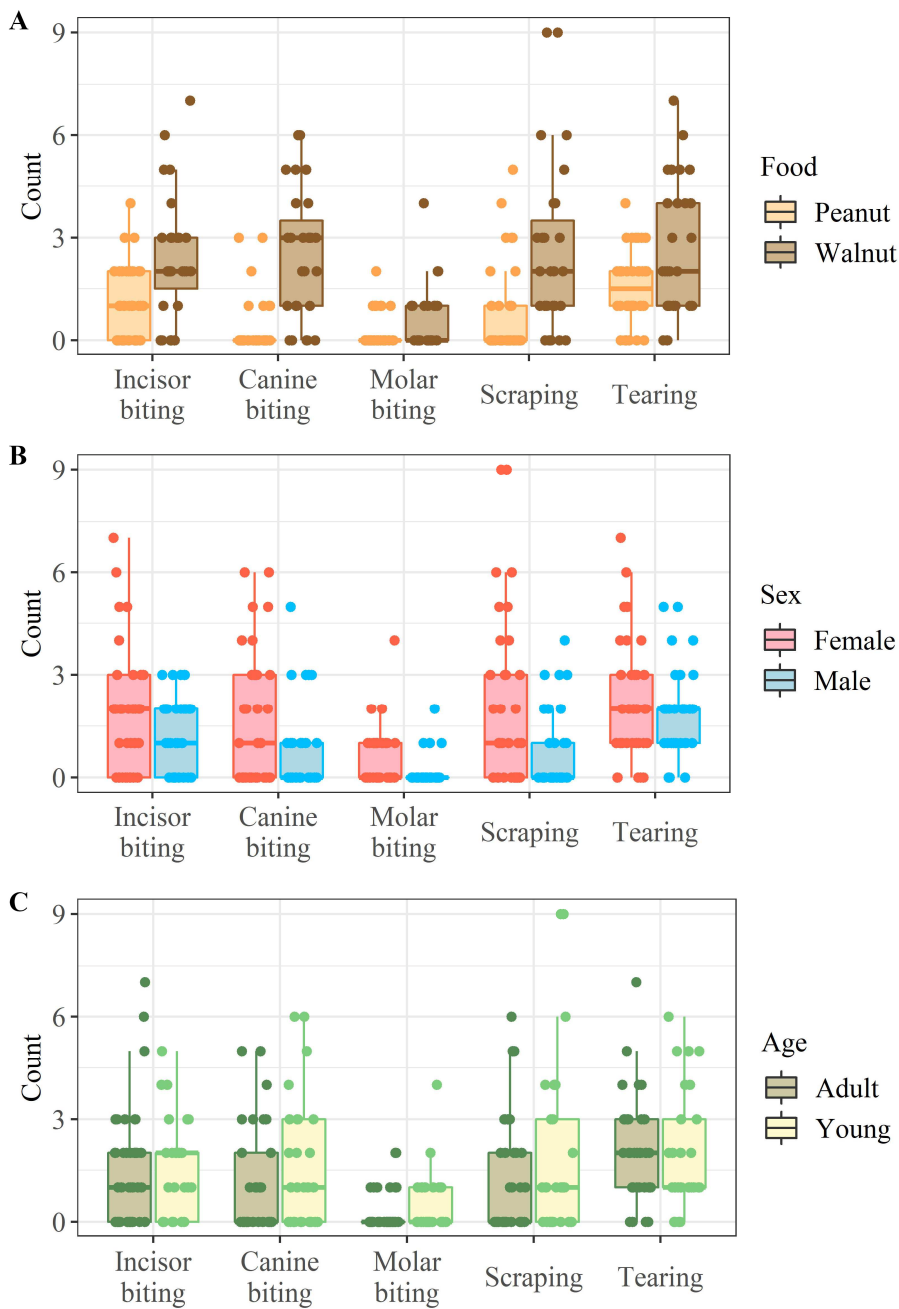
174

175 **3.2 Effect of food hardness, age and sex**

176

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

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



193

194 **Figure 2.** Count per trial for each of the five ingesting behaviors, with (A) food hardness, (B)

195 age and (C) sex as factors. Middle lines correspond to the median, boxes to the first and third

196 quartiles, and whiskers to the first and ninth deciles. [2-column fitting image]

197

[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.

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199
200

201

202 **4. Discussion**

203 ***4.1 Effect of food material properties***

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

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



225

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

231 **4.2 Effect of sex-related differences in physical strength**

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

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

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

246 One possible explanation is that molar biting is used by capuchin monkeys as an alternative
247 strategy when the use of incisors is not sufficient to get through the seed's defenses. Ross et al.
248 (2016) showed that oral food processing with anterior teeth exerted more strain on the tufted
249 capuchin's jaw than post-canine use. Furthermore, monkeys almost always engaged in incisor
250 tearing (Fig. 3B), which requires strong arms and jaws to effectively tear shell fragments apart.
251 While adult males would usually succeed at removing seed shells with their incisors, female and
252 young male capuchin monkeys may struggle and eventually resort to molar biting. As biting force
253 at the molars is significantly stronger than biting force at the incisors or canines (Wright 2005),
254 molar biting could therefore facilitate ingesting by making primary cracks into the shell or even
255 catastrophic shell failure, as observed by Terborgh (1983). As a matter of fact, molar biting has
256 been reported in several primates that consumed seeds otherwise considered too challenging for
257 them, including thin-enameled folivorous monkeys such as *Alouatta caraya*, as a fallback
258 strategy when preferred foods were low (Oliveira-Filho and Galetti, 1996). However, using
259 molars to bite hard seeds comes with a risk of tooth fracture even for thick-enameled primates,
260 which might explain why *S. apella* tended to use their anterior teeth instead.

261 **4.3 Are black-tufted capuchin molars adapted to breaking seeds?**

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

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

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

287 Putting the influence of abrasive foods aside, would the reported low occurrence of hard-shell
288 breaking using molars be insufficient to drive dental adaptation? Hard foods that are only
289 consumed seasonally as fallback foods can exert a strong selective pressure on animals in the
290 wild, eventually leading to the emergence of (dental) adaptations (Lambert et al., 2004). While
291 fallback foods are expected to apply more selection on processing than on ingesting adaptations
292 (Marshall and Wrangham, 2007), the necessity to ingest some foods using molars to break their
293 protective shell could have played a central role in the evolution of tufted capuchins' molar
294 morphology. It should also be noted that studies of black-tufted capuchin's dental microwear
295 have shown on multiple occasions that it does use its molars to process hard food (e.g., Teaford,
296 1985; Daegling et al., 2011; Scott et al., 2012). In fact, its average microwear complexity (Asfc)
297 is very close to that of *C. atys* (Daegling et al., 2011), although Asfc shows more dispersion in *S.*
298 *apella* (Ungar et al., 2017). This may reflect the recent expansion of the black-tufted capuchin
299 monkey's distribution during the Pleistocene which could have broadened its dietary range,
300 introducing more hard foods in its diet (Delgado et al., 2015). Still, it suggests that the occurrence
301 of molar seed breaking could be higher in the wild. The feeding experiments described in this
302 paper were conducted in captivity and the monkeys could not freely choose food items available
303 to wild conspecifics that could have required more molar processing. Conditions in captivity
304 could also have led to a higher prevalence of dental and oral diseases, preventing them from
305 using their molars to break seed shells (Fecchio et al., 2019).

306 **5. Conclusions**

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

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

324 **Data availability**

325 Numeric data and R code will be made available on Researchgate
326 ([https://www.researchgate.net/publication/338067653_Low_occurrence_of_molars_use_in_capu](https://www.researchgate.net/publication/338067653_Low_occurrence_of_molars_use_in_capuchins_code_and_raw_data)
327 [chins_code_and_raw_data](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
328 demand.

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