

RESEARCH ARTICLE

Feeding postural behaviors and food geometric and material properties in bearded capuchin monkeys (*Sapajus libidinosus*)

Myra F. Laird¹  | Zeenia Punjani¹ | Rachel R. Oshay¹ | Barth W. Wright²  |
Mariana Dutra Fogaça^{3,4} | Adam van Casteren⁵  | Patrícia Izar⁶ |
Elisabetta Visalberghi⁷ | Dorothy Fragazy⁸ | David S. Strait^{9,10}  |
Callum F. Ross¹¹  | Kristin A. Wright¹² 

¹Department of Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, USA

²Department of Surgery, University of Kansas Medical Center, Kansas City, Kansas, USA

³Department of Biomedical Sciences, Institute of Population Genetics, University of Veterinary Medicine, Vienna, Austria

⁴Neotropical Primates Research Group – NeoPREGo, São Paulo, Brazil

⁵Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

⁶Department of Experimental Psychology, University of São Paulo, São Paulo, Brazil

⁷Institute of Cognitive Sciences and Technologies, National Research Council (CNR), Rome, Italy

⁸Department of Psychology, University of Georgia, Athens, Georgia, USA

⁹Department of Anthropology, Washington University in St. Louis, St. Louis, Missouri, USA

¹⁰Palaeo-Research Institute, University of Johannesburg, Cnr Kingsway and University Road Auckland Park, Auckland Park, South Africa

¹¹Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois, USA

¹²Department of Biomedical Sciences, University of Missouri Kansas City School of Medicine, Kansas City, Missouri, USA

Correspondence

Myra F. Laird, University of Southern California, Department of Integrative Anatomical Sciences, Bishop Hall 401, 1333 San Pablo Street, Los Angeles, CA 90033, USA.
Email: myra.laird@usc.edu

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Abstract

Objectives: Foods that are geometrically and mechanically challenging to eat have been associated with specializations in feeding behavior and craniodental morphology across primates, and many of these foods are embedded, requiring a variety of positional behaviors during feeding. However, variation in positional behaviors in response to food properties is not well understood. Here, we examine differences in feeding postural behaviors across feeding events in relation to substrate and food geometric and material properties in a species of extractive foragers, bearded capuchins (*Sapajus libidinosus*).

Methods and materials: We coded over 1400 co-occurring postural and feeding behaviors, their durations, and relative sizes of substrate and food from videos recorded at Fazenda Boa Vista in Gilbués, Piauí, Brazil. Food material properties were measured from foods collected at the time of the video recordings.

Results: Our results suggest that bearded capuchin feeding postures significantly differ across the feeding sequence, with substrate size, and between foods of high and low toughness and elastic modulus. Feeding postures were less variable for highly

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mechanically challenging foods. Food size also had a significant effect on postural behaviors. Large foods were more likely to be associated with suspended postures and small foods with sitting and squatting. Feeding postural behaviors were best explained by a combination of substrate and food variables.

Conclusions: Our results indicate that food geometric and mechanical properties have a significant influence on feeding postural behaviors in bearded capuchins. We posit that feeding postural behaviors reflect a combination of substrate variables and food properties, and large, mechanically challenging foods have a limiting effect on postural variation.

KEYWORDS

capuchin, feeding, food size, food material properties, posture

1 | INTRODUCTION

Food geometric and mechanical properties are thought to influence primate feeding behaviors (Bouvier, 1986a, 1986b; Coiner-Collier et al., 2016; Daegling, 1992; Daegling & McGraw, 2007; Hylander, 1975; Jolly, 1970; Kay, 1975; Kinzey, 1974, 1992; Koyabu & Endo, 2009; Laird, 2017; Laird, Ross, & O'Higgins, 2020; Lucas, 2004; Rosenberger, 1992; Rosenberger & Kinzey, 1976; Silverman et al., 2001; Taylor, 2006; but see Ross et al., 2012 and Ross & Iriarte-Diaz, 2014). Mechanically and size-challenging foods will be placed at locations along the tooththrow that facilitate large gapes, increased muscle force, and maximize jaw mechanical advantage (e.g., Coiner-Collier et al., 2016; Greaves, 1978; Laird, Granatosky, et al., 2020; Spencer, 1998; Spencer, 1999; Spencer & Demes, 1993; Taylor & Vinyard, 2009; Vogel et al., 2009; Wright, 2005). While much attention has been paid to craniodental feeding behaviors, variation in the postcranial behaviors during feeding is not well understood. Some primates use specific postures in association with certain food items (Fleagle, 1976; Fleagle, 1984), and these differences have been proposed to reflect foraging strategies and food distribution (Fleagle, 1976; Grand, 1972; McGraw, 1998). Like craniodental feeding behaviors, it stands to reason the mechanical and geometric properties of a food item may influence postcranial behaviors relating to muscle force and positioning of the limbs during food processing and ingestion.

Previous studies have highlighted the influence of primates' body size and substrate size on locomotion and posture. For example, the balance and limb placement of small primates on a large arboreal substrate may resemble those used on the ground, while smaller substrates may require a different set of postures, particularly for larger-bodied primates (e.g., Cant, 1987a and 1987b; Cant, 1992; Cartmill, 1974; Grand, 1972; Jenkins, 1974; Schmitt, 2003; Thorpe & Crompton, 2006; Thorpe et al., 2007). While maintaining a given body posture likely requires lower muscular forces compared to locomotion, postures are more frequent and sustained over long periods of time, particularly for species that spend large amounts of their day feeding (Fleagle, 1984; McGraw, 1998; Rose, 1974). For example, primates with longer limbs adopt extended postures that increase the effective

mechanical advantage of the limb musculature (Polk, 2002). Primate postural behaviors are thought to be determined by a combination of anatomical and environmental factors (Figure 1; e.g., Laird et al., 2018; McGraw, 1998; McGraw & Sciulli, 2011; Wright et al., 2019). Similar to body and substrate size, food size and food material properties (FMPs) are expected to influence postural behavior, reflecting the need to produce muscle forces and position the body relative to the food item.

Variation in feeding postural behaviors has been related to food type in select primates. Black spider monkeys (*Ateles paniscus*) showed no difference in postures when feeding on fruits compared to leaves (Youlatos, 2002), whereas black howling monkeys (*Alouatta caraya*) were found to sit more commonly when feeding on leaves than on fruits (Bicca-Marques & Calegaro-Marques, 1993). McGraw (1998) found that African colobines more frequently used a reclining posture post-prandial compared to cercopithecines, and they suggest that use of this posture relates to their high fiber, low energy diet. Similar results were found in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), which showed that posture varied with food type (Grueter et al., 2013). Variation in the feeding postures of arboreal species such as black spider monkeys and black howling monkeys may also be attributable to effects of body size on substrate use (Fleagle & Mittermeier, 1980; Kay, 1984), while species that are known to frequently use terrestrial substrates (e.g., Yunnan snub-nosed monkeys) may habitually adopt postures typically used on terrestrial substrates in arboreal settings.

While the relationship between food properties and feeding behaviors has been investigated in several species of primates (Bouvier, 1986a, 1986b; Coiner-Collier et al., 2016; Daegling, 1992; Daegling & McGraw, 2007; Hylander, 1975; Jolly, 1970; Kay, 1975; Kinzey, 1974, 1992; Koyabu & Endo, 2009; Laird, 2017; Laird, Ross, & O'Higgins, 2020; Lucas, 2004; Rosenberger, 1992; Rosenberger & Kinzey, 1976; Silverman et al., 2001; Taylor, 2006; but see Ross et al., 2012 and Ross & Iriarte-Diaz, 2014), it is unknown whether feeding postural behaviors also reflect differences in geometric properties (specifically food size) and FMPs. Studies of feeding behaviors have indicated that FMPs and food size play a key role in determining the

FIGURE 1 Images captured from the videos showing bearded capuchins (*Sapajus libidinosus*) in (a) squat, (b) forelimb crouch, (c) sit-in/sit-out, and (d) flexed bipedal stand postures



type of feeding behavior, the location of food placement within the mouth, and the amount of bite force (e.g., Herring & Herring, 1974; Laird, Granatosky, et al., 2020; Lucas, 2004; Perry et al., 2011; Wright, 2005). Studies of primate FMPs have focused on two measures: food toughness and elastic modulus. Toughness is defined in this context as the work needed to propagate a crack through an object, whereas elastic modulus (or stiffness) is the relationship between stress and strain within the elastic region of an object (Ashby, 2002; Lucas, 2004).

Here, we examine variation in feeding postural behaviors and their duration (s) across feeding events in relation to substrate and food geometric and material properties in wild bearded capuchins (*Sapajus libidinosus*; Table 1). The genus *Sapajus* (robust capuchins) exhibits considerable variation in postural behaviors in the wild. It has been the focus of numerous morphological comparisons, studies of primate tool use, in vivo physiological and biomechanical modeling studies, and is commonly used as an extant model of hard object feeding by fossil hominins (e.g., Ford & Hobbs, 1996; Liu et al., 2009; Ottoni & Izar, 2008; Prado et al., 2016; Ross et al., 2016; Taylor & Vinyard, 2009; Wright, 2007; Wright et al., 2009; Wright et al., 2016; Wright et al., 2019; Youlatos, 1998). Robust capuchins are primarily arboreal, but they exhibit a wide array of food processing behaviors that includes tool use (to pound, probe, and excavate) on terrestrial substrates (Visalberghi & Fragaszy, 2013). Robust capuchins also frequently engage in bipedal postures, particularly during reaching and while carrying objects (Massaro et al., 2016; Westergaard et al., 1997;

Wright et al., 2019). Importantly, our analyses focus on postural behaviors after the food items have been foraged.

1.1 | Hypotheses

Our null hypothesis is that feeding postural behaviors do not vary across the feeding event (Table 1), with substrate, with geometric properties, or with FMPs in bearded capuchins. We test four alternative hypotheses:

Hypothesis H1. *Feeding postural behaviors and their durations vary between manual behaviors, ingestive behaviors, and mastication.* Greater variation in feeding postural behaviors is expected during manual and oral-manual ingestive behaviors associated with using the limbs to process a food (such as reducing food size or removing the tough outer shell of a food). In contrast, feeding postural behaviors are expected to vary little during oral ingestive behaviors and mastication because of the lack of limb involvement.

Hypothesis H2. *Feeding postural behaviors and their durations vary with substrate.* Previous studies suggest that large-sized substrates allow for greater variation in postural behaviors and locomotion compared to small

TABLE 1 Definitions of feeding events and postural behaviors following Laird, Ross, and O'Higgins (2020) and Hunt et al. (1996)

Behavior	Definition
Feeding event	All behaviors used to process a food item from manual food processing to final swallow. Includes manual and ingestive food processing behaviors and mastication
• Manual (preingestive)	Behaviors occurring before the food item enters the oral cavity involving the limbs (e.g., rubbing or stripping a food item with the hands or cracking it using a stone hammer and anvil)
• Ingestive	Behaviors involving the introduction of foods to the oral cavity. Includes oral and oral-manual behaviors
• Mastication	Chewing cycles, cyclic intraoral food processing occurring on the postcanine dentition during which the lower jaw moves upward and medially near minimum gape
Posture	Body positioning during feeding events
• Angled sit-in	Weight is supported by the ischia with the hip and knee tightly flexed on an angled substrate
• Flexed bipedal stand	Standing on the hindlimbs with flexed hip and knee. No support from other body parts
• Forelimb crouch	Quadrupedal with the elbows flexed but not the knees
• Hindlimb crouch	Quadrupedal with the knees flexed but not the elbows
• Quadrumanous-suspend	Suspended with equal support from each limb and a pronograde trunk
• Quadrupedal stand	Quadrupedal with extended elbows and knees
• Sit-in	Weight is supported by the ischia with the hip and knee tightly flexed.
• Sit-in/Sit-out	Weight is supported by the ischia with one hip and knee tightly flexed and the other outstretched
• Sit-out	Weight is supported by the ischia with the hip and knees outstretched
• Squat	Weight is supported by the feet with the hip and knees tightly flexed. No weight is placed on the ischia
• Tail/hindlimb-suspend	Suspension with support from the extended hindlimbs and tail
• Tripedal stand	Quadrupedal with extended elbows and knees, but weight is borne by the two hindlimbs and one forelimb

substrates (e.g., Cant, 1987a and 1987b; Cartmill, 1974; Jenkins, 1974; Schmitt, 2003; Thorpe & Crompton, 2006; Thorpe et al., 2007), and postural variation during feeding is not expected to differ. As such, we predict that larger arboreal and terrestrial substrates will be associated with increased feeding postural variation and

longer feeding postural durations compared to smaller arboreal substrates.

Hypothesis H3. *Feeding postural behaviors and their durations vary with FMPs.* Mechanically challenging foods, with higher toughness and elastic modulus values, are predicted to require greater amounts of force and manipulation during feeding, and bearded capuchins are expected to limit the postures used for these foods in order to position the body relative to the food item.

Hypothesis H4. *Feeding postural behaviors and their durations vary with food geometric properties.* Foods of larger size are expected to present challenges for manual and ingestive behaviors that result in decreased variation in feeding postures in order to improve body position while accessing the food.

Hypothesis H5. *Variation in feeding postural behaviors is best explained using a combination of substrate and food mechanical and geometric properties.* The effects of substrate and food geometric and mechanical properties on feeding postures are not expected to be independent, for example, large food items are unlikely to be found on terrestrial substrates (e.g., fruits from trees of the family Lecythidaceae). As such, we predict that variation in feeding postural behaviors is likely best explained using a combination of substrate and food variables.

2 | MATERIALS AND METHODS

2.1 | Behavioral data collection

Behavioral data and FMPs were collected from *Sapajus libidinosus* at Fazenda Boa Vista in Gilbués, Piauí, Brazil (9° 39'S, 45° 25'W). The site is in the Cerrado-Caatinga (open woodland) ecotone at 420 m a.s.l. (Howard et al., 2012; Oliveira & Marquis, 2002; Visalberghi & Frigaszy, 2013). Precipitation at the site is seasonally variable with the most rainfall occurring from November–April (Oliveira & Marquis, 2002). During the dry season, the bearded capuchins at Fazenda Boa Vista increase their fallback food consumption (Wright, 2004). Bearded capuchins, like other capuchin species, are primarily arboreal quadrupeds that leap and climb to varying degrees and use a variety of substrates (Gebo, 1992; Wright, 2007; Wright et al., 2019; Youlatos, 1998, 1999). The bearded capuchins at Fazenda Boa Vista use terrestrial substrates 27% of daytime (Wright et al., 2019). Our data collection took place from May–June 2015 in the dry season when soft fruits were unavailable.

A total of 1437 feeding behavior observations were obtained from over 30 h of video recordings of 15 (4 males, 11 females) adult and subadult wild bearded capuchin monkeys (SOM Table S1; SOM

Table S2). Although sex differences in FMPs have been noted for robust capuchins (Thiery & Sha, 2020), males and females were combined in the analyses to increase the total sample size. The analyses also included data from six subadults that were over 2 years of age. Chalk-Wilayto et al. (2016) found that subadult and adult bearded capuchins at Fazenda Boa Vista consumed foods of similar FMPs. Data collection was approved by the Brazilian National Council for Scientific and Technological Development (CNPq permit #000511/2015-3), Sistema de Autorização e Inforação em Biodiversidade (SISBIO permit #28689-6), and the Institutional Animal Care and Use Committees at Kansas City University of Medicine and Biosciences (protocol 629,641-1) and the University of Albany (protocol 14-009). All data were collected in accordance with the relevant guidelines and regulations.

Videos of capuchin feeding behaviors were captured using Sony Handycam video cameras (HD CRX405) for a period of approximately 1 month, from May to June 2015. This data recording period does not capture annual or seasonal shifts in foods, but the dry season is when bearded capuchins consume the most mechanically challenging foods (Wright, 2004). All recordings were opportunistic. Daily follows of groups of wild bearded capuchins commenced early in the morning and began with the first focal animal encountered. Recording continued until the individual went out of view. Subsequently, the next animal encountered would be filmed until out of view. For each focal animal video segment, the age, sex, and, if known, name of the individual was recorded in the audio of the video recording, as well as the encountered food items. Individual and food identifications were reviewed and updated in the laboratory (Table 2). Each usable video sequence was then viewed frame-by-frame to code all feeding and postural behaviors performed by the focal individual. Feeding

behaviors were classified as either manual, ingestive or mastication (following Laird, Wright, et al., 2020; Table 1). Feeding postural behaviors were based on Hunt et al. (1996). The durations of these behaviors were calculated using the video frame rate (30 frames per second; Table 3). Intra-observer reliability was assessed by coding the behavior and duration for four of the videos on three separate occasions. There were no significant differences between coding instances (f -value = 0.05, $df = 1$, $p = 0.82$).

2.2 | FMPs testing

At the time of video recording, sample foods were collected from the same source (in order of preference, branch, tree, growth stage) from which the animal obtained their food item. In some instances, the actual food item being consumed was dropped by the capuchin and collected for testing. The FMPs for different parts of the foods were measured using a Lucas Scientific FLS-1 portable mechanical tester (Darvell et al., 1996; Lucas et al., 2001, 2009). Toughness was defined as the work needed to initiate and propagate a given crack area through the food item (Ashby, 2002; Lucas, 2004), and was measured using scissor and wedge tests. These tests are widely used in investigations into primate dietary mechanics and in all cases, toughness is calculated by dividing the work of fracture by the crack area giving a value of $J m^{-2}$ (Lucas et al., 2011). It was not possible to measure all foods in this study using a single type of test, and we acknowledge that some of the differences between toughness values in this study may reflect mechanical differences between tests. Elastic modulus is defined as the ratio of stress to strain in the elastic region and is defined in units of pressure (MPa) (Ashby, 2002; Lucas, 2004) and

TABLE 2 Food material property classifications. Scientific names follow Santos (2015) and Laird et al., (2020)

Family	Scientific name	Common name	Elastic modulus FMP classification	Toughness FMP classification	Average elastic modulus (SD) (MPa); number of tests	Average toughness (R) (SD) ($J m^{-2}$); number of tests
?	?	Berry	Low	Low	0.02 (0.02); $n = 12$	2371.39 (2227.02); $n = 2$
Bromeliaceae	?	Bromeliad leaf	—	Low	—	547.09 (333.64); $n = 2$
Formicidae	?	Insects	Low	Low	6.56 (1.13); $n = 3$	845.43 (219.96); $n = 3$
Poaceae	<i>Saccharum</i> sp.	Cane	Low	High	2.17 (0.94); $n = 7$	4957.66 (4000.96); $n = 12$
Lecythidaceae, Anacardiaceae, Leguminosae- Caesalpinaceae, Leguminosae- Fabaceae	<i>Emmotum nitens</i> / <i>Lecythis</i> sp., <i>Anacardium occidentale</i> ^a , <i>Copaifera langsdorffi</i> ,?	Fruit	High	Low	15.15 (15.40); $n = 21$	2093.36 (2990.17); $n = 28$
Palmae-Arecaceae	<i>Orbignya</i> sp.	Palm-Piaçava	High	Low	46.18 (48.02); $n = 14$	1575.58 (2447.18); $n = 19$
Fabaceae	?	Pod	Low	Low	0.15 (0.08); $n = 8$	1335.53 (606.30); $n = 12$
Poaceae	?	USO ^b	—	High	—	4076.40 (2969.28); $n = 8$
Palmae-Arecaceae	<i>Astrocaryum campestre</i>	Palm-Tucum	High	Low	48.23 (29.36); $n = 9$	1924.64 (691.41); $n = 18$

^aFood material properties and behaviors were collected for the accessory hypocarp (also known as the pseudo-fruit or apple) of fruta de caju (cashew fruits or cashew nuts).

^bUnderground storage organ (USO).

TABLE 3 Average duration and SD for each feeding postural behavior

Feeding postural behavior	Average duration (s)	SD
Angled sit-in	11.13	10.09
Flexed bipedal stand	6.28	7.08
forelimb crouch	6.66	7.91
Hindlimb crouch	0.20	—
Quadrumanous-suspend	3.43	—
Quadrupedal stand	1.20	—
Sit-in	17.32	20.36
Sit-in/Sit-out	24.13	21.10
Sit-out	6.97	—
Squat	21.26	27.31
Tail/hindlimb-suspend	5.33	3.38
Tripedal stand	8.50	—

was tested using compression (primarily blunt-indent) and three- and four-point bending tests. Such tests use semi-hemispherical probes or a series of crossbars to load a material for a set period of time, the displacement is then held, and the relaxation behavior of the material is recorded (blunt-indent only). Here we used instantaneous modulus from these tests as it is more relevant when contextualizing how food behaves in the oral cavity during ingestion or mastication (van Casteren et al., 2016). While FMP values were obtained from most food tissue types, it was not always possible to precisely match tissue types to the recorded feeding behaviors. Therefore, FMP values were grouped into 'high' and 'low' categories with cut-off points at 3000 J m^{-2} for toughness and 15 MPa for elastic modulus (Table 2). Foods with FMP values that fall into both categories were classified as 'high & low,' such as, for example, fruit with a hard exocarp but softer mesocarp.

2.3 | Substrate and food size

During laboratory data collection, arboreal substrates and food items were classified into size groups relative to the individual animal being filmed (Bezanson et al., 2012). Arboreal substrates were classified as 'small' if their diameter was less than half the length of each subject's hand, 'medium' if the substrate was up to the length of the animal's hand, and 'large' if the substrate's diameter exceeded the animal's hand length. Terrestrial substrates were analyzed as a separate group within substrate size. All foods were selected by the animal (not provisioned), and the resulting food sample varied in size (from insects to sugar cane stalks). Food item size was classified as 'small' if the diameter of the food item was less than half the length of each subject's jaw length (gonial angle to mandibular symphysis), 'medium' if the food diameter was between half of the animal's jaw length to the full jaw length, and 'large' if the food diameter exceeded the animal's jaw length.

2.4 | Analyses

All analyses were completed in R statistical software (R Core Team, 2013). Postural variation in each hypothesis was assessed using multi-variate generalized linear mixed-effects models using Markov chain Monte Carlo techniques in the R package "MCMCglmm" (Hadfield, 2010). For hypothesis five, a series of MCMCglmm models were constructed with combinations of substrate and food variables as explanatory variables. Models including elastic modulus failed to converge due to sample size and were excluded from the comparison. This package allows for multiple categorical response variables while including random effects. Models were iteratively constructed and compared using deviance information criterion (DIC) with individual, sex, food, and weight added as random variables (SOM Table S3). Sex, food, and weight failed to improve the models in DIC comparisons and only individual was included as a random variable in the final models. Sex differences in capuchin FMPs have been noted in previous studies (e.g., Thiery & Sha, 2020), and the lack of sex differences in our models likely reflects the relatively low number of males. To visualize differences between the categorical variables within each hypothesis, we used multiple correspondence analyses (MCA) performed using the 'FactoMineR' (Lê et al., 2008) and 'Factoextra' (Kassambra & Mundt, 2017) packages. An MCA is similar to a principal components analysis in that it captures relationships among qualitative variables using frequencies to create factor scores to visualize variation between categories.

The durations of feeding postural behaviors were summed per behavior within a feeding event. For example, if a feeding posture was 'sit-in' for the first part of ingestion and changed to 'squat' for the rest of ingestion and mastication, duration was summed separately for 'sit-in' and 'squat.' As durations were grouped by feeding postural behavior, other categorical variables were grouped such that if manual and ingestive behaviors occurred during squatting, the feeding event was classified as 'manual/ingestive.' The relationships between durations of feeding postural behaviors and the feeding event, substrate size, FMPs, and food size were tested using linear mixed models fit by maximum likelihood with individual and food as random effects. Post-hoc Tukey comparisons of generalized linear mixed-effects models (R package 'lme4,' Bates et al., 2015) were performed in the R package 'multicomp' with a Bonferroni Holm correction (Hothorn et al., 2008). Significance was set at $p < 0.05$.

3 | RESULTS

Hypothesis H1. *Feeding postural behaviors and the feeding event—between manual behaviors, ingestive behaviors, and mastication.*

Across all foods, five feeding postural behaviors were used during manual behaviors, 15 during ingestion, and seven during mastication. Within the ingestive behaviors, nine postures were used during oral-manual ingestive behaviors, and six postures were used during oral

ingestive behaviors. Most posture changes took place during ingestive behaviors, followed by manual behaviors. There was only one recorded instance of feeding posture change during mastication.

Results from the MCMCglmm model suggest significant differences between postures and feeding events for most of the comparisons (SOM Table S4). Sitting postures were not related to manual behaviors, and behaviors such as quadrupedal stand and forelimb crouch were not related to ingestive behaviors. Results of an MCA for feeding event and feeding postural behaviors showed significant differences ($\chi^2 = 327.02$, $p < 0.01$). Dimension one captured 57.6% of the total variation with low values associated with oral-manual ingestion and mastication and postures such as squat and sit-in (Figure 2). High values on dimension one captured postures used during manual behaviors, namely flexed bipedal stand, which is associated with tool use while processing palm nuts. The second dimension captured

41.3% of the variance with high values distinguishing postures used during oral ingestion and mastication and low values indicating feeding postural behaviors during oral-manual and manual behaviors.

The feeding postural behaviors with the longest average durations were squat, sit-out, and sit-in/sit-out. Across all foods, there were no differences in duration of postures during feeding events (manual behaviors, ingestive behaviors, and mastication) (all $p > 0.05$; SOM Table S5; Figure 3a).

Hypothesis H2. Feeding postural behaviors and substrate.

Across all foods, seven feeding postures were used on small arboreal substrates, six on medium arboreal substrates, two on large arboreal substrates, and eight on terrestrial substrates. Results of the

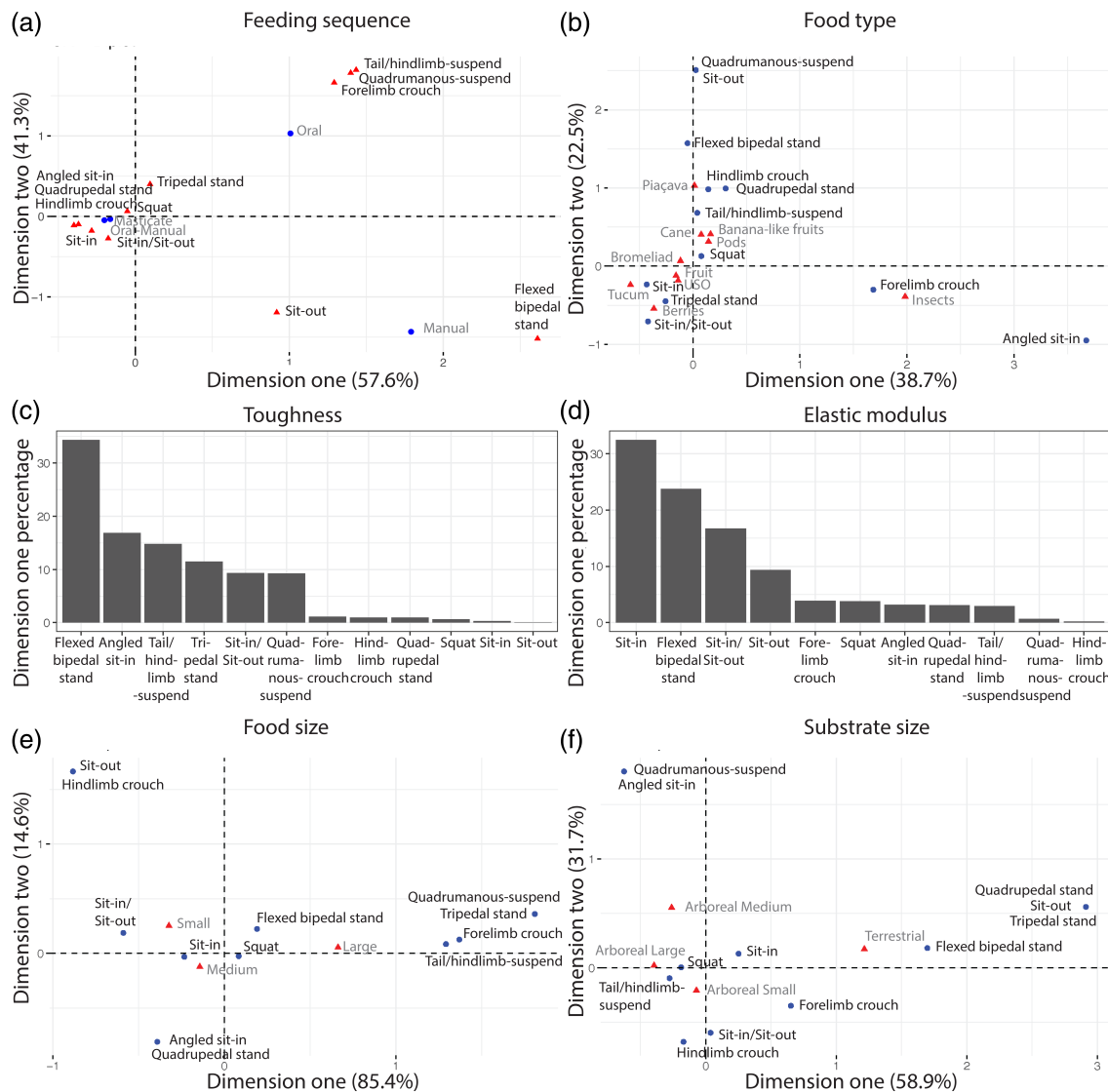


FIGURE 2 Results of the multiple correspondence analysis for (a) elements of the feeding sequence, (b) food type, (c) food toughness, (d) food elastic modulus, (e) relative food size, and (f) relative substrate size. Panels A, B, E, and F are bivariate plots of the first and second dimension with feeding postural behaviors (in blue) clustering near the categorical variable (in red). Panels C and D are univariate plots showing the percent contribution of each feeding postural behavior

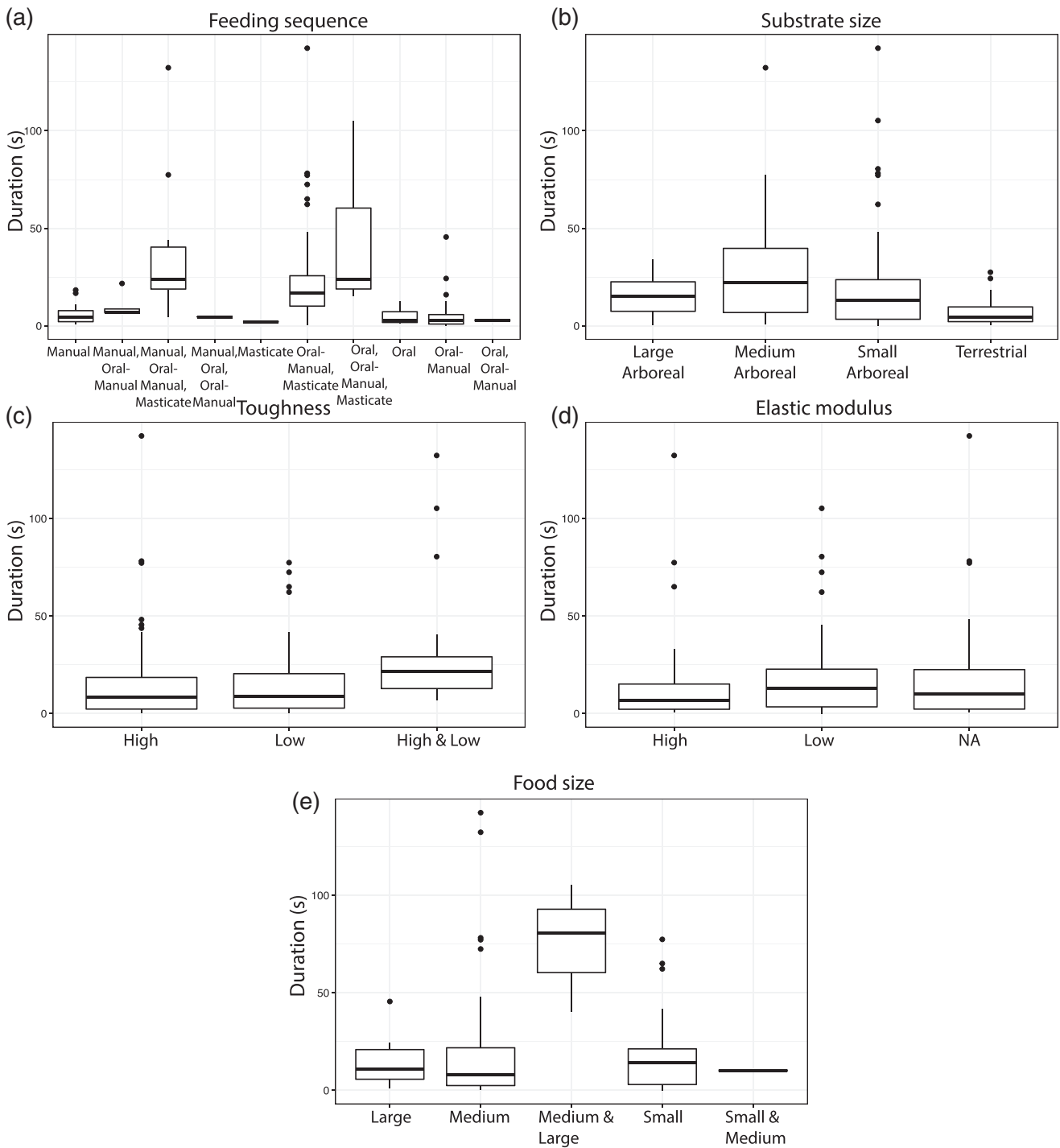


FIGURE 3 Boxplots showing differences in duration for (a) elements of the feeding sequence, (b) relative substrate size, (c) food toughness, (d) food elastic modulus, and (e) relative food size. Arboreal substrates were classified as ‘small’ if their diameter was less than half the length of each subject’s hand, ‘medium’ if the substrate was up to the length of the animal’s hand, and ‘large’ if the substrate’s diameter exceeded the animal’s hand length. Similarly, food item size was classified as ‘small’ if the diameter of the food item was less than half the length of each subject’s jaw length (gonial angle to mandibular symphysis), ‘medium’ if the food diameter was between half of the animal’s jaw length to the full jaw length, and ‘large’ if the food diameter exceeded the animal’s jaw length. The median is represented by a horizontal line inside the boxes, and the upper and lower bound of the boxes corresponds with the 25% and 75%. The whiskers extend 1.5 times the interquartile range in either direction

MCMCglmm model suggest that almost all postural behaviors were related to their arboreal or terrestrial substrate (SOM Table S6). For substrate size, sitting, flexed bipedal stand, and quadrupedal stand

postures occurred significantly more on large and terrestrial substrates, whereas tail/hindlimb suspended postures were significantly more common on small substrates (SOM Table S7). An MCA of

feeding postures and substrate yielded significant variation ($\chi^2 = 419.57$, $p < 0.01$). Dimension one explained 58.9% of the variation and primarily captured differences between terrestrial, high values on dimension one, and arboreal substrates, low values (Figure 2). Terrestrial substrates were associated with feeding postures including the standing postures (flexed bipedal, quadrupedal, and tripodal) and sit-out. In contrast, arboreal substrates were associated with crouching, sitting, squatting, and suspended postures. Dimension two captured 31.7% of the variation and primarily explained differences in arboreal substrate size. Smaller substrates were more likely to be associated with crouched postures, but postures used for large and small substrates were grouped closer than postures for medium substrates.

Across the entire dataset, the bearded capuchins spent 60.51% of their time on small arboreal substrates, 23.63% of the time on medium arboreal substrates, 5.76% of the time on large arboreal substrates, and 10.10% of time on terrestrial substrates. A linear mixed model indicated that durations of feeding postural behaviors on small and medium arboreal substrates were significantly longer than feeding postural behaviors on terrestrial substrates (both $p < 0.01$; SOM Table S5; Figure 3b).

Hypothesis H3. Feeding postural behaviors and FMPs.

Nine feeding postures were used for foods with high-toughness values and 10 for foods with low-toughness values. Five feeding postures were used for foods with high-elastic modulus values and nine for foods with low-elastic modulus values. The MCMCgmm model results suggest higher toughness values were significantly associated with flexed bipedal stand, sit-in, and squat (SOM Table S8), but higher elastic modulus values were only associated with flexed bipedal stand, sit-in/sit-out, sit-out, squat, and tail/hindlimb-suspend (SOM Table S9). Across all hypotheses, elastic modulus followed by toughness as explanatory variables were the best fit for the dataset. Multiple correspondence analyses of high and low FMP values were significant for toughness ($\chi^2 = 68.04$, $p < 0.01$) and elastic modulus ($\chi^2 = 135.96$, $p < 0.01$; Figure 2).

Feeding postural behaviors for foods with a combination of low- and high-toughness values were significantly longer in duration compared to foods of either low toughness or high toughness (both $p < 0.01$; SOM Table S5; Figure 3c). There were no significant differences in feeding posture duration for high- and low-elastic modulus foods (Figure 3d).

Hypothesis H4. Feeding postural behaviors and food size.

Across all foods, six feeding postures were used for foods of small size, eight for foods of medium size, and seven for foods of large size. The MCMCgmm model results suggest tail/hindlimb-suspend and quadrupedal stand were significantly associated with larger food sizes, whereas sit-in and squat postures were significantly associated with a variety of food sizes (SOM Table S10). An MCA of food size and feeding postural behaviors yielded significant differences ($\chi^2 = 222.90$,

$p < 0.01$). Dimension one explained 85.4% of variation with low values capturing postures such as sit-in and squat associated with small and medium food sizes (Figure 2). High values on dimension one captured tail/hindlimb-suspend and quadrumanous-suspend postures used while processing large food items. The second dimension captured 14.6% of the variance differentiating between postures. Low values distinguished quadrupedal stand and angled sit-in, whereas hindlimb crouch and sit-out represented high values of dimension two.

Feeding postural behaviors for medium/large food sizes were significantly longer in duration compared to all other food sizes (all $p < 0.01$; SOM Table S5; Figure 3e). There were no significant differences among other food sizes.

Hypothesis H5. Feeding postural behaviors and the combination of substrate and food properties.

Based on DIC values, the best fit MCMCgmm model included substrate size and food toughness as explanatory variables indicating that feeding postural behaviors are best explained by a combination of substrate size and FMPs. The subsequent best-fitting model added substrate type as an explanatory variable. Each explanatory variable in both top fitting models was significantly related to feeding postural behaviors (SOM Table S11).

The best fit model of feeding postural durations included substrate type and food size. Thus, feeding postural duration is best explained by a combination of substrate and food geometric properties (SOM Table S12).

4 | DISCUSSION

Primates are thought to use a range of behaviors to address the biomechanical challenges of feeding and the foods—behavioral flexibility (Norconk & Veres, 2011). Broadly, behavioral flexibility (sometimes called behavioral plasticity, but see Strier, 2017) is the ability to modify behavior for a short time in response to a stimulus, such as a food. Studies of force-gape tradeoffs, bite and muscle forces, and feeding behaviors in primates suggest behavioral flexibility during primate feeding relates to the biomechanical configuration of the feeding system and the foods (Coiner-Collier et al., 2016; Laird, Granatosky, et al., 2020; Laird, Wright, et al., 2020; Ross et al., 2016; Ross & Iriarte-Diaz, 2019; Taylor & Vinyard, 2009; Wright, 2005). While the feeding and locomotor systems are infrequently related (but see Granatosky et al., 2019), our results suggest both systems are behaviorally flexible in response to food items.

Our first hypothesis posited that bearded capuchins would have varied feeding postural behavior across the feeding event, particularly during manual and ingestive behaviors. Our results suggest the greatest variation in feeding postures occurred during oral-manual ingestive behaviors and to a lesser extent during manual behaviors for particular foods. Oral ingestive behaviors had half the number of feeding posture changes as oral-manual ingestive behaviors. We found only one change in feeding postures during mastication indicating that

the posture assumed during manual or ingestive behaviors was usually maintained until the end of mastication, resulting in longer postural durations. The rarity of posture changes during mastication may reflect the animal adopting postures during chewing that are energetically efficient. Alternatively, mastication and bolus formation for swallowing are thought to minimize the risk of aspiration and choking (Prinz & Lucas, 1997), and the locomotor system may play a role in providing stability of the head to minimize these risks. Distinguishing between these hypotheses requires future investigation.

Previous studies of primates suggest the behaviors used during ingestion may be food-specific (Laird, Wright, et al., 2020; Ungar, 1994), and it is likely that feeding postural behaviors will vary both *within* and *across* food types. While we were unable to test *within*-food relationships due to small sample sizes, food geometric properties and FMPs are expected to change within a food item and across the feeding sequence. For example, removing the hard outer layer of a fruit both reduces the size and alters the mechanical properties of the food. We assume that some of the variation captured in feeding postural behaviors relating to FMPs and food size reflects *within*-food and *within*-sequence variation.

The relationship between body size, substrate size, and positional behavior (postural and locomotor behaviors) has been well studied in primates (e.g., Cant, 1987a and 1987b; Cant, 1992; Cartmill, 1974; Fleagle & Mittermeier, 1980; Gebo, 1992; Jenkins, 1974; Schmitt, 2003; Thorpe & Crompton, 2006; Thorpe et al., 2007). We found that bearded capuchins showed the largest differences in feeding postural behavior between arboreal and terrestrial substrates, but smaller postural differences were noted on arboreal substrates of varying size. This finding suggests postures during feeding are consistent with posture changes relating to substrate balance and coordination (Stevens, 2006). The difference in feeding postures between arboreal and terrestrial substrates likely reflects a combination of substrate stability, food distribution, and postural requirements during food processing. Terrestrial foods were associated with infrequent postures used to access a particular type of food that are likely unevenly distributed. These postures include flexed bipedal stand used while cracking palm nuts with hammer stones and forelimb crouch used to extract underground tubers. Toussaint et al. (2013) suggest that small arboreal substrates increase hand use during postures and locomotion. Our data indicate that feeding postures, including hand use, were used across all three sizes of arboreal substrates. This difference likely relates to the generalist feeding strategy of bearded capuchins in our sample and that their food resources are less frequently acquired on terminal branches of small size. In this sense, substrate size may have a limited impact on feeding postures in bearded capuchins compared to other primates that frequently exploit terminal branch resources. Grand (1972) noted that terminal branches present a challenge for arboreal mammals such as primates, and that medium and larger-bodied species may need to employ specific feeding postures, such as sitting on a larger part of the substrate and reaching forward to the terminal part of the branch, or suspension underneath smaller substrates, to accommodate feeding on peripheral parts of tree branches. Primates of different sizes rely on food resources that are associated with terminal

branches and adopt postures that allow them to exploit the terminal branch environment. For example, Dunbar and Badam (2000) found that, like the bearded capuchins in our study, juvenile bonnet macaques (*Macaca radiata*) used postures such as sitting or crouching on lateral branches while reaching forward to grasp more vertically oriented terminal branches in order to feed on flowers, thereby spreading their body weight over multiple substrates. Larger-bodied species use suspensory postures to feed in terminal branches. McGraw (1998) found that colobine (*Colobus badius*, *C. polykomos*, and *C. verus*) and cercopithecine species (*Cercopithecus diana*, *C. campbelli*, and *C. atys*) all frequently fed in a small branch environment and when doing so used sitting positions while reaching for food items. Gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) use orthograde suspension and sitting postures to feed in terminal branches (Fleagle, 1976; Grand, 1972), and orangutans (*Pongo abelii*) use pronograde suspensory orientation to feed on fruits located in the terminal branch environment (Myatt & Thorpe, 2011). We also note that our analyses do not take other aspects of substrate into account, such as compliance or orientation, although these variables have been related to postural behaviors in other studies (Dagosto & Gebo, 1998; Mekonnen et al., 2018).

The influence of substrate size, FMPs, and food size on feeding postures is likely to vary seasonally and with sociobiology. Previous studies suggest that seasonal variation can result in changes in primate postural behavior (Dagosto, 1995; Wright, 2007). Our data were collected during the dry season, when bearded capuchins exploit the most mechanically challenging food items (Visalberghi et al., 2008; Wright, 2005). Work at Fazenda Boa Vista suggests that non-palm fruit abundance is either consistent throughout the year (Spagnoletti et al., 2012) or may in some years be higher in the wet season (Izar et al., 2012). Palm nuts are found to be more abundant during the dry season (Izar et al., 2012; Spagnoletti et al., 2012); whereas insects are markedly more abundant in the wet season (Spagnoletti et al., 2012). Seasonal shifts in food availability from the dry to the wet season may result in less time spent on terrestrial substrates and reduced postural variability. The seasonal availability of preferred foods will also change food competition and group sociality (Verderane et al., 2013), and these dynamics along with predation risk likely have an impact on feeding postures, their duration, and frequency. Some foods in our dataset, such as fruits, tended to be more clumped than foods such as insects, likely increasing food competition. High-ranking female gray-cheeked mangabeys (*Lophocebus albigena*) have been shown to have longer feeding durations compared to low-ranking females (Chancellor & Isbell, 2009), and the number of predator scans decreased during manual feeding behaviors in ursine colobus monkeys (*Colobus vellerosus*; Teichroeb & Sicotte, 2012). These comparisons suggest our data potentially overestimate postural changes, duration, and frequency, as some postural variation may relate to sociobiological factors. Incorporating sociobiological variables into future studies will provide a broader context for postural changes and the relationships between posture and food availability.

Food geometric and material properties have a significant influence on oral food processing in wild and captive primates (e.g., Coiner-Collier et al., 2016; Laird, Wright, et al., 2020; Norconk

et al., 2009; Perry & Hartstone-Rose, 2010; Ross et al., 2016; Vinyard et al., 2008; Wright, 2005). Strepsirrhine data suggest food geometric and material properties have a significant influence on grasping strategies (Peckre et al., 2019), and food type is thought to influence posture in select wild primates (e.g., Bicca-Marques & Calegario-Marques, 1993; Grueter et al., 2013; McGraw, 1998). To our knowledge, this paper is the first to relate food geometric and material properties to positional behaviors, specifically posture. Our results indicate, for bearded capuchins, feeding postures significantly differ between foods of high and low toughness and elastic modulus, and feeding postures are less variable for highly mechanically challenging foods. These results suggest that mechanically challenging foods may constrain variation in feeding postures through two possible mechanisms. First, bearded capuchins assumed a limited number of postures because of force constraints. While we did not measure muscle forces, feeding postural variation may relate to maximizing mechanical advantage for manual and ingestive behaviors, particularly for foods of higher toughness and stiffness. For example, a crouched posture used when extracting tubers allows them to use their forelimbs and hindlimbs to push against the terrestrial substrate. Additional analyses are needed to evaluate this suggestion. Second, mechanically challenging foods may be more likely to occur on substrates that limit posture. For example, tubers are buried in the ground, requiring the individual to assume select postures during extraction. Constrained feeding postures for mechanically challenging foods may also reflect a combination of these possibilities.

Food size had a significant effect on postural behaviors in bearded capuchins. Large foods were more likely to be associated with suspended postures whereas small foods were associated with sitting and squatting. We propose this variation reflects two aspects of food size. First, foods can be classified depending on whether they can be held in the hands. Small foods generate low magnitude moments on the limbs, so the limbs are relatively unconstrained in posture. In contrast, large foods will generate large moments and therefore are more likely to impact limb posture. The second aspect of food size dictating feeding posture is when large food items, such as sugar cane, double as both the food item and the substrate. These large food items result in feeding postural behaviors that both support the animal's body weight and position the oral cavity or hands for food processing. This relationship mirrors the influence of body size and substrate size on posture (Jenkins, 1974). Our data also suggest that foods reduced from large to medium sizes were associated with significantly longer durations of feeding postural behaviors compared to other food sizes. This indicates that bearded capuchins engaged in food size reduction presumably to meet the force-gape constraints of the feeding system and suggests that some variation in postural behaviors reflects *within*-food variation in food size.

Our results support the idea that feeding postural behaviors are best explained using a combination of substrate and food geometric and mechanical properties. Posture is inherently dependent on an animal's substrate. For example, suspensory postures are unlikely to occur on terrestrial substrates, but postures during feeding are also influenced by required food access. However, it is worth noting the

strong influence of geometric properties on postural behavior, given that this parameter is infrequently measured or reported from the field. We propose that substrate provides the first set of constraints in feeding postures, and food properties are a second. In this sense, feeding postural behaviors reflect spheres of influence similar to those proposed for mandibular morphology (Ross & Iriarte-Diaz, 2014). This also implies that substrate provides an incomplete view of postural variation during feeding, which is likely dependent on the substrate and food. Our results suggest large, embedded, and/or mechanically challenging foods have a larger influence on feeding postures.

While associations between locomotion and dietary categories in primates are tenuous at best (Fleagle, 1984; Gebo, 2011), the data presented here suggest feeding postural behaviors can reflect aspects of diet, specifically FMPs and food size. In the same way that studies of FMPs have reshaped our understanding of craniodental morphology and feeding behaviors (Ross et al., 2012), our results suggest similar hierarchical approaches can elucidate flexibility in postural behaviors during feeding. Future work testing the relationships between feeding postural behaviors and FMPs and size at other sites and in taxa will improve the generalizability of these results.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

All data to support the findings of this study are available in the supplementary material of this article.

AUTHOR CONTRIBUTIONS

Myra F. Laird: Conceptualization (lead); data curation (lead); formal analysis (lead); supervision (equal); writing – original draft (lead). **Zeenia Punjani:** Data curation (lead); methodology (equal); writing – review and editing (equal). **Rachel R. Oshay:** Data curation (lead); methodology (equal); writing – review and editing (equal). **Barth W. Wright:** Data curation (supporting); funding acquisition (lead); methodology (equal); resources (equal); writing – review and editing (equal). **Mariana Dutra Fogaça:** Data curation (supporting); methodology (supporting); writing – review and editing (equal). **Adam van Casteren:** Data curation (supporting); methodology (supporting); writing – review and editing (equal). **Patrícia Izar:** Investigation (equal); resources (equal); supervision (equal); writing – review and editing (equal). **Elisabetta Visalberghi:** Resources (equal); writing – review and editing (equal). **Dorothy M. Fragaszy:** Investigation (equal); resources (equal); writing – review and editing (equal). **David S. Strait:** Funding

acquisition (equal); methodology (equal); resources (equal); writing – review and editing (equal). **Callum F. Ross:** Funding acquisition (equal); methodology (equal); resources (equal); writing – review and editing (equal). **Kristin A. Wright:** Funding acquisition (equal); methodology (equal); resources (equal); writing – review and editing (equal).

ORCID

Myra F. Laird  <https://orcid.org/0000-0002-8636-0407>

Barth W. Wright  <https://orcid.org/0000-0001-9477-6499>

Adam van Casteren  <https://orcid.org/0000-0002-2993-8874>

David S. Strait  <https://orcid.org/0000-0002-3572-1663>

Callum F. Ross  <https://orcid.org/0000-0001-7764-761X>

Kristin A. Wright  <https://orcid.org/0000-0002-6431-1081>

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