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# The Light Bite: Red-Nosed Cuxiu (*Chiropotes albinasus*, Primates) Exploit Differential Penetrability of Hard Fruit Husks When Selecting Dental Puncture Sites

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## ABSTRACT

The Amazonian primate *Chiropotes albinasus* (red-nosed cuxiu) is a specialist on seeds of hard-husked unripe fruit. These are accessed with specialized processing behavior, involving highly modified canines and incisors. This is energetically demanding and carries a high dental damage risk. Hypothesizing that red-nosed cuxiu process foods in ways that minimize both energetic expenditure and maximize dental safety, we predicted that individuals would selectively bite fruit husks at locations that were easiest to penetrate. Sutures were the easiest area to penetrate for all the 11 analyzed red-nosed cuxiu diet species with functioning (non-fused) sutures. Quantification of bite mark locations on these fruits showed significant clustering along the lower-penetrability areas (sutures) in 8 of 11 species (72.7%). This pattern did not exist for another 10 species that lacked sutures; bites did not cluster on the thinnest (and most easily penetrated) parts of the husk for 9 of these 10 species (90%). For four species that were functionally indehiscent due to fused or thick sutures, penetrability was lowest at the face (2 species) and suture (2 species). Thus, despite robust crania, mandibles, and dentition that appear highly suited for resisting forces generated by powerful biting action, red-nosed cuxiu deploy a more refined technique and often select the weakest areas of fruits for their seed-accessing bite sites, especially when the fruits are dehiscent with unfused sutures.

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## PORTUGUESE

O primata amazônico *Chiropotes albinus* (cuxiu-de-nariz-vermelho) é especialista em sementes de frutos verdes de casca dura. Estas são acessadas com um comportamento de processamento especializado, envolvendo caninos e incisivos altamente modificados. Isto é energeticamente exigente e acarreta alto risco de danos dentários. Hipotetizando que o cuxiu-de-nariz-vermelho processa alimentos de maneiras que minimizam tanto o gasto energético quanto maximizam a segurança dentária, previmos que os indivíduos morderiam seletivamente as cascas dos frutos em locais que fossem mais fáceis de penetrar. As suturas foram a área mais fácil de penetrar para todas as 11 espécies de cuxiu-de-nariz-vermelho analisadas com suturas funcionais (não fundidas). A quantificação dos locais das marcas de mordidas nestes frutos mostrou agrupamento significativo ao longo das áreas de menor penetrabilidade (suturas) em 8 de 11 espécies (72.7%). Este padrão não existiu para outras 10 espécies que não tinham suturas; As mordidas não se agruparam nas partes mais finas (e mais facilmente penetradas) da casca em 9 dessas 10 espécies (90%). Para quatro espécies que eram funcionalmente indeiscentes devido a suturas fundidas ou espessas, a penetrabilidade foi menor na face (2 espécies) e na sutura (2 espécies). Assim, apesar dos crânios, mandíbulas e dentição robustos que parecem altamente adequados para resistir às forças geradas por uma poderosa ação de mordida, o cuxiu-de-nariz-vermelho emprega uma técnica mais refinada e frequentemente seleciona as áreas mais fracas dos frutos para seus locais de mordida de acesso às sementes, especialmente quando os frutos são deiscentes com suturas não fundidas.

## 1 | Introduction

It is common for foraging studies to focus on optimizing time/energy by maximizing energetic gain and minimizing time expenditure (Aristizabal et al. 2017; da Dias Silva et al. 2020; Felton et al. 2009; Hohmann 2009). However, in mammals, the role of both minimizing deployed force and risk of breakage to teeth has been studied mainly in carnivores (Mann et al. 2017). Direct contact with bone can blunt or fracture the canine teeth of carnivorous mammals (Lawn et al. 2013; Van Valkenburgh 2009; Van Valkenburgh and White 2021), with strong negative impacts on survivorship (Goodrich et al. 2011; Patterson 2023). Accordingly, to reduce the danger of dental damage, as well as reducing the time spent subduing prey, carnivores organize bites so that the points of their canines slip into softer areas between the neck vertebrae of prey. This action is known to occur in extant felines (Mazzolli 2013; Pollock et al. 2022; Seidensticker and McDougal 1993), and there is strong fossil evidence that it also occurred in extinct species (Anyonge 1996; Binder and Van Valkenburgh 2010; Brown 2014; Diedrich 2021).

Rarely have such tactics been investigated in plant-eating species. However, such considerations are also pertinent for primate species that regularly practice durophagy (the eating of hard and resistant food items). An example of such durophagy occurs in the Pitheciidae, a family of South American primates composed of two sub-families, the Callicebinae (*Callicebus*, *Cheracebus*, and *Plecturocebus*) and the Pitheciinae (*Cacajao*, *Chiropotes*, and *Pithecia*). While Callicebinae largely eat insects and soft fruit (DeLuycker 2024), Pitheciinae specialize in the seeds of unripe fruits (Ayres 1986, 1989; Van Roosmalen et al. 1988; Kinzey and Norconk 1990, 1993; Barnett and Brandon-Jones 1997; Boubli 1999; Barnett et al. 2005; Barnett, Bezerra, et al. 2013; Barnett, Bowler, et al. 2013; Barnett et al. 2016; Shaffer 2013; Ledogar et al. 2018; Norconk 2021). This is especially the case for *Cacajao* and *Chiropotes* where the majority of fruits from families dominant in the diet (e.g., Euphorbiaceae, Fabaceae, Lecythidaceae, and Sapotaceae: Ayres 1989; Barnett, Bezerra, et al. 2013; Barnett, Bowler, et al. 2013; Boyle et al. 2016; Pinto et al. 2018) are hard-husked. This is either because the layers surrounding the seeds are fibrous and/or highly lignified or suberized (e.g., Euphorbiaceae,

Fabaceae, Lecythidaceae), or have yet to soften as part of the maturation process (e.g., Sapotaceae). To allow for these diets, members of the genera *Cacajao* and *Chiropotes* show distinct cranial, dental, and behavioral specializations for sclerocarpic foraging (Bouvier 1986; Kay 1990; Rosenberger 1992; Kinzey 1992; Kinzey and Norconk 1990, 1993; Anapol and Lee 1994; Norconk et al. 2009; Ledogar et al. 2013; Püschel et al. 2018). For this, individuals puncture the outer surface of a fruit (hereafter termed the “husk”: Jackson 2004) with their robust canines (Figure S4), before using the procumbent incisors (Figure S4) to remove seeds with either a tweezer-like or scraping action. Both *Cacajao* and *Chiropotes* species have well-developed mandibles and canines that provide a powerful biting force, while procumbent incisors are well-suited to seed extraction (Barnett et al. 2016; Kinzey and Norconk 1990, 1993; Shaffer 2013).

Enlarged, fiber-dense, cranial and mandibular adductor muscles are associated with durophagy and are well developed in both Pitheciidae (Anapol et al. 2008; Norconk 2021) and other mammalian taxa (e.g., carnivorans, Harano and Asahara 2022). However, while bite force mechanics have been well studied (e.g., Ledogar et al. 2018; Püschel et al. 2018; Deutsch et al. 2020), the energetics behind them are much less well known (Anapol et al. 2008; Van Casteren et al. 2022). In primates, the energetic costs of dental preparation of food are considered to be less than those of locomotion (Granatosky and Ross 2020). However, the well-established links between increased muscle mass and energetic demands (Muchlinski et al. 2012; Pontzer 2015), and the demonstration by Wall et al. (2023) that adductor muscle use is responsible for the greatest part of energetic expenditure during feeding, make it likely that saving energy via behavioral optimization of biomechanical capacity enhances fitness. This is especially likely in pitheciines where several hundred hard-husked individual fruits may be eaten in a day (AA Barnett unpublished data, 2025).

Overall, some 95% of the diet of *Chiropotes* species consists of seeds attained via sclerocarpic foraging (Mittermeier and van Roosmalen et al. 1981; Van Roosmalen et al. 1988; Ayres 1989; Kinzey and Norconk 1990, 1993; Barnett, Bowler, et al. 2013; Shaffer 2013), although members of the genus can become generalists, using insects, leaves, gum, and flowers

when seed availability is limited (Shaffer 2013). This general dietary pattern for *Chiropotes* species is exhibited by the red-nosed cuxiu (*Chiropotes albinasus*), a 3–3.5 kg member of the genus with a distribution restricted to the Madeira–Xingu interfluvium, including the forests along the Rio Tapajós, Brazil (Pinto et al. 2018). Given the large number of individual fruits that they process in a day, individual pitheciin primates run the risk of blunting, chipping, fracturing, or snapping their teeth due to the repeated stresses involved (Klukkert 2019; Ledogar et al. 2018). The golden-backed uacari (*Cacajao ouakary*), a close relative of the red-nosed cuxiu (Kay et al. 2013), selectively bites hard fruits at their weakest spots (Barnett et al. 2016). As this parallels the way in which felines inset their canines into the weakest spots between vertebrae, this may be a tactic to reduce the likelihood of food-processing related canine damage (Barnett et al. 2016), since the frequency of canine damage in pitheciines is low (even if ablation is high: See Appendix S2, Table S3, Figure S5).

Given that the red-nosed cuxiu also risks canine damage when processing the hard fruits that dominate its diet, we therefore hypothesize that individuals of this species bite fruits in ways that minimize the risk of dental damage, similar to felines and the golden-backed uacari. Consequently, we predicted that, when biting hard-husked fruits, red-nosed cuxiu would bite at the weakest point on a husk, and that:

Prediction (1) on a dehiscent fruit this bite location would be sutures (the natural lines of weakness along which such a fruit breaks to release the seed[s] within); and Prediction (2) on an indehiscent fruit (one with no sutures, or functionally indehiscent due to fused sutures), this bite location would be at the thinnest point of the husk.

## 2 | Methods

### 2.1 | Study Site

As part of a broader primatological (Barnett et al. 2017; Barnett, Bezerra, et al. 2013, Barnett, Bowler, et al. 2013; Barnett, dos Santos-Barnett, et al. 2023; Barnett, Stone, et al. 2023; dos Santos-Barnett et al. 2022; Jucá et al. 2020; Tomanek et al. 2020) and ecological (de Oliveira et al. 2020) initiative, the study was conducted along the mid-Tapajós River, centering on the mouth of Jamanxim River, Pará State, Brazil (Figure 1). Between October 2013 and December 2014, a survey team of two to three people searched for primates from boats (both sides of the river and covering 125 km on each bank) between 0530 and 1830 h, and via a system of five terrestrial trails from 0600 to 1000 h and 1400 to 1800 (Figure 1). The latter totalled 36 km in length, with individual trail lengths varying from 4 to 9 km. We covered each river and land transect three times a month. While primates in the region were not habituated to humans, hunting pressure was low at the time of the survey (de Oliveira et al. 2020), and red-nosed cuxiu showed little fear of the researchers. Despite this, a distance of 10 m was maintained from any observed feeding group to avoid provoking a flight reaction by the monkeys. Whenever feeding red-nosed cuxiu were encountered, the feeding tree species were noted, and GPS locations were recorded.

### 2.2 | Fruit Collection

To test our hypothesis that red-nosed cuxiu bite fruits at the weakest part of the husk, the distribution of bite marks were analyzed on the husks of dehiscent and indehiscent fruits from 27 tree species observed being eaten by red-nosed cuxiu at the Tapajós study site (Barnett, Bezerra, et al. 2013). These species analyzed here were selected from the 41 whose fruits were recorded by Barnett, Bezerra, et al. (2013) as being eaten by red-nosed cuxiu on the mid-Tapajós, as the fruits were (i) retrievable and (ii) present in sufficient numbers for statistical analysis.

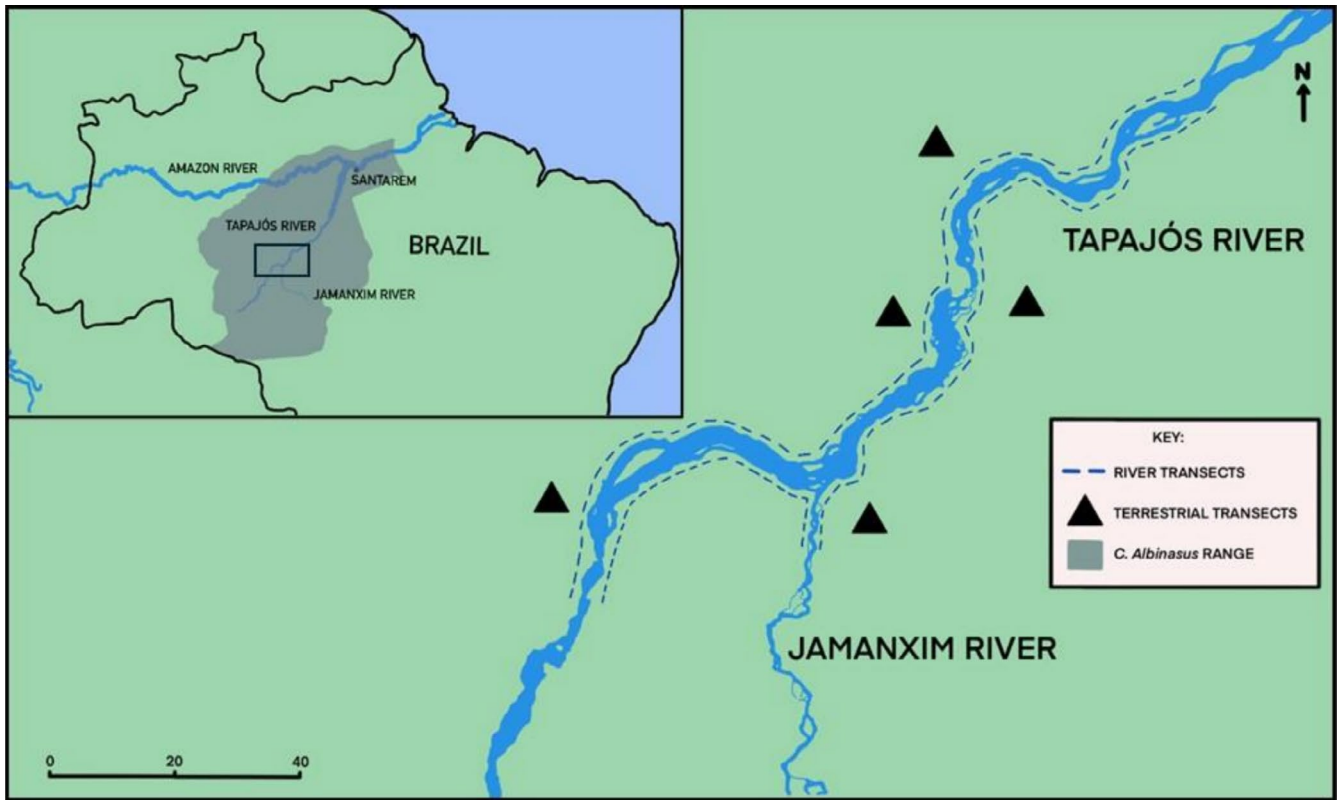
Fruits that had been fed upon by red-nosed cuxiu were collected from under trees in which groups of the species had been observed feeding (Figure S6). Fruits were removed from the ground as soon as the animals had left the feeding site. Whole fruits, at the same ripeness stage as those on which the animals had been feeding (determined by comparative color, size, shape, and hardness), were collected for penetrability analysis, using a combination of those fruits knocked to the ground during feeding bouts and others retrieved from branches (using a pole-mounted horticultural pruner or cord-mounted commando saw, depending on the height of the target branch: see Barnett 1995). Fruits with fungal infestations were excluded. Plants were identified using general (e.g., Gentry 1993; Ribeiro et al. 1999) or group-specific (e.g., Mori and Prance 1990) floras, with Roosmalen (1985) being used specifically for fruits. Taxonomy of identified taxa was checked against World Flora Online (<https://wfoplantlist.org/>) to ensure that nomenclature was current.

Fruits of 17 of the 27 species had sutures ( $N=654$  individual fruits), of which six species ( $N=204$  individual fruits) were functionally indehiscent due to fused sutures (a situation where the suture, though clearly observable, is composed of tissue that no longer contains the central line that, through suberization and apoptosis, otherwise results in the lateral separation of tissues that ends in dehiscence: Ballester and Ferrándiz 2017; Roberts et al. 2002). Thus, though morphologically in possession of a suture, such fruits are functionally indehiscent. The fruit of the remaining 10 tree species ( $N=161$  individual fruits) lacked any form of suture.

### 2.3 | Measuring Penetrability

Suture penetrability and face penetrability were recorded on a total of 462 freshly collected fruits from 15 of the 17 sutured species studied (11 species with non-fused sutures and 4 species with fused sutures; Table 1). Penetrability data are missing for two species with fused sutures (*Dalium* sp. and *Swartzia polyphylla*), although bite preferences were recorded for these two species (Table 2).

Penetrability was quantified using a prosthetic *Chiropotes* canine mounted on a standard fruit penetrometer to maximize repeatability (Facchini FT 011 Fruit Firmness Tester, marketed by International Ripening Company, Norfolk, VA 23502-2095; Barnett et al. 2015). Here, a lower number indicates a softer fruit and thus higher penetrability. The prosthetic



**FIGURE 1** | Location of the study site (mid-Rio Tapajós) showing the seven transects (two river transects); five terrestrial transects, and (inset) the site in relation to the geographical range of the red-nosed cuxiu, *Chiropotes albinasus*.

*Chiropotes* canine was used instead of the standard penetrometer head due to the smaller width of the prosthetic (1.25 mm) and flared shape compared to the width and shape of the standard cylindrical penetrometer head (7.8 mm). In consequence, the prosthetic canine provided more analogous results for the force required by the red-nosed cuxiu to penetrate the  $\leq 1$  mm-wide sutures (see image in Barnett et al. 2015). Some studies of fruit penetrability have taken just one penetrometer measurement per face, considering that more than one puncture in the husk of the same fruit might make it easier to penetrate (e.g., Mourthé et al. 2008). However, Barnett et al. (2016) showed that this is not the case in fruits eaten by the golden-backed uacari (*Cacajao ouakary*), a close relative of the red-nosed cuxiu (*Chiropotes albinasus*). The fruits studied by Barnett et al. (2016) included both the genera and species studied here. Nevertheless, it was considered prudent for the current study to take a single husk face measurement and a single suture measurement per fruit, regardless of whether the fruit had one suture (e.g., Fabaceae) or multiple sutures (e.g., Euphorbiaceae).

The fruit tester gave values in  $\text{kg}/\text{mm}^2$ . This was converted to Megapascals (MPa), the international unit for measuring material breakage (e.g., Lucas et al. 2000; Mourthé et al. 2008; with  $1 \text{ kg}/\text{mm}^2 = 9.80665 \text{ MPa}$ ). Both units appear in Table 1. Table 1 also lists fruits as “hard”/“not hard”, based on the ease with which a human fingernail could invade the husk surface. For species classified by this qualitative assessment as “hard,” eight of 11 had a penetrometer value exceeding  $3 \text{ kg}/\text{mm}^2$  (29.42 MPa), while three of four species so classified as ‘soft’ had a value of  $< 2 \text{ kg}/\text{mm}^2$  (19.61 MPa). The penetrometer values for the

intermediate species (*Abuta* cf. *panurensis*, *Chaunochiton loranthoides*, *Couratari* cf. *tenuicarpa*, and *Swartzia polyphylla*) and the reasons for their allocation to this category are discussed in Appendix S1.

## 2.4 | Quantifying Bite-Mark Location

For species with sutures, bite mark location was noted to see if they occurred more frequently along these areas of natural weakness than elsewhere on the fruit surface (Prediction 1). For sutured fruit (and following Barnett et al. 2016), bite mark scars were scored as positive if they lay either side of the suture at a distance within 10% of the fruit diameter, or if the bite had occurred directly on the suture, and negative if they appeared elsewhere on the husk surface (“face” in Table 1).

For the 10 species of tree whose husks lacked sutures, bite mark location was recorded as lying within or outside the areas which prior measurements with calipers of husk thickness from 10 transversally sectioned fruits of each species (AA Barnett unpublished data, 2025) had identified as the thinnest part (Prediction 2). Fruits lacking sutures were divided into three similar-sized sections based on proximity to the peduncle (proximal, medial, distal), and the number of bite marks in each was counted. Lists of plant species, forms, and fruit types analyzed are given in Table 2 (sutured species) and Table 3 (non-sutured species). Only fruits that red-nosed cuxiu had opened successfully ( $N=803$  individual fruits: 653 with sutures, 150 without) were analyzed. The very small proportion ( $N=51$ ,  $< 6\%$ ) of the 854 fruit originally collected that had been bitten into but not opened were excluded.

**TABLE 1** | Differences in penetrability of faces and sutures of 15 species<sup>a</sup> with sulcate fruits (11 were dehiscient with non-fused sutures and 4 were functionally indehiscent with fused sutures) eaten by the red-nosed cuxiu (*Chiropotes albinasus*) on the Rio Tapajós, Pará State, Brazil. The lower the value, the easier the part is to penetrate. One face/suture measure per fruit.

<b>Family Species</b> (NH = not hard; H = hard; FS = fused sutures/functionally indehiscent)	<b>N penetrometer</b> measures (face, suture)	<b>Penetrability value for</b> face mean $\pm$ SD (range) kg/mm <sup>2</sup> (MPa)	<b>Penetrability value</b> for suture mean $\pm$ SD (range) (kg/mm <sup>2</sup> /MPa)	<b>Which location had lowest</b> penetrability? (Wilcoxon signed-rank test)	<b>% difference in</b> penetrability of suture versus face
Non-fused sutures					
Apoocynaceae					
<i>Malouetia flavescens</i> NH	30, 30	1.73 $\pm$ 0.17 (1.4–2.0)	0.84 $\pm$ 0.05 (0.8–0.9)	Suture ( $W=900, p<0.001$ )	–51.45
<i>Tabernaemontana</i> sp. NH	28, 28	1.39 $\pm$ 0.25 (0.9–1.8)	0.71 $\pm$ 0.05 (0.6–0.8)	Suture ( $W=784, p<0.001$ )	–48.97
Euphorbiaceae					
<i>Hevea spruceana</i> H	40, 40	3.06 $\pm$ 0.59 (1.8–3.8)	1.71 $\pm$ 0.24 (1.3–2.1)	Suture ( $W=1558, p<0.001$ )	–44.24
<i>Mabea niida</i> H	60, 60	2.75 $\pm$ 0.22 (2.1–3.3)	1.86 $\pm$ 0.25 (1.4–2.5)	Suture ( $W=3565, p<0.001$ )	–32.24
Lecythidaceae					
<i>Couratari stellata</i> H	25, 25	9.64 $\pm$ 0.19 (9.2–9.9)	6.31 $\pm$ 0.42 (5.5–6.9)	Suture ( $W=625, p<0.001$ )	–34.55
<i>Couratari</i> cf. <i>tenuicarpa</i> H (brittle)	25, 25	2.30 $\pm$ 0.19 (1.8–2.6)	1.73 $\pm$ 0.08 (1.6–1.9)	Suture ( $W=625, p<0.001$ )	–24.56
<i>Eschweilera albiflora</i> H	25, 25	22.36 $\pm$ 1.96 (17.65–25.50)	16.97 $\pm$ 0.78 (15.70–18.63)	Suture ( $W=615, p<0.001$ )	–35.52
<i>Eschweilera obversa</i> H	25, 25	4.76 $\pm$ 0.65 (3.1–6.0)	3.07 $\pm$ 0.32 (2.3–3.7)	Suture ( $W=619, p<0.001$ )	–46.32
<i>Lecythis lurida</i> H	25, 25	55.90 $\pm$ 8.63 (39.23–72.57)	30.00 $\pm$ 7.65 (17.65–41.19)	Suture ( $W=549, p<0.001$ )	–13.40
Menispermaceae					
		54.52 $\pm$ 4.22 (47.07–63.74)	47.86 $\pm$ 4.22 (40.20–56.88)		

(Continues)

TABLE 1 | (Continued)

Family Species (NH = not hard; H = hard; FS = fused sutures/functionally indehiscent)	N penetrometer measures (face, suture)	Penetrability value for face mean $\pm$ SD (range) kg/mm <sup>2</sup> (MPa)	Penetrability value for suture mean $\pm$ SD (range) (kg/mm <sup>2</sup> /MPa)	Which location had lowest penetrability? (Wilcoxon signed-rank test)	% difference in penetrability of suture versus face
<i>Abuta cf. panurensis</i> NH	34, 34	2.4 $\pm$ 0.19 (2.0–2.8) 23.54 $\pm$ 1.86 (19.61–27.46)	1.67 $\pm$ 0.18 (1.4–1.9) 16.67 $\pm$ 1.77 (14.70–18.63)	Suture ( $W = 1156, p < 0.001$ )	–30.56
Myristicaceae					
<i>Iryanthera sagoitiana</i> NH	23, 23	1.7 $\pm$ 0.22 (1.4–2.3) 16.67 $\pm$ 2.16 (13.73–20.59)	1.20 $\pm$ 0.12 (0.9–1.4) 11.77 $\pm$ 1.18 (8.83–13.73)	Suture ( $W = 527, p < 0.001$ )	–30.48
Fused sutures (functionally indehiscent)					
Fabaceae					
<i>Inga alba</i> H (brittle), FS	25, 25	2.47 $\pm$ 0.16 (2.1–2.7) 24.22 $\pm$ 1.56 (20.59–26.47)	1.54 $\pm$ 0.19 (1.1–1.9) 16.96 $\pm$ 10.98 (10.78–18.63)	Suture ( $W = 625, p < 0.001$ )	–37.44
<i>Inga heterophylla</i> H (brittle), FS	25, 25	2.29 $\pm$ 1.13 (2.1–2.5) 22.45 $\pm$ 11.08 (20.59–24.51)	1.30 $\pm$ 0.22 (0.8–1.6) 12.45 $\pm$ 2.16 (7.85–15.69)	Suture ( $W = 625, p < 0.001$ )	–43.46
<i>Macrolobium acacifolium</i> H, FS	50, 50	3.05 $\pm$ 0.17 (2.5–3.6) 29.91 $\pm$ 1.67 (20.59–34.32)	5.39 $\pm$ 0.45 (4.7–6.3) 52.86 $\pm$ 1.41 (46.09–61.78)	Face ( $W = 0, p < 0.001$ )	76.66
Oilacaceae <sup>b</sup>					
<i>Chaunochiton loranthoides</i> H, FS	42, 42	2.08 $\pm$ 0.06 (2.0–2.2) 23.54 $\pm$ 1.86 (19.61–21.77)	2.80 $\pm$ 0.15 (2.6–3.1) 27.36 $\pm$ 1.47 (26.48–30.40)	Face ( $W = 0, p < 0.001$ )	34.63

<sup>a</sup>Penetrability data for *Dalium* sp. and *Swarzizia polyphylla* fruits were not available.

<sup>b</sup>Placed in Aptandraceae by some authorities.

**TABLE 2** | Comparison of bite preference by red-nosed cuxiu (*Chiropotes albinasus*) against the weakest part of the husk of sutured fruit (non-fused and fused sutures) from 17 plant species.

Family Species	Fruit type (hardness; suture ± fused)	N Fruits	N Bites (%)			Bite point preference ( $\chi^2$ test)	Weakest part of fruit husk	Preference for weakest part?
			Face only	Suture only	Face and suture			
Non-fused sutures								
Apocynaceae								
<i>Malouetia flavescens</i>	Not hard; unfused	62	15 (24.2%)	27 (43.5%)	20 (32.3%)	None ( $\chi^2 = 3.60$ ; $p = 0.17$ )	Suture	No
<i>Tabernaemontana</i> sp.	Not hard; unfused	35	5 (14.3%)	19 (54.3%)	11 (31.4%)	Suture ( $\chi^2 = 8.59$ ; $p < 0.001$ )	Suture	Yes
Euphorbiaceae								
<i>Hevea spruceana</i>	Hard; unfused	40	1 (2.5%)	35 (87.5%)	4 (10.0%)	Suture ( $\chi^2 = 54.06$ ; $p = 0.014$ )	Suture	Yes
<i>Mabea nitida</i>	Hard; unfused	24	1 (4.2%)	19 (79.2%)	4 (16.7%)	Suture ( $\chi^2 = 23.67$ ; $p < 0.001$ )	Suture	Yes
Lecythidaceae								
<i>Couratari stellata</i>	Hard; unfused	44	0 (0.0%)	43 (97.7%)	1 (2.3%)	Suture ( $\chi^2 = 83.41$ ; $p < 0.001$ )	Suture	Yes
<i>Couratari</i> cf. <i>tenuicarpa</i>	Hard (but brittle); unfused	52	1 (1.9%)	50 (96.2%)	1 (1.9%)	Suture ( $\chi^2 = 93.80$ ; $p < 0.001$ )	Suture	Yes
<i>Eschweilera albiflora</i>	Hard; unfused	49	3 (6.1%)	45 (91.8%)	1 (2.0%)	Suture ( $\chi^2 = 76.85$ ; $p < 0.001$ )	Suture	Yes
<i>Eschweilera obversa</i>	Hard; unfused	94	7 (7.4%)	84 (89.4%)	3 (3.2%)	Suture ( $\chi^2 = 135.33$ ; $p < 0.001$ )	Suture	Yes
<i>Lecythis lurida</i>	Hard; unfused	37	1 (2.7%)	35 (94.6%)	1 (2.7%)	Suture ( $\chi^2 = 63.49$ ; $p < 0.001$ )	Suture	Yes
Menispermaceae								
<i>Abuta</i> cf. <i>panurensis</i>	Not hard; unfused	41	22 (53.7%)	14 (34.1%)	5 (12.2%)	Face ( $\chi^2 = 11.05$ ; $p = 0.004$ )	Suture	No
Myristicaceae								
<i>Iryanthera sagotiana</i>	Not hard; unfused	29	12 (41.4%)	8 (27.6%)	9 (31.0%)	None ( $\chi^2 = 0.95$ ; $p = 0.62$ )	Suture	No

(Continues)

TABLE 2 | (Continued)

Family Species	Fruit type (hardness; suture ± fused)	N Bites (%)			Bite point preference ( $\chi^2$ test)	Weakest part of fruit husk	Preference for weakest part?	
		N Fruits	Face only	Suture only				Face and suture
Fused sutures (functionally indehiscent)								
Olacaceae								
<i>Chaunochiton loranthoides</i>	Hard; fused	18	2 (11.1%)	12 (66.7%)	4 (22.2%)	Suture ( $\chi^2 = 9.53$ ; $p = 0.009$ )	Face	No
Fabaceae								
<i>Inga alba</i>	Hard (but brittle); fused	47	34 (72.3%)	9 (19.1%)	4 (8.5%)	Face ( $\chi^2 = 33.76$ ; $p < 0.001$ )	None	No
<i>Inga heterophylla</i>	Hard (but brittle); fused	50	35 (70.0%)	2 (4.0%)	13 (26.0%)	Face ( $\chi^2 = 34.45$ ; $p < 0.001$ )	Suture	No
<i>Dalium</i> sp.	Hard; fused	32	30 (93.8%)	1 (3.1%)	1 (3.1%)	Face ( $\chi^2 = 53.41$ ; $p < 0.001$ )	n/a <sup>a</sup>	n/a <sup>a</sup>
<i>Macrolobium acacifolium</i>	Hard; fused	46	44 (95.7%)	0 (0.0%)	2 (4.3%)	Face ( $\chi^2 = 81.79$ ; $p < 0.001$ )	Face	Yes
<i>Swartzia polyphylla</i>	Not hard; fused	17	11 (64.7%)	3 (17.6%)	3 (17.6%)	Face ( $\chi^2 = 7.73$ ; $p = 0.021$ )	n/a <sup>a</sup>	n/a <sup>a</sup>

<sup>a</sup>Penetrability data for *Dalium* sp. and *Swartzia polyphylla* fruits were not available.

TABLE 3 | Bite preferences among proximal, medial, and distal sectors of 10 species of indehiscent (non-sutured) fruits: general location preference versus preference at thinnest sector of the fruit.

Family Species	N Fruits	N Bites	Sector (%)			General preference for a sector? ( $\chi^2$ test)	Thinnest sector	Preference at thinnest sector? ( $\chi^2$ test)
			Proximal	Medial	Distal			
Chrysobalanaceae								
<i>Licania canescens</i>	8	12	3 (25.0%)	5 (41.7%)	4 (33.3%)	No ( $\chi^2 = 0.51$ ; $p = 0.78$ )	Sectors equal	N/A; sectors equal
Humeriaceae								
<i>Endopleura uchi</i>	17	23	6 (26.1%)	9 (39.1%)	8 (34.8%)	No ( $\chi^2 = 0.60$ ; $p = 0.74$ )	Sectors equal (though mesocarp rugose)	N/A; sectors equal
Myrtaceae								
<i>Calyptanthus</i> sp.	10	10	3 (30.0%)	5 (50.0%)	2 (20.0%)	No ( $\chi^2 = 1.48$ ; $p = 0.48$ )	Medial	No ( $\chi^2_1 = 1.31$ ; $p = 0.25$ )
<i>Eugenia</i> sp.	9	9	3 (33.3%)	4 (44.4%)	2 (22.2)	No ( $\chi^2 = 0.72$ ; $p = 0.70$ )	Medial	No ( $\chi^2_1 = 0.53$ ; $p = 0.47$ )
Polygalaceae								
<i>Moutabea guinensis</i>	14	19	5 (26.3%)	7 (36.8%)	7 (36.8%)	No ( $\chi^2 = 0.39$ ; $p = 0.82$ )	Sectors equal	N/A; sectors equal
Rubiaceae								
<i>Duroia</i> sp.	14	14	3 (21.4%)	7 (50.5%)	4 (28.6%)	No ( $\chi^2 = 1.92$ ; $p = 0.38$ )	Medial	No ( $\chi^2_1 = 1.83$ ; $p = 0.18$ )
Sapotaceae								
<i>Chromolaucuma rubiflora</i>	21	21	9 (42.9%)	3 (14.3%)	9 (42.95)	No ( $\chi^2 = 3.33$ ; $p = 0.19$ )	Proximal and Distal	No ( $\chi^2_1 = 3.33$ ; $p = 0.068$ )
<i>Manilkara bidentata</i>	22	28	10 (35.7%)	5 (17.9%)	13 (46.4%)	No ( $\chi^2 = 3.28$ ; $p = 0.19$ )	Proximal and Distal	No ( $\chi^2_1 = 2.90$ ; $p = 0.088$ )
<i>Pouteria bilocularis</i>	13	14	6 (42.9%)	2 (14.3%)	6 (42.9%)	No ( $\chi^2 = 2.22$ ; $p = 0.33$ )	Proximal and Distal	No ( $\chi^2_1 = 2.22$ ; $p = 0.14$ )
<i>Pouteria cuspidata</i>	20	20	9 (45.0%)	2 (10.0%)	9 (45.0%)	No ( $\chi^2 = 4.79$ ; $p = 0.091$ )	Proximal and Distal	Yes ( $\chi^2_1 = 4.79$ ; $p = 0.029$ )

Sutured fruits had a range of husk hardnesses and occurred in both dehiscent and functionally indehiscent forms (Figure 2). In indehiscent species, husk thickness varied both between and within the husk itself (Figure 3).

## 2.5 | Statistical Analysis

We tested if there were differences in penetrability of the suture and face locations for each of the sulcate fruit species using Wilcoxon signed-rank tests. We then tested if there was a difference in the number of bites on the suture versus the face for the sulcate species using Chi-Square tests, allowing us to determine if there was a bite preference for the weakest area of the sulcate fruits.

For the 10 indehiscent fruits, we tested if there was a difference in general bite location (proximal, medial, and distal sectors) using chi-square tests. Then, using prior information on the thinnest sectors of the fruits, we coded each bite based on whether it was at the thinnest sector (given that some fruits had both the proximal

and distal sectors as the thinnest). We then used chi-square tests to test if bite location occurred more often at the thinnest section than what was predicted based on the number of thinnest sections (i.e., some species had one sector that was thinnest, while other species had two sectors that were equally thinnest). All tests were completed in R 4.4.1 (R Foundation for Statistical Computing 2024).

## 3 | Results

### 3.1 | Variation in Force Needed to Experimentally Penetrate Fruit Husk at Sutures/Face of Dehiscent Fruits

All 11 (100%) sulcate species with non-fused sutures, the force needed to penetrate the suture was lower than the face (range: 12.33%–51.50% lower; mean: 36.24%; see Table 1 for details on each species). There was also a difference in penetrability in all four species with fused sutures, but the face had lower penetrability for two species (*Chaunochiton loranthoides* and



**FIGURE 2** | Examples of sutured fruits sampled for this study, showing the range of suture types and husk hardnesses. Sutured but functionally indehiscent, (A) *Chaunochiton loranthoides* (Olacaceae)–fused sutures form thickened ridges, (B) *Macrolobium acaciifolium* (Fabaceae)–fused sutures form thickened grooves; Sutured and dehiscent, (C) *Eschwieleria tenuifolia* (Lecythidaceae)–leathery fruit with single non-fused suture, (D) *Hevea spruceana* (Euphorbiaceae)–hard fruit with three non-fused sutures; (E) *Malouetia flavescens* and *Tabernaemontana* sp. (both Apocynaceae)–both soft fruit, each with a single non-fused suture. Though possessing sutures, *C. loranthoides* and *M. acaciifolium* are functionally indehiscent, while those of *E. tenuifolia*, *H. spruceana*, *M. flavescens*, and *T. abernaemontana* sp. do dehisce.



**FIGURE 3** | Examples of unsutured (and so indehiscent) fruits sampled for this study, showing the range of husk thicknesses, both between species and within a single fruit. (A) *Eugenia* sp. (Myrtaceae); (B) *Pouteria cuspidata* (Sapotaceae); (C) *Manilkara bidentata* (Sapotaceae); (D) *Licania canescens* (Chrysobalanaceae).

*Macrolobium acaciifolium*), and the suture had lower penetrability for two species (*Inga alba* and *I. heterophylla*; Table 1).

### 3.2 | Preference for Bite Site on Dehiscent (Sutured) Fruits Compared to Weakest Part of the Fruit Husk

Of the 17 tree species with sutured fruits, red-nosed cuxiu clustered their bites at the suture for 8 of the 11 (72.7%) dehiscent species and for 1 of the 6 (16.7%) functionally indehiscent species. Bites were clustered at the fruit's face for 1 of 11 (9.1%) dehiscent species and 5 of 6 (83.3%) functionally indehiscent species (Table 2). These bite preferences were located at the weaker area of the fruit for 8 of 11 (72.7%) dehiscent species (these 8 species all had sutures as the weakest area) and 1 of 4 (25.0%) indehiscent species (as 2 species did not have penetrability data associated with them). For the 3 dehiscent species where red-nosed cuxius did not display a bite preference for the suture (*Abuta* cf. *panurensis*, *Malouetia flavescens*, and *Iryanthera sagotiana*), the face was the weakest part of the fruit. None of these fruits were highly sclerotized, with each showing low penetrability values for both the face and suture (Table 1).

### 3.3 | Preference for Bite Site on Non-Sutured (Indehiscent) Fruits

There was no general bite preference pattern among proximal, medial, and distal sectors for fruits from any of the 10 indehiscent species (Table 3). For 3 of the fruit species, there was no difference in thinness among the three sections of the fruits. For the remaining 7 species, 3 species were thinnest at the medial sector, and 4 species were thinnest at the proximal and distal sectors. For the 7 species where there were differences in fruit

thinness, bite preference for the thinnest sectors was demonstrated in only 1 species: *Pouteria cuspidata* (Table 3, Figure 3).

## 4 | Discussion

For all 11 dehiscent species with functioning (non-fused) sutures eaten by red-nosed cuxiu and analyzed here, sutures were the easiest area of the husk to penetrate. Quantification of bite mark locations on these fruits showed significant clustering along sutures in 8 of these species (72.7%). This provides support for our Prediction 1 that for dehiscent fruit, bite locations would be concentrated on the sutures. The 10 species lacking sutures did not show this pattern, as bites did not cluster on the thinnest (and most easily penetrated) parts of the husk. For a further 5 species which had sutures, but the fruits were functionally indehiscent, bites were clustered at the sutures for one species and clustered at the face for 5 species. When examining these bite preferences with the areas that were easier to penetrate, only 1 of 4 species had bites clustered on the weaker area of the fruit. Therefore, other elements of foraging optimality may, instead, be operating and driving bite-site choice. Among these is the ease of manipulation, which is a key element in minimizing processing time. The ergonomics of pitheciine foraging have been explored by da Dias Silva et al. (2020) for a species of *Cacajao*, the genus most closely related to *Chiropotes*. Their study showed that when selecting *Aldina latifolia* (Fabaceae) across a range of sizes, golden-backed uacaris (*Cacajao ouakary*) experimented with large fruit, but processed those in the mid-range that allowed ease of manual manipulation and dental positioning. None of the fruits considered here are as large as those of *A. latifolia* (which may reach 13 cm in length). However, the per-unit cost-benefit of diet item processing (*sensu* Ménard and Vallet 1997) may explain apparent anomalies observed here, especially if the ergonomics of foraging are optimized to both minimize

processing time and the risk of dental damage. In the functionally indehiscent *Maclobium acaciifolium*, the fused suture is heavily sclerotized, leaving the faces of the single-seeded pod as the weakest entry point, which is where red-nosed cuxiu bite sites occurred. However, for a further 5 species, the structurally weakest areas were not those used by red-nosed cuxiu to access the seeds within.

For the 4 fruit species (1 dehiscent and 3 functionally indehiscent) in which cuxiu preferred to bite the harder part of the fruit, it is possible that fruit shape or other physical characteristics may influence the selection of bite penetration sites. For example, in *Chaunochiton loranthoides* (Olacaceae) the sutures are fused into prominent ridges on the surface of an otherwise smooth surface. Bites were concentrated at the base of these, possibly as this provides a reliable place to wedge the canine tip prior to biting. Both *Inga* (Fabaceae) species have a fruit that is long, thin, and with a husk that is hard, but thin and therefore brittle and easily penetrated. Accordingly, there would be little to gain in dental security spending the extra time required to position canines on the more sclerotized area surrounding the suture; indeed, it might be hard to manipulate such a long fruit to do so effectively. This may also apply to one of the two species where no preferential area was recorded, one (*Malouetia flavescens*, Apocynaceae), whose pencil-thick pods may reach 25 cm in length. Significantly, a preference for sutures was recorded in the shorter (to 14 cm), broader (to 1.5 cm) pods of *Tabernamontana* (Apocynaceae), even though these are not sclerotized. This could be due to the deep groove of the suture providing a convenient insertion point for the canines. The lack of bite-site preference in *Iryanthera sagotiana* (Myristicaceae) may be due to the low penetrability of both the face and suture (means of  $1.7 \pm 0.22/16.67 \pm 2.16$  and  $1.2 \pm 0.12/11.77 \pm 1.17$  kg/mm<sup>2</sup>/MPa, respectively). For *Abuta* cf. *panurensis* (Menispermaceae) the preferred bite site lay on the face, despite the suture having a lower penetrability value. This may occur because the suture is very narrow (a width of <0.5 mm) and so it is difficult to access effectively with a canine tip. In addition, fruit of this species are small (6 mm diameter), so the handling and manipulation associated with accurate positioning of the canine may be too time-consuming an investment to compensate for the small energetic yield of the seed (a 4 mm sphere). In contrast, why locational selectivity occurred in *Pouteria cuspidata* is unclear since the fruit are neither the largest nor smallest of the analyzed Sapotaceae (Pennington 1990), nor do the fruits vary in husk or pulp thickness.

Finally, it should be noted that none of the fruits used had been fed on, since the actions associated with feeding would have damaged fruits in ways that would have made it hard to measure suture penetrability in a repeatable manner (especially as they were no longer whole and so lacked intrinsic mechanical auto-support of an entire fruit). Because of this, we cannot unambiguously assert that the measured values were what foraging red-nosed cuxiu actually met, as they might possess means of choosing fruits with the lowest penetrability values. Accordingly, our data compares penetrability values of fruits these animals would have encountered on trees and records the penetrability of their faces and sutures.

Although the strength of the pitheciin bite (~145 N at the canine in *Chiropotes*; Ledogar et al. 2018) would be more than capable

of penetrating the studied fruits at any point on their surfaces, for the majority of the fruits studied, bite sites were not randomly dispersed over the fruit surface. For just over half of the fruit species, bite marks concentrated on or around the suture, notably when the suture is generally found to be the weakest sector of the fruit. For one of the species (*Maclobium acaciifolium*), where the suture was not the weakest point, the face of the fruit was the chosen bite site. Thus, the choice of bite site in these instances is likely to be mediated by strategies to (i) avoid damage to the tips of the canines (which are key to effective penetration), (ii) save energy on each of the multitude of bites that occur throughout the day, or a combination of both. That this may be the latter is shown by the results of Barnett et al. (2015), whose simulations with a prosthetic canine found that those with broken tips required greater force to penetrate the surface of test fruits than those where the canine tips were intact. That this may be significant for species like *Chiropotes* (and related genera like *Cacajao*) can be seen in the fact that fruits with prominent sutures, such as the Euphorbiaceae and Lecythidaceae, form prominent parts of their diets (Barnett, Bezerra, et al. 2013; Barnett, Bowler, et al. 2013; Pinto et al. 2018). Moreover, although sutures will rupture in dehiscent fruits when ripe, their role as access points for pitheciines is accentuated by the predominance of unripe fruit and their seeds in the subfamily Pitheciinae (Norconk 2021).

However, that the overall situation is complex and influenced by multiple factors can be seen in *Inga* and *Malouetia*, where the shape of the fruit and the time constraints of handling long, thin, forms may override the impetus to bite at more easily penetrated sutures. There is also the consideration that, for all three of these species, the husk is resistant but brittle (i.e., they are stress-limited; Lucas 2004), so that catastrophic failure of the seed husk material (Lucas et al. 2009) may occur more quickly when force is applied to areas other than the suture. For *Abuta*, it seems likely that small size and extremely narrow sutures mean that this form of selectivity could not be deployed. For non-sutured species, it seems likely that differences in thickness in sectors of the husk do play a role in bite site choice, with a preference being on the thinner sectors. However, more extensive sampling is required before that can be fully confirmed. As the strategy is likely to be a combination of canine-tip maintenance and optimization of time/energy constraints, such sampling is highly desirable as the non-sutured family Sapotaceae is a prominent component of the diet of members of the genus *Chiropotes* and other members of the subfamily pitheciinae (Ayres 1989; Norconk 2021).

That focusing bites on sutures when opening dehiscent fruits is not restricted just to the red-nosed cuxiu can be seen from the fact that black-bearded cuxiu (*Chiropotes sagulatus*) at Brownsberg Nature Park, Suriname, have also been observed to open a variety of fruits along sutures (J Ledogar unpublished data, 2025). These include *Carapa guianensis* (Meliaceae), *Clusia grandiflora* (Clusiaceae), and *Qualea* sp. (Vochysiaceae), in addition to a number of unidentified fruits. Furthermore, many of the plant genera included here were shown to be treated in a similar manner by the golden-backed uacari (Barnett et al. 2016). This processing mechanism matches well with the suggestions in the literature that, for durophagous species, there will be strong selection for the precise application of bite forces (Ross and

Iriarte-Díaz 2014; Granatosky and Ross 2020; Wall et al. 2023). While studies such as Ross and Iriarte-Díaz (2014), Granatosky and Ross (2020) and Wall et al. (2023) refer to the precision of dental occlusion, the current study has clearly shown that another form of precision is being applied by durophagous pitheciines.

Results of the current study indicate that this processing technique may be deployed widely in pitheciin primates. Consequently, studies should be performed to confirm such bite specificity in sakis (genus *Pithecia*), the third member of the subfamily Pitheciinae to which *Cacajao* and *Chiropotes* belong. It would be interesting to see if this behavior is also present in the smaller and more basal titis (subfamily Callicibinae), where the canines are enlarged but not to the extent as in the Pitheciinae. For pitheciines, analysis of body size and bite mechanics has been conducted for *Pithecia*, *Chiropotes*, and *Cacajao* (Ledogar et al. 2018), and for titi monkeys by Püschel et al. (2018), but neither considered the possibility of bite selectivity indicated by the current study. Consequently, a study based on pitheciin body and jaw size would allow an analysis of the potential influences of masseter muscle volume on bite penetration points selection and enhance our understanding of foraging in this highly specialized clade of primates (Norconk and Veres 2011; Norconk 2021).

However, such behavior patterns are unlikely to be found in other neotropical mammals feeding on hard-husked fruits, as they either use their powerful molars (capuchin monkeys: Wright 2005; peccaries: Hendges et al. 2019) and tools (capuchins: Visalberghi et al. 2008) to crush the husks prior to extracting the seeds. Squirrels are notable seed predators and, in the Amazon, *Sciurus spiciceps* feeds on the same seed species as pitheciines (Cintra and Horna 1997; Barnett 2010). Like pitheciines, they deploy teeth at the front of the dental arcade (incisors) to access seeds, but a pitheciines-like bite specificity does not appear to have been recorded in this group (Casanovas-Vilar and van Dam 2013; Cox et al. 2012; Koyabu et al. 2009). This may be due to the relatively small size of sciurids in general, and the incisors' central position in the dental arc, both of which limit the size of a curved object that can be partially engulfed in the buccal cavity when biting takes place (da Dias Silva et al. 2020). Thus, the dental morphology so characteristic of the Pitheciinae (Norconk 2021) is not only finely adapted to sclerocarpic foraging (Kinzey 1992) but, as reported here, to its finessed deployment, reflecting the fact that the sub-family is unique among primates in using canines in food processing and not social display (da Dias Silva et al. 2020).

#### Author Contributions

**Adrian A. Barnett, Gemma Penhorwood, Sarah A. Boyle, Ben Klinkenberg:** conceptualization. **Adrian A. Barnett, Tadeu G. de Oliveira:** funding acquisition. **Adrian A. Barnett, Gitana N. Cavalcanti, Tadeu G. de Oliveira:** investigation. **Adrian A. Barnett:** methodology, project administration, resources and validation. **Adrian A. Barnett and Sarah A. Boyle:** software. **Adrian A. Barnett and Sarah A. Boyle:** supervision. **Adrian A. Barnett, Gemma Penhorwood, Ellie Little, Rebecca Bonham, Maisie Carter, Sarah A. Boyle, Richelly S. Andrade, Tereza C. Santos-Barnett, Renann H. P. Dias da Silva, Lucy M. Todd, Jen Muir, Marcelo**

**Menzenes, Gitana N. Cavalcanti, Tadeu G. de Oliveira, Justin A. Ledogar, Ben Klinkenberg:** visualization. **Adrian A. Barnett, Sarah A. Boyle, Renann H. P. Dias da Silva:** writing – original draft. **Adrian A. Barnett, Gemma Penhorwood, Ellie Little, Rebecca Bonham, Maisie Carter, Sarah A. Boyle, Richelly S. Andrade, Tereza C. Santos-Barnett, Renann H. P. Dias da Silva, Lucy M. Todd, Jen Muir, Marcelo Menzenes, Gitana N. Cavalcanti, Tadeu G. de Oliveira, Justin A. Ledogar, Ben Klinkenberg:** writing – review and editing.

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#### Disclosure

The authors have nothing to report.

#### Conflicts of Interest

The authors declare no conflicts of interest.

#### Data Availability Statement

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.g79cnp63n>.

#### References

- Anapol, F., and S. Lee. 1994. "Morphological Adaptation to Diet in Platyrrhine Primates." *American Journal of Physical Anthropology* 94, no. 1: 239–261. <https://doi.org/10.1002/ajpa.1330940208>.
- Anapol, F., N. Shahnoor, and C. F. Ross. 2008. "Scaling of Reduced Physiologic Cross-Sectional Area in Primate Muscles of Mastication." In *Primate Craniofacial Function and Biology*, 201–216. Springer US. [https://doi.org/10.1007/978-0-387-76585-3\\_10](https://doi.org/10.1007/978-0-387-76585-3_10).
- Anyonge, W. 1996. "Microwear on Canines and Killing Behavior in Large Carnivores: Sabre Function in *Smilodon Fatalis*." *Journal of Mammalogy* 77, no. 4: 1059–1067. <https://doi.org/10.2307/1382786>.
- Aristizabal, J. F., J. M. Rothman, L. M. García-Ferriá, and J. C. Serio-Silva. 2017. "Contrasting Time-Based and Weight-Based Estimates of Protein and Energy Intake of Black Howler Monkeys (*Alouatta pigra*)." *American Journal of Primatology* 79, no. 4: 1–8. <https://doi.org/10.1002/ajp.22611>.
- Ayres, J. M. 1986. "Uakaris and Amazonian Flooded Forest." Ph.D. Thesis, University of Cambridge.
- Ayres, J. M. 1989. "Comparative Feeding Ecology of the Uakari and Bearded Saki, *Cacajao* and *Chiropotes*." *Journal of Human Evolution* 18, no. 7: 697–716. [https://doi.org/10.1016/0047-2484\(89\)90101-2](https://doi.org/10.1016/0047-2484(89)90101-2).
- Ballester, P., and C. Ferrándiz. 2017. "Shattering Fruits: Variations on a Dehiscent Theme." *Current Opinion in Plant Biology* 35: 68–75. <https://doi.org/10.1016/j.pbi.2016.11.008>.
- Barnett, A. A. 1995. "Primates. Expedition Advisory Centre, Royal Geographical Society, London." Expedition Field Techniques Series, No. 6.

- Barnett, A. A. 2010. "Diet, Habitat, Use and Conservation Ecology of the Golden-Backed Uacari, *Cacajao melanocephalus* Ouakary, in Jaú National Park, Amazonian Brazil (PhD Thesis, Roehampton University)." [https://pure.roehampton.ac.uk/ws/portalfiles/portal/442220/Barnett\\_thesis\\_combined.pdf](https://pure.roehampton.ac.uk/ws/portalfiles/portal/442220/Barnett_thesis_combined.pdf).
- Barnett, A. A., B. Bezerra, P. Santos, et al. 2016. "Foraging With Finesse: A Hard-Fruit-Eating Primate Selects the Weakest Areas as Bite Sites." *American Journal of Physical Anthropology* 160, no. 1: 113–125. <https://doi.org/10.1002/ajpa.22935>.
- Barnett, A. A., B. M. Bezerra, M. Oliveira, H. M. Queiroz, and T. R. Defler. 2013. "Cacajao ouakary in Brazil and Colombia: Patterns, Puzzles and Predictions." In *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*, edited by L. Veiga, A. Barnett, S. Ferrari, and M. Norconk, 179–195. Cambridge University Press. <https://doi.org/10.1017/CBO9781139034210.022>.
- Barnett, A. A., M. Bowler, B. M. Bezerra, and T. R. Defler. 2013. "Ecology and Behaviour of Uacaris (Cacajao)." In *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*, edited by L. Veiga, A. Barnett, S. Ferrari, and M. Norconk, 151–172. Cambridge University Press. <https://doi.org/10.1017/CBO9781139034210.020>.
- Barnett, A. A., and D. Brandon-Jones. 1997. "The Ecology, Biogeography and Conservation of the Uakaris, *Cacajao* (Pitheciinae)." *Folia Primatologica* 68, no. 1: 223–235.
- Barnett, A. A., C. V. de Castilho, R. L. Shapley, and A. Anicacio. 2005. "Diet, Habitat Selection and Natural History of *Cacajao melanocephalus* Ouakary in Jaú National Park, Brazil." *International Journal of Primatology* 26, no. 4: 949–969. <https://doi.org/10.1007/s10764-005-5331-5>.
- Barnett, A. A., T. C. dos Santos-Barnett, J. Muir, et al. 2023. "Beans With Bugs: Covert Insectivory and Infested Seed Selection by the Red-Nosed Cuxiu Monkey, *Chiropotes albinasus*." *Biotropica* 55, no. 2: 579–593. <https://doi.org/10.1111/btp.13207>.
- Barnett, A. A., P. J. P. Santos, A. S. Boyle, and B. M. Bezerra. 2015. "An Improved Technique Using Dental Prostheses for Field Quantification of the Force Required by Primates for the Penetration of Fruit." *Folia Primatologica* 86, no. 2: 398–410. <https://doi.org/10.1159/000434677>.
- Barnett, A. A., J. M. Silla, T. de Oliveira, et al. 2017. "Run, Hide or Fight: Anti-Predation Strategies in Endangered Red-Nosed Cuxiú (*Chiropotes Albinasus*, Pitheciidae) in South-Eastern Amazonia." *Primates* 58, no. 2: 353–360. <https://doi.org/10.1007/s10329-017-0596-9>.
- Barnett, A. A., A. I. Stone, P. Shaw, et al. 2023. "When Food Fights Back: Cebid Primate Strategies of Larval Paper Wasp Predation and the High-Energy Yield of High-Risk Foraging." *Austral Ecology* 48, no. 2: 719–742. <https://doi.org/10.1111/aec.13287>.
- Binder, W. J., and B. Van Valkenburgh. 2010. "A Comparison of Tooth Wear and Breakage in Rancho La Brea Sabertooth Cats and Dire Wolves Across Time." *Journal of Vertebrate Paleontology* 30, no. 1: 255–261. <https://doi.org/10.1080/02724630903413016>.
- Boubli, J. P. 1999. "Feeding Ecology of Black-Headed Uacaris (*Cacajao melanocephalus Melanocephalus*) in Pico da Neblina National Park, Brazil." *International Journal of Primatology* 20, no. 2: 719–749. <https://doi.org/10.1023/A:1020704819367>.
- Bouvier, M. 1986. "Biomechanical Scaling of Mandibular Dimensions in New World Monkeys." *International Journal of Primatology* 7, no. 23: 551–567. <https://doi.org/10.1007/BF02736661>.
- Boyle, S. A., C. L. Thompson, A. DeLuycker, et al. 2016. "Geographic Comparison of Plant Genera Used in Frugivory Among the Pitheciids *Cacajao*, *Callicebus*, *Chiropotes*, and *Pithecia*." *American Journal of Primatology* 78, no. 2: 493–506. <https://doi.org/10.1002/ajp.22422>.
- Brown, J. 2014. "Jaw Function in *Smilodon Fatalis*: A Reevaluation of the Canine Shear-Bite and a Proposal for a New Forelimb-Powered Class 1 Lever Model." *PLoS One* 9, no. 10: 1–14. <https://doi.org/10.1371/journal.pone.0107456>.
- Casanovas-Vilar, I., and J. van Dam. 2013. "Conservatism and Adaptability During Squirrel Radiation: What Is Mandible Shape Telling Us?" *PLoS One* 8, no. 4: e61298. <https://doi.org/10.1371/journal.pone.0061298>.
- Cintra, R., and V. Horna. 1997. "Seed and Seedling Survival of the Palm *Astrocaryum murumuru* and the Legume Tree *Dipteryx micrantha* in Gaps in Amazonian Forest." *Journal of Tropical Ecology* 13, no. 1: 257–277. <https://doi.org/10.1017/S0266467400010440>.
- Cox, P. G., E. J. Rayfield, M. J. Fagan, A. Herrel, T. C. Pataky, and N. Jeffery. 2012. "Functional Evolution of the Feeding System in Rodents." *PLoS One* 7, no. 4: e36299. <https://doi.org/10.1371/journal.pone.0036299>.
- da Dias Silva, R. H. P., M. Castro-Sá, F. Baccaro, P. Tomacek, and A. A. Barnett. 2020. "Juggling Options: Optimal Selection of Size-Weight Combinations of *Aldina latifolia* (Fabaceae) Pods by *Cacajao ouakary* (Pitheciidae)." *Biotropica* 52, no. 6: 1275–1285. <https://doi.org/10.1111/btp.12835>.
- de Oliveira, T. G., D. Mazim, O. Q. Vieira, et al. 2020. "Nonvolant Mammal Megadiversity and Conservation Issues in a Threatened Central Amazonian Hotspot in Brazil." *Tropical Conservation Science* 9, no. 2: 1–16. <https://doi.org/10.1177/1940082916672340>.
- DeLuycker, A. 2024. "Diet and Feeding Ecology of the Critically Endangered San Martín Titi Monkey (*Plecturocebus oenanthe*) in Peru." *International Journal of Primatology* 45, no. 1: 104–126. <https://doi.org/10.1007/s10764-021-00256-w>.
- Deutsch, A. R., E. Dickinson, K. C. Leonard, F. Pastor, M. N. Muchlinski, and A. Hartstone-Rose. 2020. "Scaling of Anatomically Derived Maximal Bite Force in Primates." *Anatomical Record* 303, no. 7: 2026–2035. <https://doi.org/10.1002/ar.24284>.
- Diedrich, C. G. 2021. "Top Predators at War—Ice Age Lions Versus Competing Spotted Hyenas." *Acta Zoologica* 102, no. 4: 365–385. <https://doi.org/10.1111/azo.12345>.
- dos Santos-Barnett, T. C., T. C. Cavalcante, S. A. Boyle, et al. 2022. "Pulp Fiction: Why Some Populations of Ripe-Fruit Specialists, *Ateles chamek* and *A. marginatus*, Prefer Insect-Infested Foods." *International Journal of Primatology* 43, no. 2: 384–408. <https://doi.org/10.1007/s10764-022-00284-0>.
- Felton, A. M., A. Felton, J. T. Wood, et al. 2009. "Nutritional Ecology of *Ateles chamek* in Lowland Bolivia: How Macronutrient Balancing Influences Food Choices." *International Journal of Primatology* 30, no. 3: 675–696. <https://doi.org/10.1007/s10764-009-9367-9>.
- Gentry, A. H. 1993. *A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru) With Supplementary Notes*. University of Chicago Press.
- Goodrich, J. M., I. V. Seryodkin, D. G. Miquelle, L. L. Kerley, H. B. Quigley, and M. G. Hornocker. 2011. "Effects of Canine Breakage on Tiger Survival, Reproduction and Human-Tiger Conflict." *Journal of Zoology* 285, no. 2: 93–98. <https://doi.org/10.1111/j.1469-7998.2011.00819.x>.
- Granatosky, M. C., and C. F. Ross. 2020. "Differences in Muscle Mechanics Underlie Divergent Optimality Criteria Between Feeding and Locomotor Systems." *Journal of Anatomy* 237, no. 4: 1072–1086. <https://doi.org/10.1111/joa.13279>.
- Harano, T., and M. Asahara. 2022. "Correlated Evolution of Craniodental Morphology and Feeding Ecology in Carnivorans: A Comparative Analysis of Jaw Lever Arms at Tooth Positions." *Journal of Zoology* 318, no. 2: 135–145. <https://doi.org/10.1111/jzo.13005>.
- Hendges, C. D., B. D. Patterson, N. C. Cáceres, G. M. Gasparini, and C. F. Ross. 2019. "Skull Shape and the Demands of Feeding: A Biomechanical Study of Peccaries (Mammalia, Cetartiodactyla)." *Journal of Mammalogy* 100, no. 2: 475–486. <https://doi.org/10.1093/jmammal/gyz061>.

- Hohmann, G. 2009. "The Diets of Non-Human Primates: Frugivory, Food Processing, and Food Sharing." In *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*, edited by J.-J. Hublin and M. P. Richards, 1–14. Springer. [https://doi.org/10.1007/978-1-4020-9699-0\\_1](https://doi.org/10.1007/978-1-4020-9699-0_1).
- Jackson, B. D. 2004. *Dictionary of Botanical Names and Terms: With Their English Equivalents*. Laurier Books, Ltd.
- Jucá, T., S. Boyle, G. Cavalcanti, et al. 2020. "Being Hunted High and Low: Do Differences in Nocturnal Sleeping and Diurnal Resting Sites of Howler Monkeys (*Alouatta nigerrima* and *A. discolor*) Reflect Safety From Attack by Different Types of Predator?" *Biological Journal of the Linnean Society* 131, no. 2: 203–219. <https://doi.org/10.1093/biolinnean/blaa102>.
- Kay, R. F. 1990. "The Phyletic Relationships of Extant and Fossil Pitheciinae (Platyrrhini, Anthropoidea)." *Journal of Human Evolution* 19, no. 1: 175–208. <https://doi.org/10.1016/B978-0-12-260345-7.50011-4>.
- Kay, R. F., D. J. Meldrum, and M. Takai. 2013. "Pitheciidae and Other Platyrrhine Seed Predators." In *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*, edited by L. Veiga, A. Barnett, S. Ferrari, and M. Norconk, 3–12. Cambridge University Press. <https://doi.org/10.1017/CBO9781139034210.005>.
- Kinzey, W. G. 1992. "Dietary and Dental Adaptations in the Pitheciinae." *American Journal of Physical Anthropology* 88, no. 4: 499–514. <https://doi.org/10.1002/ajpa.1330880406>.
- Kinzey, W. G., and M. A. Norconk. 1990. "Hardness as a Basis of Fruit Choice in Two Sympatric Primates." *American Journal of Physical Anthropology* 81, no. 1: 5–15. <https://doi.org/10.1002/ajpa.1330810103>.
- Kinzey, W. G., and M. A. Norconk. 1993. "Physical and Chemical Properties of Fruit and Seeds Eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela." *International Journal of Primatology* 14: 207–227. <https://doi.org/10.1007/BF02192632>.
- Klukkert, Z. S. 2019. "The Functional Morphology of Ingestion in the Platyrrhine Sclerocarpic Harvesters (Platyrrhini, Primates)." (Doctoral Dissertation, City University of New York). [https://academicworks.cuny.edu/gc\\_etds/3257](https://academicworks.cuny.edu/gc_etds/3257).
- Koyabu, D. B., T. Oshida, N. X. Dang, et al. 2009. "Craniodental Mechanics and the Feeding Ecology of Two Sympatric Callosiurine Squirrels in Vietnam." *Journal of Zoology* 279, no. 4: 372–380. <https://doi.org/10.1111/j.1469-7998.2009.00629.x>.
- Lawn, B. R., H. Chai, A. Barani, and M. B. Bush. 2013. "Transverse Fracture of Canine Teeth." *Journal of Biomechanics* 46, no. 9: 1561–1567. <https://doi.org/10.1016/j.jbiomech.2013.03.018>.
- Ledogar, J., T. Luk, J. Perry, D. Neaux, and S. Wroe. 2018. "Biting Mechanics and Niche Separation in a Specialized Clade of Primate Seed Predators." *PLoS One* 13, no. 1: 1–26. <https://doi.org/10.1371/journal.pone.0190689>.
- Ledogar, J. A., J. M. Winchester, E. M. St. Clair, and D. M. Boyer. 2013. "Diet and Dental Topography in Pitheciine Seed Predators." *American Journal of Physical Anthropology* 150, no. 1: 107–121. <https://doi.org/10.1002/ajpa.22181>.
- Lucas, P. W. 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge University Press.
- Lucas, P. W., P. J. Constantino, J. Chalk, et al. 2009. "Indentation as a Technique to Assess the Mechanical Properties of fallback Foods." *American Journal of Physical Anthropology* 140, no. 4: 643–652. <https://doi.org/10.1002/ajpa.21026>.
- Lucas, P. W., I. M. Turner, N. J. Dominy, and N. Yamashita. 2000. "Mechanical Defences to Herbivory." *Annals of Botany* 86, no. 5: 913–920. <https://doi.org/10.1006/anbo.2000.1261>.
- Mann, S., B. Van Valkenburgh, and M. Hayward. 2017. "Tooth Fracture Within the African Carnivore Guild: The Influence of Intraguild Competition and Resource Availability." *Journal of Zoology* 303, no. 4: 261–269. <https://doi.org/10.1111/jzo.12488>.
- Mazzolli, M. 2013. "Lethal Biting Behaviour of Pumas (Carnivora, Felidae) Interpreted From Fractured Skull of Prey." *Neotropical Biology & Conservation* 8, no. 1: 63–66. <https://doi.org/10.4013/nbc.2013.81.08>.
- Ménard, N., and D. Vallet. 1997. "Behavioral Responses of Barbary Macaques (*Macaca sylvanus*) to Variations in Environmental Conditions in Algeria." *American Journal of Primatology* 43, no. 4: 285–304. [https://doi.org/10.1002/\(SICI\)1098-2345\(1997\)43:4<285::AID-AJP1>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1098-2345(1997)43:4<285::AID-AJP1>3.0.CO;2-T).
- Mittermeier, R. A., and M. G. van Roosmalen. 1981. "Preliminary Observations on Habitat Utilization and Diet in Eight Surinam Monkeys." *Folia Primatologica* 36, no. 1-2: 1–39.
- Mori, S. A., and G. T. Prance. 1990. "Lecythidaceae-Part II: The Zygomorphic-Flowered New World Genera (*Couropita*, *Corythophora*, *Bertholletia*, *Couratari*, *Eschweilera*, & *Lecythis*), With a Study of the Secondary Xylem of Neotropical Lecythidaceae by Carl de Zeeuw." *Flora Neotropica Monographs* 21: 1–376. <http://www.jstor.org/stable/4393724>.
- Mourthé, Í. M. C., K. B. Strier, and J. P. Boubli. 2008. "Seed Predation of *Mabea fistulifera* (Euphorbiaceae) by Northern Muriquis (*Brachyteles hypoxanthus*)." *Neotropical Primates* 15, no. 2: 40–45. <https://doi.org/10.1896/044.015.0202>.
- Muchlinski, M. N., J. J. Snodgrass, and C. J. Terranova. 2012. "Muscle Mass Scaling in Primates: An Energetic and Ecological Perspective." *American Journal of Primatology* 74, no. 5: 395–407. <https://doi.org/10.1002/ajp.21990>.
- Norconk, M. A. 2021. "Historical Antecedents and Recent Innovations in Pitheciid (Titi, Saki, and Uakari) Feeding Ecology." *American Journal of Primatology* 83, no. 6: e23177. <https://doi.org/10.1002/ajp.23177>.
- Norconk, M. A., and M. Veres. 2011. "Physical Properties of Fruit and Seeds Ingested by Primate Seed Predators With Emphasis on Sakis and Bearded Sakis." *Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* 294, no. 12: 2092–2111. <https://doi.org/10.1002/ar.21506>.
- Norconk, M. A., B. W. Wright, N. L. Conklin-Brittain, and C. J. Vinyard. 2009. "Mechanical and Nutritional Properties of Food as Factors in Platyrrhine Dietary Adaptations." In *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology and Conservation*, edited by P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, and K. B. Strier, 279–311. Springer Press.
- Patterson, B. D. 2023. "The Man-Eaters of Tsavo and the Untapped Potential of Natural History Collections." *Curator: The Museum Journal* 66, no. 3: 523–531.
- Pennington, T. D. 1990. "Sapotaceae." *Flora Neotropica Monograph* 52: 1–770.
- Pinto, L. P., R. F. S. da Silva, A. C. M. Oliveira, A. A. Barnett, L. M. Veiga, and E. Z. F. Setz. 2018. "Diet and Foraging Behavior of *Chiropotes albinus* (I. Geoffroy & Deville 1848) at Two Sites in South-Eastern Brazilian Amazonia." In *La primatologia en Latinoamérica 2—A primatologia na America Latina 2*, edited by B. Urbani, M. Kowalewski, R. G. T. da Cunha, S. de la Torre, and L. Cortés-Ortiz, 199–218. Instituto Venezolano de Investigaciones Científicas.
- Pollock, T., O. Panagiotopoulou, D. Hocking, and A. Evans. 2022. "Taking a Stab at Modelling Canine Tooth Biomechanics in Mammalian Carnivores With Beam Theory and Finite-Element Analysis." *Royal Society Open Science* 9, no. 10: e220701. <https://doi.org/10.1098/rsos.220701>.
- Pontzer, H. 2015. "Energy Expenditure in Humans and Other Primates: A New Synthesis." *Annual Review of Anthropology* 44, no. 1: 169–187. <https://doi.org/10.1146/annurev-anthro-102214-013925>.

Püschel, T. A., J. Marcé-Nogué, T. M. Kaiser, R. J. Brocklehurst, and W. I. Sellers. 2018. "Analyzing the Sclerocarpus Adaptations of the Pitheciidae Mandible." *American Journal of Primatology* 80, no. 5: e29. <https://doi.org/10.1002/ajp.22759>.

R Foundation for Statistical Computing. 2024. "R Version 4.4.1."

Ribeiro, S. J. E. L., M. J. G. Hopkins, A. Vicentini, et al. 1999. "Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra firme na Amazonia Central." Manaus: DFID-Instituto Nacional de Pesquisas da Amazônia. [https://ppbio.inpa.gov.br/en/Identification\\_Guides](https://ppbio.inpa.gov.br/en/Identification_Guides).

Roberts, J. A., K. A. Elliott, and Z. H. Gonzalez-Carranza. 2002. "Abscission, Dehiscence, and Other Cell Separation Processes." *Annual Review of Plant Biology* 53, no. 1: 131–158. <https://doi.org/10.1146/annurev.arplant.53.092701.180236>.

Roosmalen, M. G. M. 1985. *Fruits of the Guianan Flora*. National Herbarium of the Netherlands.

Rosenberger, A. L. 1992. "The Evolution of Feeding Niches in New World Monkeys." *American Journal of Physical Anthropology* 88, no. 3: 525–562. <https://doi.org/10.1002/ajpa.1330880408>.

Ross, C. F., and I. Iriarte-Diaz. 2014. "What Does Feeding System Morphology Tell Us About Feeding?" *Evolutionary Anthropology* 23, no. 1: 105–120. <https://doi.org/10.1002/evan.21410>.

Seidensticker, J., and C. McDougal. 1993. "Tiger Predatory Behaviour, Ecology and Conservation." *Symposium of the Zoological Society of London* 65: 105–125. <https://doi.org/10.1093/oso/9780198540670.003.0006>.

Shaffer, C. A. 2013. "Feeding Ecology of Northern Bearded Sakis (*Chiropotes sagulatus*) in Guyana." *American Journal of Primatology* 75, no. 6: 568–580. <https://doi.org/10.1002/ajp.22134>.

Tomanek, P., Í. Mourté, and A. A. Barnett. 2020. "Calls for Concern: Matching Alarm Response Levels to Threat Intensities in Three Neotropical Primates." *Acta Oecologia* 109, no. 2: e103646. <https://doi.org/10.1016/j.actao.2020.103646>.

Van Casteren, A., J. R. Codd, K. Kupczik, G. Plasqui, W. I. Sellers, and A. G. Henry. 2022. "The Cost of Chewing: The Energetics and Evolutionary Significance of Mastication in Humans." *Science Advances* 8, no. 33: eabn8351. <https://doi.org/10.1126/sciadv.abn8351>.

Van Roosmalen, M. G., R. A. Mittermeier, and J. G. Fleagle. 1988. "Diet of the Northern Bearded Saki (*Chiropotes satanas*): A Neotropical Seed Predator." *American Journal of Primatology* 14, no. 1: 11–35.

Van Valkenburgh, B. 2009. "Costs of Carnivory: Tooth Fracture in Pleistocene and Recent Carnivorans." *Biological Journal of the Linnean Society* 96, no. 1: 68–81. <https://doi.org/10.1111/j.1095-8312.2008.01108.x>.

Van Valkenburgh, B., and P. A. White. 2021. "Naturally-Occurring Tooth Wear, Tooth Fracture, and Cranial Injuries in Large Carnivores From Zambia." *PeerJ* 9: e11313. <https://doi.org/10.7717/peerj.11313>.

Visalberghi, E., G. Sabbatini, N. Spagnoletti, et al. 2008. "Physical Properties of Palm Fruits Processed With Tools by Wild Bearded Capuchins (*Cebus libidinosus*)." *American Journal of Primatology* 70, no. 9: 884–891. <https://doi.org/10.1002/ajp.20578>.

Wall, C. E., J. B. Hanna, M. C. O'Neill, M. Toler, and M. F. Laird. 2023. "Energetic Costs of Feeding in 12 Species of Small-Bodied Primates." *Philosophical Transactions of the Royal Society B* 378, no. 1891: 20220553.

Wright, B. W. 2005. "Craniodental Biomechanics and Dietary Toughness in the Genus *Cebus*." *Journal of Human Evolution* 48, no. 5: 473–492. <https://doi.org/10.1016/j.jhevol.2005.01.006>.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** [btp70113-sup-0001-DataS1.docx](https://doi.org/10.1111/bcp.20113).