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RESEARCH ARTICLE

Ontogenetic changes in bite force and gape in tufted capuchins

Myra F. Laird[1,*], Cláudia Misue Kanno[2], Caitlin B. Yoakum[3], Mariana Dutra Fogaça[4,5], Andrea B. Taylor[6], Callum F. Ross[7], Janine Chalk-Wilayto[8], Megan A. Holmes[9], Claire E. Terhune[10] and José Américo de Oliveira[2]

ABSTRACT

Bite force and gape are two important performance metrics of the feeding system, and these metrics are inversely related for a given muscle size because of fundamental constraints in sarcomere length–tension relationships. How these competing performance metrics change in developing primates is largely unknown. Here, we quantified *in vivo* bite forces and gapes across ontogeny and examined these data in relation to body mass and cranial measurements in captive tufted capuchins, *Sapajus* spp. Bite force and gape were also compared across geometric and mechanical properties of mechanically challenging foods to investigate relationships between bite force, gape and food accessibility (defined here as the ability to breach shelled nuts). Bite forces at a range of gapes and feeding behavioral data were collected from a cross-sectional ontogenetic series of 20 captive and semi-wild tufted capuchins at the Núcleo de Procriação de Macacos-Prego Research Center in Araçatuba, Brazil. These data were paired with body mass, photogrammetric measures of jaw length and facial width, and food geometric and material properties. Tufted capuchins with larger body masses had absolutely higher *in vivo* bite forces and gapes, and animals with wider faces had absolutely higher bite forces. Bite forces and gapes were significantly smaller in juveniles compared with subadults and adults. These are the first primate data to empirically demonstrate the gapes at which maximum active bite force is generated and to demonstrate relationships to food accessibility. These data advance our understanding of how primates meet the changing performance demands of the feeding system during development.

KEY WORDS: Performance, Feeding, *Sapajus*, Primate, Craniodental morphology

INTRODUCTION

A primate's ability to access and break down food items is dependent on two key performance metrics of the feeding system: bite force and gape (Herring and Herring, 1974; Hylander, 2013). Bite force is the product of jaw elevator muscle force and the bony geometry of the facial skeleton, i.e. lever arms of the jaw muscles and location of the bite point along the toothrow. Moreover, under the constrained lever model of the biting apparatus, bite forces are modulated by neural control factors, such that bite force increases posteriorly along the toothrow until the first or second molar, then decreases at more distal molars (Hylander, 1975; Greaves, 1978; Radinsky, 1981; Spencer, 1999; Thompson et al., 2003; Ross et al., 2018). Importantly, however, bite forces are also moderated by gape (Herring and Herring, 1974; Lindauer et al., 1993; van Eijden and Turkawski, 2001; Dumont and Herrel, 2003; Eng et al., 2009; Williams et al., 2009), primarily because the length–tension relationship of skeletal muscle sarcomeres imposes a fundamental constraint on whole muscle length–tension relationships, which change with gape (Anapol and Herring, 1989; Eng et al., 2009; Ross and Iriarte-Diaz, 2019; Taylor et al., 2019). Muscle fibers (and sarcomeres) generate maximum force at a narrow range of optimal lengths, and lower forces at lengths shorter or longer than their optimum. Hence, as gape increases or decreases, changes in jaw muscle length (stretch) are associated with changes in maximum available muscle force and bite force capacity for a specific muscle size (Fig. 1) (Herring and Herring, 1974; Taylor et al., 2009, 2019). The available data suggest that for masseter (at least), maximum muscle force is generated at a few degrees of gape, decreasing slightly at minimum gape, as well as across the wide range of larger gapes (Anapol and Herring, 1989; Dechow and Carlson, 1986, 1990; Eng et al., 2009; Taylor et al., 2009; Williams et al., 2009; Santana, 2016). Hence, the potential bite force–gape trade-off is particularly important for animals that depend on large, mechanically challenging foods requiring relatively wide gapes and relatively high bite forces.

The precise nature of the relationship between gape, muscle stretch and maximum available muscle force capacity is moderated by static and dynamic muscle architecture – muscle mass, muscle fiber/fascicle length and angulation, and, hence, physiological cross-sectional area (PCSA) (Madeira and de Oliveira, 1979; Powell et al., 1984; Azizi et al., 2008; Taylor and Vinyard, 2009, 2013; Taylor et al., 2009, 2020; Laird et al., 2020a). Modifications to these aspects of jaw elevator muscle morphology have been shown to enable the maintenance of large muscle and bite forces at wide gapes in adult tufted capuchins (*Sapajus* spp.) compared with untufted capuchins (*Cebus* spp.) (Taylor and Vinyard, 2009), and in adult male *Macaca fascicularis* relative to conspecific females (Terhune et al., 2015), or to allow low force gouging at large gapes in adult tree-gouging marmosets (Taylor et al., 2009; Eng et al., 2009). These studies demonstrate that selection can act on different components of the masticatory system in order to circumvent the theoretical trade-off between bite force and gape.

There are data on ontogenetic changes in bite force, but these data were collected at controlled gapes (e.g. Dechow and Carlson, 1990). In an ontogenetic sample of macaques, stimulated maximum

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[1]Department of Basic and Translational Sciences, University of Pennsylvania, Philadelphia, PA 19104-6030, USA. [2]Universidade Estadual Paulista (UNESP), Research Center 'Núcleo de Procriação de Macacos-Prego', Araçatuba Dental School, Araçatuba - SP, 16018-805, Brazil. [3]Department of Anatomy, Arkansas Colleges of Health Education, Fort Smith, AR 72916, USA. [4]Department of Biomedical Sciences, Institute of Population Genetics, University of Veterinary Medicine, Vienna, Austria. [5]Neotropical Primates Research Group – NeoPReGo. [6]Department of Foundational Biomedical Sciences, Touro University California, Vallejo, CA 94592, USA. [7]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA. [8]Department of Biomedical Sciences, Mercer University School of Medicine, Savannah, GA 31404, USA. [9]Department of Family Medicine and Community Health, Duke University School of Medicine, Durham, NC 27710, USA. [10]Department of Anthropology, University of Arkansas, Fayetteville, AR 72701, USA.

*Author for correspondence (mflaird@upenn.edu)

M.F.L., 0000-0002-8636-0407; M.D.F., 0000-0002-6776-9389; C.F.R., 0000-0001-7764-761X

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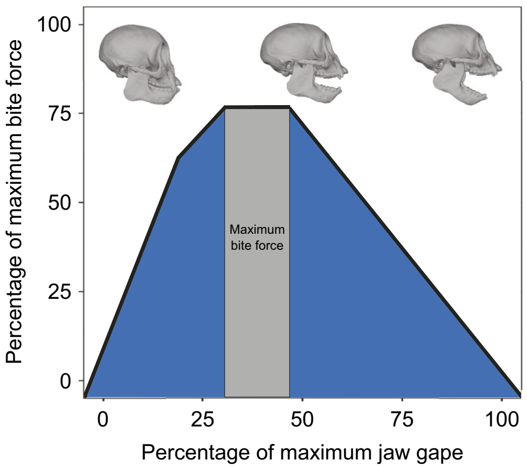

Fig. 1. Theoretical bite force–gape curve that reflects a muscle length–tension curve. Muscle fibers generate maximum force at an optimal length, and muscle fibers operating at lengths shorter or longer than their optimum (i.e. large gapes) result in reduced bite forces. A *Sapajus apella* skull illustrates changes in gape.

occlusal bite forces were isometrically related to jaw length and outpaced body mass (Dechow and Carlson, 1990). Ontogenetic changes in bite force in grey mouse lemurs (*Microcebus murinus*) are correlated with changes in body mass and cranial width (Chazeau et al., 2013), and differences in bite force are heritable (Zablocki-Thomas et al., 2021). Bite force data from humans also support increased force production across ontogeny (Edmonds and Glowacka, 2020). There have also been some attempts to estimate ontogenetic changes in gape on the basis of body mass and craniofacial morphology (Dechow and Carlson, 1986; Weijs et al., 1989). Adult *in vivo* gapes and jaw lengths suggest positive allometry across catarrhines (Hylander, 2013) but not necessarily cercopithecids (Taylor et al., 2020), and maximum ingested food sizes scale isometrically with body mass and jaw length in adult strepsirrhines (Perry and Hartstone-Rose, 2010) and negatively in anthropoids (Perry et al., 2015; Paciulli et al., 2020). Measures of maximum bony gape are positively correlated with body mass across adult primates (Fricano and Perry, 2019). However, it is unknown how primate *in vivo* gapes vary with body mass and craniofacial morphology during development. In infant rabbits, maximum gapes at weaning are larger than those in adults, which could be related to a variety of factors such as ontogenetic differences in motor control, craniofacial shape, and jaw muscle architecture (Weijs et al., 1989). These rabbit data suggest that *in vivo* bite forces and gapes may be inversely related, such that juvenile primates favor larger *in vivo* gapes over bite forces, whereas adults favor higher *in vivo* bite forces at the expense of gape.

The ontogeny of the bite force–gape trade-off, which is important for understanding the relationship between ontogenetic changes in feeding system morphology and performance, has been examined in nonprimate mammals (Weijs et al., 1987; Anapol and Herring, 1989; Langenbach and Weijs, 1990), but is less well studied in primates. Many papers have documented developmental changes in the geometry of the mammalian facial skeleton resulting in large shifts in muscle leverage and force production (e.g. Enlow, 1966; Herring, 1985; Boughner and Dean, 2008; Terhune et al., 2020). For example, longer jaws in macaques are associated with larger jaw elevator muscles, which are thought to relate to maintaining bite forces as the ratio of bite point lever arm to muscle lever arms increase (Antón, 1999). Similarly, overall craniofacial size, including facial width, is linked to increased muscle force estimates (Weijs and Hillen, 1985; Koolstra et al., 1988; Hannam and Wood, 1989; van Spronsen et al., 1992; Raadsheer et al., 1999). There are fewer studies of ontogenetic changes in muscle architecture. Adult *M. fascicularis* have relatively longer fibers and larger jaw–elevator PCSAs than juveniles (Dickinson et al., 2018), but PCSAs and fascicle lengths in mouse lemurs (*M. murinus*) increase during development and then plateau in adults (Leonard et al., 2020). Neonatal common marmosets do not have relatively longer fibers compared with non-gouging cotton-top tamarins, in contradistinction to the adult pattern (Mork, 2012), suggesting that the onset of feeding and muscle plasticity accounts for at least some of the changes in fiber architecture observed during ontogeny. Together, these studies suggest that there are age-related changes in the relationship between bite force and gape that might impact feeding performance. However, to our knowledge, there are no *in vivo* data on ontogenetic changes in both bite force and gape in any non-human primates, a knowledge gap limiting understanding of the mechanistic underpinnings of ontogenetic changes in feeding performance.

Research goals and hypotheses

In this study, we quantified and examined changes in bite forces and gapes at the anterior dentition across an ontogenetic sample of tufted capuchins (*Sapajus* spp.). Tufted capuchins have served as model species for studies aimed at understanding the mechanics of hard-object feeding as well as for studies drawing paleobiological inferences about feeding behavior and diet in extinct taxa (Daegling, 1992; Wright, 2005). The trade-off between bite force and gape provides a theoretical limit to the geometric (size) and mechanical (force) properties of ingested foods. However, primates are known to circumvent biomechanical constraints through behavioral flexibility (Norconk and Veres, 2011; McGraw and Daegling, 2012). 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 particular situation (Amici et al., 2018), for example, using manual behaviors to reduce food size. Behavioral data suggest that some primates may indeed use manual behaviors to circumvent bite force–gape constraints. For example, tool use in wild tufted capuchins allows them to access hard foods that exceed their bite force capabilities, resulting in improved diet quality (Wright et al., 2009; Izar et al., 2022). Therefore, we also investigated behavioral flexibility related to food access. *Cercocebus* frequently uses the postcanine toothrow to access hard foods, whereas *Lophocebus* relies on the anterior dentition (Daegling and McGraw, 2007; McGraw et al., 2011). These mangabeys use behavioral modifications to access hard foods by carefully selecting less mechanically challenging food items and exploiting weaknesses in the foods themselves (McGraw and Daegling, 2020; Geissler et al., 2021). Thus, pairing *in vivo* experiments with behavioral flexibility data allows us to examine the extent to which bite force–gape curves reflect food accessibility, particularly for large, mechanically challenging foods that may require additional manipulation. Here, we present data on ontogenetic changes in bite force and gape, and test a series of hypotheses about their relationship to morphological and performance variables:

Hypothesis 1: Maximum *in vivo* bite forces and linear gapes are positively correlated with body mass and craniomandibular measurements in tufted capuchins

Animals with larger body masses, jaw lengths and facial widths are expected to produce higher bite forces. Previous primate studies have demonstrated a positive relationship between jaw length, facial width and bite force when examined ontogenetically (e.g. jaw length, Dechow and Carlson, 1990; jaw length and facial width, Chazeau et al., 2013). Hence, we predicted that *in vivo* maximum recorded bite forces of tufted capuchins would be positively correlated with body mass, jaw length and facial width during ontogeny and among adults. Maximum recorded gapes were also expected to increase with body mass. As we expected jaw length to vary with body mass, we also expected jaw length relative to body mass to increase with both bite force and gape. The null hypothesis is that body mass and cranial measurements have no relationship to maximum or relative bite forces and gapes in tufted capuchins.

Hypothesis 2: Maximum *in vivo* bite forces are inversely related to gape and vary across ontogeny in tufted capuchins

Theoretical and experimental data suggest that jaw muscle and bite forces increase until the muscles reach their optimal lengths and then decrease with increasingly larger gapes (Herring and Herring, 1974; Eng et al., 2009; Williams et al., 2009; Taylor et al., 2019). However, the decrease in force will likely be moderated by where the gape falls on the animal's 'whole jaw system' length–tension curve; gapes slightly larger than optimal will be associated with a slight decrease in bite force, and gapes much larger than optimal will exhibit a large decrease in bite force. At any particular age, 'whole system' bite force–gape curves should resemble those of sarcomeres or whole fiber – convex superiorly – but the precise shape will be a function of the combined gape–length–tension relationships of all jaw elevator muscles. The null hypothesis is that bite force–gape curves are not convex and do not change across ontogeny.

Hypothesis 3: Bite force–gape curves constrain food accessibility and biting location in tufted capuchins

Bite force–gape curves are expected to explain the limit of accessible food size in terms of gape, and food fracture properties in terms of bite force at a given gape, and determine the location along the toothrow where foods are fractured. As such, foods that demand performance outside of the bite force–gape curve are expected to be inaccessible at a particular location on the toothrow in the absence of behaviors that make such items accessible. The null hypothesis is that bite force–gape curves do not reflect food accessibility or biting location in tufted capuchins.

MATERIALS AND METHODS

In vivo bite force, gape and feeding data were collected from 20 captive and semi-wild tufted capuchins (*Sapajus* spp.) over a 3-week period in May–June 2022 at the Núcleo de Procriação de Macacos-Prego Research Center at the Faculdade de Odontologia-Campus de Araçatuba-UNESP, Araçatuba, Brazil. The capuchins in the sample population were hybrids of *Sapajus libidinosus* and *Sapajus nigritus*. In geographically distinct areas, these species differ in their dietary composition in that *S. libidinosus* spend more time foraging fruits and flowers, whereas *S. nigritus* spend more time foraging leaves (Izar et al., 2012). However, the hybrids in our Araçatuba sample ate the same foods, and the animals exhibit few differences in coloration, suggesting similar levels of hybridization. The semi-wild individuals are provisioned but free ranging, whereas the captive animals are permanently held at the Núcleo de Procriação de Macacos-Prego Research Center. All semi-wild individuals were released at the end of the study. The captive sample was only composed of adults, and there were no differences between maximum bite force or gape between the semi-wild and captive adults (Mann–Whitney *U*-test; bite force P=0.13; gape P=0.60). All experiments were reviewed and approved by the UNESP-Araçatuba Ethics Committee on the Use of Animals (00151-2019), the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio-77908-1) and the University of Southern California Institutional Animal Care and Use Committee (21294).

Animals in this study were grouped into three age categories: juvenile (three animals: two females, one male; prior to the first molars in occlusion), subadult (seven animals: three females, four males; first to second molars in occlusion) and adult (10 animals: four females, six males; third molars in occlusion; Table S1). Dental eruption was assessed through opportunistically collected photographs. Each animal was weighed using a digital scale except for two adult males (capuchins 24 and 26). Body masses for these individuals were estimated as the average of all the other adult males (3.35 kg). Body masses for the sample (excluding capuchins 24 and 26) ranged from 0.65 to 3.95 kg (Table S1).

Bite force data

A total of 1505 bites were collected across a range of gapes (5–40 mm). For each individual, the highest bite force at each gape was retained for analysis. Bite forces were collected using a custom-built bite force transducer based on a model described by Herrel and colleagues (e.g. Verwaijen et al., 2002; Aguirre et al., 2003; Herrel et al., 2001, 2004, 2005; Fig. S1). Briefly, the animal bites on the ends of two metal plates fixed to a compressive piezoelectric load cell (Kistler 9203). The metal plates were wrapped in cushioned athletic tape to protect the animal's teeth, and the animals were trained to bite on the plates for a week before data recording. The spacing between the bite plates, resulting in gape (in mm), was controlled by an adjustable micrometer (Mitutoyo 152-103). Output from the load cell was amplified (Kistler handheld amplifier-5995A) and passed through an analog-to-digital converter (Adafruit Industries ADS1115) to a Raspberry Pi 4 Model B where data collection was controlled using custom Python code. Biting was incentivized by a liquid strawberry yogurt reward administered through a plastic cannula attached to the underside of the top bite plate. All bites were monitored during recording and training, and biting was loosely threshold trained (similar to van der Meijden et al., 2023). The animal had to elicit stronger and stronger bites in order to receive the reward, and the reward was withheld if the animal used lower forces than their previous bites. If an animal became frustrated and or lost interest in biting because of a lack of reward, they were given a small amount of yogurt and the bite plates or the force threshold was reduced to reinforce the activity. Reward was only given for bites on the incisors. Gape was increased at 5 mm intervals until the animal was no longer willing to bite, and notes on voluntary bite location (incisors, canines or postcanine dentition) were recorded during the experiments. All analyses were conducted on maximum force and gape values recorded on the anterior dentition. Only a handful of bites were recorded on the postcanine dentition, and the sample was too small for comparative analyses. The recorded postcanine bite forces were also not collected using the same training regime as the animals were only rewarded for incisor bites.

Separate experiments were conducted to calculate a calibration factor between the amplified output values and Newtons of force. The bite plates were statically loaded three times with 100, 200 and 500 g weights at 10, 15 and 20 mm of gape. For each weight, these data suggested there were no significant differences in amplified force values between gapes, and a standard corrective factor could be applied to convert amplified forces to Newtons.

Morphological measurements

Cranial and jaw measurements for each individual were recorded using photogrammetry. Distance calibrated photographs were taken of each animal following methods described in Dunham et al. (2018) using a Bushnell Prime 1800 6×24 laser rangefinder and a Canon Rebel XS DSLR camera. These calibrated images were used to measure jaw length and facial width in Fiji (ImageJ v 2.1.0/1.53c). Jaw length was defined as the distance from the opening of the external auditory meatus to the skin superficial to infradentale (Fig. 2A). Bizygomatic breadth has been correlated with bite forces in mouse lemurs (Vuarin et al., 2013; Rakotoniaina et al., 2016; Thomas et al., 2015; Zablocki Thomas et al., 2018) and presumably reflects the size of the masticatory muscles. We could not consistently take this measurement from photos of capuchins because the shape of the zygomatic could not be consistently distinguished from facial hair. Instead, facial width was measured as the distance between the left and right lateral canthus of the eyes (Fig. 2B). This measure provides an estimate of facial width but does not capture variation in the size of the masticatory muscles. For all animals, jaw length and facial width measurements were recorded in at least three separate images and averaged (Table S1). Relative jaw length and facial width were calculated by dividing these measures by body mass, all logarithmically transformed.

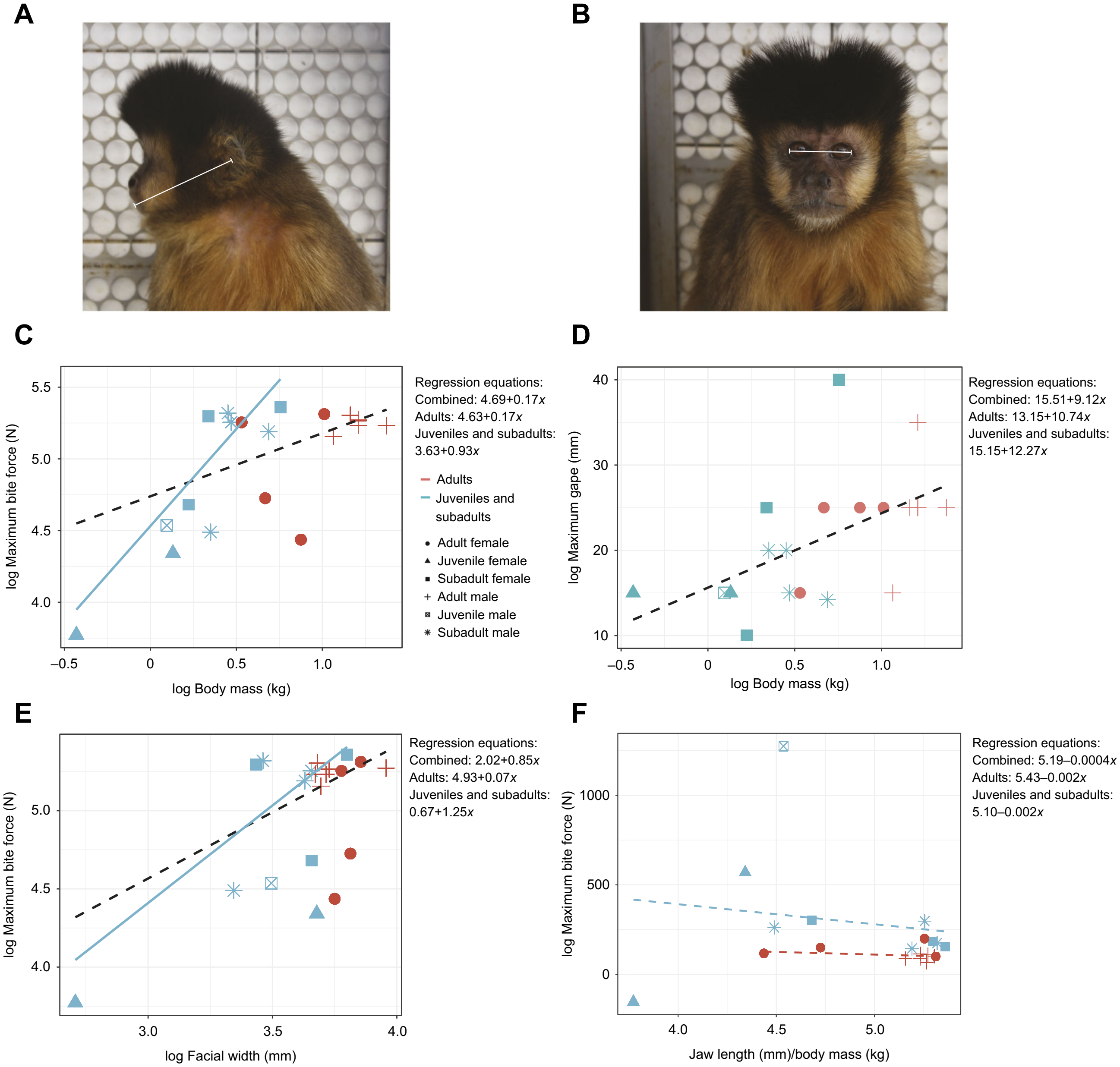

Fig. 2. Relationships between maximum bite force and gape with body mass and cranial morphology. (A) Lateral and (B) anterior photographs of an adult female tufted capuchin (*Sapajus* spp.). The anterior image shows the measurement of facial width between the right and left lateral canthi of the eyes, and the lateral photo shows the measurement of jaw length from the opening of the external auditory meatus to the skin over infradentale. (C–F) Relationships between (C) body mass and maximum bite force, (D) body mass and maximum gape, (E) facial width and maximum bite force, and (F) jaw length relative to body mass and maximum bite force. Tufted capuchins with larger body masses and wider faces had higher bite forces, particularly in juveniles and subadults. Non-significant regression lines are not shown, and the black dashed line shows the regression line for all individuals.

Table 1. Geometric and material properties of the experimental foods

Nut	Mass (g)	Length (mm)	Height (mm)	Width (mm)	Force to failure (N)
Brazil nut in shell (*n*=8)	8.54±1.225	40.28±5.508	26.55±3.546	19.56±1.952	614.46±111.498
English walnut in shell (*n*=8)	11.48±0.838	35.49±1.105	32.97±0.871	31.00±0.632	233.39±46.217
Peanut in shell (*n*=9)	3.02±0.459	39.49±3.402	16.53±1.248	16.01±1.305	64.63±18.557

Brazil nut and peanut width were used as proxies for gape at ingestion, but English walnuts were too large to place fully in the mouth. Instead, the capuchins would wedge their teeth along the walnut seam at an estimated gape of 19.44±2.02 mm. Data are means±s.d.

Feeding trials

Feeding trials were conducted using three foods: peanuts in shell, Brazil nuts in shell and English walnuts in shell (Table 1). These foods were selected to cover a range of food geometric and material properties and to be resistant to manual deformation. Previous studies have used foods cut into cubes of various sizes such as melon and sweet potato to estimate maximum bite size (e.g. Perry and Hartstone-Rose, 2010), but this approach did not yield accurate data for our tufted capuchin sample because of their propensity to manipulate foods manually. An FLS-II portable universal tester (Lucas Scientific) was used to measure the amount of force (N) needed to fracture the nuts in shell. All three nut types were obtained from a commercially available source in the USA (www.nuts.com). Although these nuts were the same species given to the experimental individuals, they are not from the same sample provided to the Araçatuba capuchins. Weight, maximum length, height, width and force to fracture were recorded eight times for each nut type (Table 1). Food size was not related to force to fracture in these nuts, as Brazil nuts require the highest amount of force to fracture but were intermediate in size between peanuts and walnuts. To obtain force to fracture, each nut was slowly compressed between two brass plates until fracture, and resultant force was measured with a 1000 kN load cell. Nuts were oriented with the long axis parallel to the compression plate surfaces, similar to how the experimental capuchins positioned them on the tooth row. During the behavior trials, each animal was presented with the nuts in random order on at least five different days for a minimum of 30 min (maximum of 1 h) each day and the feeding bouts were coded as either accessed (i.e. the outer shell was fully fractured to reach the kernel) or discarded (i.e. the shell was not fractured or minimally fractured without accessing the kernel). Location on the toothrow of the initial shell fracture was also recorded for accessed feeding bouts. There were no trials in which animals successfully used their hands (e.g. pounding against cage) to initially fracture the walnut, peanut or Brazil nut shells. For the analyses, feeding bouts were summarized for each animal by food type as accessed in all bouts, discarded in all bouts, or a mix of accessed and discarded, and bite location was coded as incisors or postcanine dentition for any accessed bout (Table S1).

Analyses

All analyses were conducted in R v. 3.6.2 (https://www.r-project.org/) using the ggplot2 (Wickham, 2016), ggsci (https://CRAN.R-project.org/package=ggsci) and readxl packages (https://CRAN.R-project.org/package=readxl). For all analyses, bite force, gape, body mass, facial width and jaw length were logarithmically transformed. The highest recorded bite force and gape for each animal was defined as maximum bite force and maximum gape. These measures were used to test all three hypotheses.

Hypothesis 1 was tested using a series of linear models with body mass, jaw length or facial width as the explanatory variable and maximum bite force or maximum gape as the response variable.

Hypothesis 2 was first tested using nonparametric statistics because of the small sample size and because most variables did not pass a Shapiro–Wilk normality test. Kruskal–Wallis and pairwise Wilcoxon rank sum tests were used to test for differences in maximum bite forces and maximum gape between age categories. Mann–Whitney *U*-tests were used to test for differences in maximum bite force and maximum gape between sexes within each age group. Hypothesis 2 also tested differences in bite force–gape curve shape across animals. Custom R code was written to calculate the radius of curvature fit across three bite force–gape points. The first point was the gape at maximum bite force and the other two were the maximum bite forces for gapes on either side of the first point. For most individuals, these were the maximum bite forces recorded at 10, 15 and 20 mm of gape. The radius of curvature calculation fits a circle to this series of points and measures the radius of the circle; wider curves have a larger radius of curvature. Kruskal–Wallis and pairwise Wilcoxon rank sum tests were used to test for differences in the radius of curvature between age categories. Significance for all analyses was set at $\alpha<0.05$.

For hypothesis 3, differences in body mass, maximum bite forces and maximum gapes between food accessibility categories (accessed, discarded, or a mix of accessed and discarded) and bite location (incisor and postcanine) were tested using Kruskal–Wallis and pairwise Wilcoxon rank sum tests.

RESULTS

Hypothesis 1

Maximum recorded anterior bite force was positively correlated with body mass across all individuals (P=0.01, r^2=0.33; Fig. 2C, Table 2), and across juveniles and subadults (P<0.01, r^2=0.73), but not across adults only (P=0.30, r^2=0.18; Table S2). Importantly, these relationships remain significant if the analyses are rerun excluding the individual capuchin with the smallest body mass, which is more than one standard deviation below the mean. Maximum recorded gape was also positively correlated with body mass across all individuals (P=0.02, r^2=0.29; Table 2, Fig. 2D), but not when age categories were analyzed separately (Table S2). Neither bite force nor gape were correlated with jaw length across all individuals, adults, or juveniles and subadults (Table S2). Bite force was positively correlated with facial width across all animals, and in juveniles and subadults; in other words, animals with wider faces had higher bite forces (all individuals: P<0.01, r^2=0.28; adults: P=0.35, r^2<0.01; juveniles and subadults: P<0.01, r^2=0.48; Table 2, Fig. 2E).

Jaw length and facial width were both positively correlated with body mass (Table S2), and we were interested in how bite force and gape scaled with jaw length, and how bite force scaled with facial width after standardizing the cranial measures by body mass. Bite forces were negatively correlated with jaw length relative to body mass in all individuals, adults, and juveniles and subadults, but explained little of the variation (all individuals: P<0.01, r^2=0.04; adults: P<0.01, r^2=0.06; juveniles and subadults: P<0.01, r^2=0.03; Table S2; Fig. 2F); in other words, as relative jaw length increased,

Table 2. Significant linear regressions for hypothesis 1 across all individuals

H1 comparison	Model variable	Estimate and slope	s.e.	*t*	*P*	R^2
Maximum bite force∼log body mass	(Intercept)	4.34	0.23	18.59	<0.01	
	Body mass (kg)	0.3	0.11	2.8	0.01	0.33
Maximum gape∼log body mass	(Intercept)	15.51	2.69	5.76	<0.01	
	Body mass (kg)	9.12	3.55	2.57	0.02	0.29
Maximum bite force∼Jaw length relative to body mass	(Intercept)	5.19	0.01	395.33	<0.01	
	Jaw length/body mass	<0.01	<0.01	−6.96	<0.01	0.04
Maximum bite force∼Facial width relative to body mass	(Intercept)	5.19	0.01	383.23	<0.01	
	Facial width/body mass	−0.01	<0.01	−6.68	<0.01	0.04
Maximum gape∼Facial width relative to mass body	(Intercept)	8.81	0.08	113.14	<0.01	
	Facial width/body mass	−0.04	0.01	−4.74	<0.01	0.02

All other results and separate comparisons for adults and juveniles and subadults are found in Table S2.

bite force decreased. Gape was not correlated with jaw length relative to body mass in any of the age categories (Table S2). Bite force was negatively correlated with facial width relative to body mass in all age categories, but again explained little of the variation (all individuals: $P<0.01$, $r^2=0.04$; adults: $P<0.01$, $r^2=0.14$; juveniles and subadults: $P=0.04$, $r^2=0.01$; Table 2; Table S2). Residuals of bite force and jaw length relative to body mass, and bite force and facial width relative to body mass, were both significantly higher in juveniles and subadults, suggesting greater variability in bite force compared with adults ($P<0.001$).

Hypothesis 2

Within adults, average maximum bite force steeply increased until 16.79 mm average maximum gape for females and 16.35 mm average maximum gape for males (log female gape=2.82; log male gape=2.79), then gradually declined across larger gapes, although some individuals increased bite forces at larger gapes (Table 3, Fig. 3A). For subadults, average maximum bite forces sharply increased until 17.84 mm average maximum gape for females (log gape=2.88) and 13.80 mm average maximum gape for males (log gape=2.62), and gradually declined with larger gapes. The juvenile sample was limited by the number of animals and recorded gapes, but the available data showed a sharp increase in average maximum bite force until 9.26 mm average maximum gape in females (log gape=2.23) and 10.00 mm average maximum gape in males (log gape=2.30) followed by a gradual decrease in bite forces, similar to the pattern observed in subadults and adults.

Maximum bite forces for each animal were grouped by age category (juvenile, subadult and adult) to test for differences across ontogeny. There were significant differences in maximum bite force between age categories, with bite forces in juveniles being significantly lower than both subadults and adults ($P=0.05$ and 0.04; Fig. 3B; Table S3). There were no significant differences in maximum bite forces between subadults and adults ($P=0.74$). Bite forces relative to body mass were significantly higher in subadults, followed by juveniles, and lowest in adults (all $P<0.01$). Similarly, maximum gapes for each animal were significantly lower in juveniles compared with subadults and adults ($P=0.01$ and 0.02; Table S3), and maximum gape relative to body mass was significantly higher in juveniles, followed by subadults, and lowest in adults (all $P<0.04$). There were no differences in maximum bite forces or maximum gapes between males and females within age categories (all $P>0.61$). There were no significant differences in the bite force–gape radius of curvature between age categories (all $P=0.99$; Table S3).

Hypothesis 3

Food accessibility was summarized for each animal and food type as accessed in all bouts, discarded in all bouts, or a mixture of accessed and discarded. All animals accessed peanuts in shell, and accessibility was only tested for Brazil nuts and walnuts. Body mass was first tested for differences between access categories for Brazil nuts and walnuts. Body mass was significantly higher for animals that accessed Brazil nuts in all bouts compared with those that discarded Brazil nuts in all bouts ($P<0.01$; Table S4). Similarly, body mass for animals that accessed walnuts in all bouts was significantly higher than body masses for animals that had mixed accessibility ($P<0.01$) and those that discarded walnuts in all bouts ($P<0.01$). Across all animals, there were no differences in maximum recorded bite forces between accessibility categories for Brazil nuts or walnuts ($P=0.14$ and 0.10; Table S4). Similarly, there were no pairwise differences in maximum gape between food accessibility categories for Brazil nuts or walnuts in our sample (Table S4).

All accessed Brazil nuts and walnuts were initially fractured on the postcanine teeth; therefore, only peanut biting location was retained for analyses. Body mass was significantly higher for animals initially fracturing peanut shells on their incisors compared with their postcanine dentition ($P<0.01$; Table S4). Maximum bite forces and gapes were significantly higher for animals initially fracturing peanut shells on their incisors compared with their postcanine dentition (bite force: $P<0.01$; gape: $P=0.02$; Table S4).

Table 3. Mean±s.d. and maximum bite force values for each age and sex group

Sex	Age	Mean maximum bite force (N)	Mean gape of maximum bite forces (mm)	Maximum recorded bite force (N)	Gape at maximum recorded bite force (mm)	Maximum recorded gape (mm)	Force at maximum recorded gape (N)
Female	Juvenile	35.61±16.493	9.26±4.472	76.83	15	15	76.83
Male	Juvenile	45.61±23.623	10.00±5.00	93.35	10	15	52.51
Female	Subadult	155.91±58.929	17.84±9.261	212.65	15	40*	33.39*
Male	Subadult	141.92±48.205	13.80±4.148	204.16	15	20	138.71
Female	Adult	102.76±46.937	16.79±5.754	202.79	15	25	112.8
Male	Adult	146.52±45.425	16.35±7.502	201.23	5	35	66.11

*One animal recorded 40 mm gape. The maximum gape without this animal is 25 mm, with a bite force of 175.72 N.

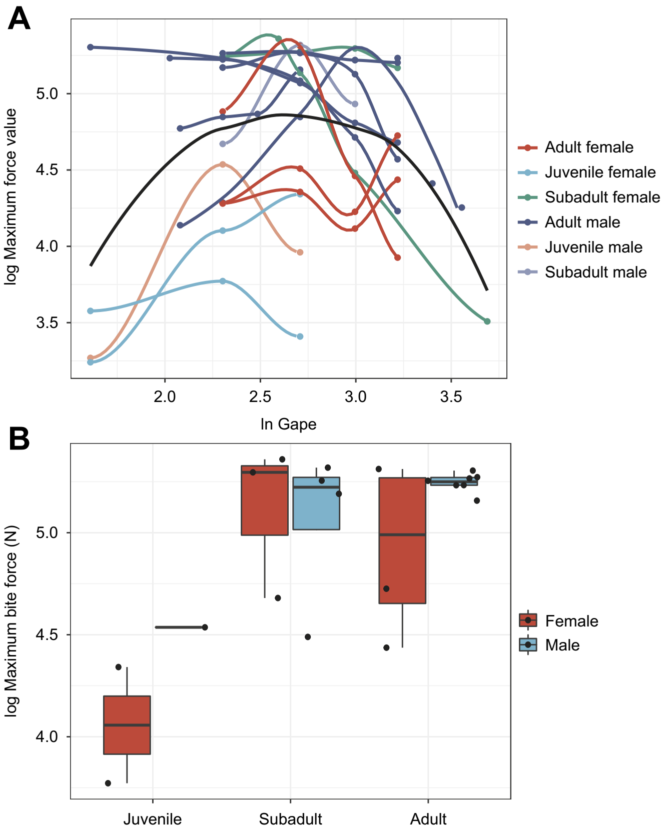

Fig. 3. Ontogenetic changes in bite force and gape. (A) Bite force–gape curves for each *Sapajus* spp. individual colored by age–sex group. The black line is a loess curve fit across all individuals. These curves suggest bite forces increase until an optimal gape followed by a decrease in bite force at larger gapes. This pattern is consistent for the entire sample and in most individual bite force–gape curves. (B) Maximum bite force compared across age categories. Juveniles have significantly lower bite forces compared with subadults and adults. There are no significant differences in bite forces between males and females within each age category. All data were logarithmically transformed.

DISCUSSION

Studies in primate evolutionary biology have sought to relate craniomandibular form to feeding ecology with varied success (e.g. Daegling and McGraw, 2001, 2007; Ross et al., 2012; Singleton, 2004; Taylor et al., 2018). However, the majority of these studies have focused on adults, and little is known about how primates maintain and/or optimize feeding performance across ontogeny. Here, we tested how two aspects of feeding performance, bite force and gape, vary across ontogeny in tufted capuchins (*Sapajus* spp.). Many of the adults were older, and age-related changes in muscle, including sarcopenia, may have resulted in lower adult bite forces compared with subadults (Yoshida and Tsuga, 2020). Future *in vivo* studies are needed to assess the generalizability of these results in other primates and across a range of foods. That being said, length–tension curves are not available for any primate feeding muscles, and these are the first primate data to empirically demonstrate the gapes at which maximum active bite force is generated and to capture *in vivo* changes in both bite force and gape. These data are therefore valuable for further advancing our understanding of the feeding system and updating existing models for how primates might meet the changing demands of the feeding system during growth and development. Here, we discuss the implications of our results on bite force–gape trade-offs across ontogeny as well as the role of these performance metrics in the developing primate feeding system.

To assess performance metrics of the tufted capuchin feeding system, it is important to contextualize our *in vivo* bite force data. There are few *in vivo* bite forces available for primates (e.g. Hylander, 1979; Dechow and Carlson, 1990; Chazeau et al., 2013) and, to our knowledge, no stimulated or *in vivo* bite force data published for capuchins. However, we can compare our *in vivo* capuchin bite forces with stimulated and *in vivo* macaque bite forces. *Sapajus apella* have slightly smaller estimates of relative superficial masseter and temporalis PCSAs (i.e. $\mathrm{PCSA}^{0.5}$/jaw length) compared with *Macaca mulatta* (Taylor and Vinyard, 2013). Thus, we might expect bite forces for a given location to be slightly lower in capuchins compared with macaques. Hylander (1975) measured *in vivo* molar bite forces in *Macaca fascicularis* that ranged between 205.0 and 333.43 N for three adult females and one subadult male. Dechow and Carlson (1990) measured molar bite forces while stimulating the masticatory muscles in *M. mulatta* and recorded a maximum force of 369.3 N in males and 286.2 N in females. We recorded a maximum incisal bite force of 212.65 N in a subadult female capuchins, which is at the lower end of the macaque *in vivo* bite forces measured by Hylander (1975), and just below the stimulated forces measured by Dechow and Carlson (1990). Importantly, both Hylander (1975) and Dechow and Carlson (1990) recorded bite forces on the molars, whereas the capuchin bite force data presented here were collected at the incisors. We expect capuchins to produce higher bite forces on the postcanine dentition, and we suggest our *in vivo* incisor bite forces are reasonable estimates of the maximum bite forces used during feeding – both of which are supported by our food accessibility and bite location data.

Bite forces and gapes vary with body mass and craniofacial morphology

Collectively, our results demonstrate that tufted capuchins with absolutely larger body masses generated higher bite forces and larger gapes. Tufted capuchins also exhibited a plateau in bite forces once reaching adult body mass, suggesting that most of the increase in absolute bite force occurs during growth. *In vivo* bite force and muscle architecture data from grey mouse lemurs also suggest that the relationships between body mass and bite force plateaus in adults (Chazeau et al., 2013; Leonard et al., 2020). Our results further indicate that tufted capuchins with absolutely and relatively wider faces had higher *in vivo* bite forces, particularly in juveniles and subadults. Facial width is thought to track the size of the jaw elevator muscles and consequently bite forces (Weijs and Hillen, 1985; Hannam and Wood, 1989, van Spronsen et al., 1991, 1992; Raadsheer et al., 1999). Interestingly, absolute jaw length was not correlated (either positively or negatively) with bite force or gape in tufted capuchins. These results may reflect our relatively small sample size, particularly for juveniles.

In the absence of associated muscular changes, increasing jaw length will negatively impact bite forces on the incisors through a decrease in the ratio of muscle in-lever arm to bite point out-lever arm (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). Adult tufted capuchins have more anteriorly positioned jaw elevators than juveniles, to increase bite forces on the incisors and canines (Wright, 2005), and leverage estimates for the jaw elevator muscles increase across ontogeny in tufted capuchins compared with untufted capuchins (Cole, 1992; M. Holmes et al., unpublished). However, our data show that bite force is negatively correlated with facial widths and jaw lengths relative to body mass, suggesting that tufted capuchins with shorter and narrower faces relative to body size produced less bite force regardless of age. This suggests that shifts in relative positioning and leverage of bite point and jaw muscles may function to maintain bite force performance levels in tufted capuchins. We also note the methodological difference between our measure of facial width between the canthi of the eyes compared with bizygomatic measures used in Chazeau et al. (2013). Additional comparisons are needed to test whether these measures covary.

Increased *in vivo* bite forces and gapes with body mass in tufted capuchins suggest this taxon is not compromising bite force in favor of gape or vice versa. Notably, this pattern appears to be consistent across the range of body masses included in this study, indicating that adults show a similar pattern to juveniles and subadults. This balancing act between performance needs in the feeding system has been noted previously for capuchins: muscle architecture data from Taylor and Vinyard (2009) suggested tufted capuchins have muscular adaptations (i.e. long muscle fibers and relatively large muscle PCSAs) that allow them to maintain high bite forces at large gapes. This sharply contrasts with similar analyses in marmosets, which found that bite force is compromised in favor of large gapes associated with gouging by sacrificing muscle PCSA in favor of long muscle fibers (Taylor et al., 2009) and by reducing excursion and increased tension at large gapes (Eng et al., 2009).

Tufted capuchin bite forces and gapes vary across ontogeny

Our data show that in tufted capuchins, ‘whole system’ bite force–gape curves match theoretical expectations and data from other mammals (Herring and Herring, 1974; Dumont and Herrel, 2003; Christiansen and Adolfssen, 2005; Eng et al., 2009; Williams et al., 2009; Santana, 2016). This indicates bite forces increase with gape until the jaw muscles reach an optimal length. Gapes larger or smaller than the optimum are associated with reduced bite forces. Juvenile tufted capuchins had lower absolute maximum bite forces and gapes compared with subadults and adults, and there were no differences in bite force and gape between subadults and adults. These results support the idea that the greatest changes in bite force and gape during development occur between the eruption of M1 and M2, and the relatively small differences in growth that occur between the eruption of M2 and M3 are not associated with change in these measures of performance. Data from studies of jaw elevator muscle architecture indicate that fiber lengths mostly increase across ontogeny. For example, Dickinson et al. (2018) found that jaw elevator muscle fiber lengths were positively correlated with age in *M. fascicularis*. Leonard et al. (2020) showed a slight increase in fascicle length in younger grey mouse lemurs; however, cadaveric gape differences were not reported in Leonard et al. (2020) (see Taylor et al., 2019; Laird et al., 2020a). Future studies pairing *in vivo* maximum gapes and muscle architecture data will further our understanding of ontogenetic changes in gape.

There were no significant differences in measures of bite force–gape radius of curvature between age categories. Ideally, the radius of curvature would be calculated from a spline fit across the maximum bite forces recorded at all gapes. However, several individuals in our sample only bit the transducer at select gapes, limiting the comparability of bite force–gape curves across ontogeny. Our result does capture shape variation of the bite force–gape curve around peak bite forces, and suggests that this portion of the curve shows little variation in shape across ontogeny. Additional *in vivo* data are needed to examine shape changes in the bite force–gape curve in primates, particularly from gape extremes.

Tufted capuchin bite force–gape curves are related to food accessibility and bite location

Data from this study highlight the importance of combining primate experimental and behavioral data to address questions of food acquisition and dietary adaptations (Vinyard et al., 2009; Norconk and Veres, 2011; McGraw and Daegling, 2012; Wright et al., 2019). Our data suggest that subadults and adults are generating up to 4 times the average maximum bite force and 2–3 times the maximum recorded bite force than juveniles (Table 3), but juvenile tufted capuchins in the wild are reported to be able to access foods of similar material properties as adults (Chalk et al., 2016). Similar results have been reported in sooty mangabeys, where juveniles are reported to eat a significantly higher percentage of mechanically challenging *Sacoglottis gabonensis* seeds compared with adults (McGraw et al., 2011), as well as in a number of other primate species (e.g. Virunga gorillas: Watts, 1984; *Alouatta palliata*: Pokempner et al., 1995; *Eulemur fulvus*: Tarnaud, 2004; *Daubentonia madagascariensis*: Krakauer, 2005; *Saimiri sciureus*: Stone, 2006; *Gorilla gorilla gorilla*: Fletcher and Nowell, 2008). This suggests that juveniles must compensate for reduced bite forces compared with adults. Chalk-Wilayto et al. (2022) found that juvenile tufted capuchins have reduced food processing efficiency compared with adults, and that food processing skill development is more important than changes in variables such as body size. Our measures of food accessibility do not account for differences in food processing skill development, but future pairings of these behavioral changes with performance factors will be important for understanding food accessibility.

Our initial results based on our Brazil nut and walnut data suggest that access to food by tufted capuchins is constrained to some extent by gape. Animals with larger maximum *in vivo* gapes were not significantly more likely to access both Brazil nuts and walnuts in this sample of tufted capuchins, but gape was a better delineator of food accessibility, which reflects the positive relationships between body size, bite force, and gape. We also found that the force needed to fracture Brazil nut and walnut shells as recorded on the FLS-II tester substantially exceeded the maximum *in vivo* bite forces as recorded from the transducer for all animals (Tables 1 and 3). This difference is expected because we recorded *in vivo* transducer bite forces on the incisors, and tufted capuchins tend to breach mechanically challenging foods on the premolars (Ross et al., 2016; Laird et al., 2020b). Indeed, all Brazil nuts and walnuts were initially fractured on the premolars. *In vivo* bite forces at the premolars are higher than those at the incisors, as the ratio of muscle in-lever arm to bite point out-lever arm negatively impacts bite forces on the incisors (Greaves, 1978; Spencer and Demes, 1993; Spencer, 1998, 1999). Our data suggest that bite forces minimally increase 2.88 times from the incisors to the premolars in tufted capuchins based on the maximum bite force recorded at the incisors and the mean Brazil nut fracture force. Extraoral processing of foods could also potentially impact the relationship between force–gape and food accessibility. Primates, particularly capuchins, are known to engage in high amounts of extraoral food processing (e.g. Wright, 2005). However, we find this explanation unlikely as the foods used in this study could not be manually reduced in size, nor could the material properties be altered prior to ingestion. Capuchins do strategically place nuts to exploit weaknesses in the shell when using a hammer and anvil (Fragaszy et al., 2013), and it is likely that nut shells fractured in the mouth are also oriented to exploit variation in the nut shell.

Our bite location data were limited to peanut shells. However, tufted capuchins with larger body sizes, larger maximum bite forces and larger maximum gapes were significantly more likely to initially fracture the peanut shell on their incisors rather than their postcanine dentition. All animals with maximum *in vivo* bite forces and gapes closest to peanut shell force to fracture and peanut shell width used their premolars for initial fracture (Fig. 4). The switch from postcanine initial fracture to the incisors occurred when our animals registered maximum *in vivo* bite forces and gapes exceeding ∼30–40% of peanut size and force to fracture. These data strongly suggest that bite location relates to bite force–gape curve variation, and tests in additional species are needed to determine whether bite location occurs at a certain location on the bite force–gape curve.

Muscle PCSAs estimate maximum muscle force potential, i.e. they assume 100% activation of the muscles over their full fiber lengths and full fiber rotations. However, under normal physiological conditions, only a portion of a muscle's force is converted into bite force. Thus, other things being equal, modeled bite forces that incorporate muscle PCSAs might be expected to overestimate bite force. We note, however, that muscle force estimates derived from muscle fiber architecture (i.e. PCSAs) may underestimate maximum bite force capacity. In an interspecific analysis in bats, for example, Herrel et al. (2008) found that their modeled bite forces using muscle PCSAs underestimated their *in vivo* bite forces measured on the same individuals, though they found that the two bite force estimates were significantly correlated. Deutsch et al. (2020) used muscle architecture data to estimate maximum incisal bite forces in *S. apella* and reported an estimate of maximum incisal bite force based on total jaw–adductor PCSA of 199.67 N, which is slightly below our maximum *in vivo* bite force of 212.65 N. Holmes and Taylor (2021) estimated maximum muscle forces for the superficial masseter and temporalis using muscle PCSAs adjusted for fiber type proportions and their specific muscle tensions across a sample of five anthropoid primates. Based on their fiber-type adjusted PCSAs averaged across three individuals, adult tufted capuchins had an estimated maximum superficial masseter force capacity of 211.5±30.8 and 356.2 ±166.9 N cm^{-2} for the temporalis (Holmes and Taylor, 2021). This means that superficial masseter and temporalis muscle force capacity totals only 567.7 N cm^{-2}, whereas the force needed to fracture Brazil nuts is 614.46 N (Table 1). Without comparable data for the medial pterygoid and deep masseter, this is an underestimate of the total available muscle force and does not consider the impact of lever mechanics or differences in muscle activation on bite force production. However, we note that for most locations on the toothrow, the transformational ratio of muscle force to bite force is relatively low (Dumont et al., 2011; Cox et al., 2012). To more fully explore the relationship between bite force estimates and the force needed to fracture, we calculated bite forces using sarcomere normalized and non-sarcomere normalized PCSA values for all four jaw adductor muscles from a large (4.4 kg) adult male tufted capuchin, accounting for a range of muscle-specific tensions (calculated at both 25 and 35 N), leverage, and working- to balancing-side differences (calculated at both 1.8 and 2.0) (Table S5). Bite forces exceeded the Newtons needed to fracture a Brazil nut for 3 out of 4 estimates derived using non-normalized PCSAs (range: 496.03–897.74 N), but only with specific tension estimates of 35 N for normalized PCSAs (Table S5). [We note that our estimated range for maximal bite force exceeds the estimate of maximal incisal bite force of 199.67 N reported by Deutsch et al. (2020). Apart from potential differences between studies in specific tension and leverage, these different estimates are likely due to the fact that Deutsch et al.'s (2020) estimate is based on two adult females and a specimen of unknown sex while our estimate is based on a very large adult male. We suggest that combined, the bite force estimate reported by Deutsch et al. (2020) and our estimates more accurately represent the full range of bite forces for adult *Sapajus* spp.] Juveniles, subadults and adult females almost certainly produce lower maximum bite forces compared with this adult male, but both subadults and adult females fractured Brazil nuts. There are several things to keep in mind about these bite force estimates. Although accounting for several variables contributing to bite force, these estimates do not include factors such as muscle force orientation; biting on a transducer almost certainly generates forces that differ from bite forces used during feeding. Another is that muscle, and thus bite force, changes throughout the gape cycle, and we do not know where along the length–tension curve our normalized or non-normalized muscle force estimates fall. Our data also examined only vertical components of bite force, which do not account for the complexity of jaw movements and bite force application that occurs during mammalian feeding (e.g. Thexton et al., 1980). It is thus important to keep in mind that bite force, whether estimated *in vivo* using a transducer, *in silico* based on a mechanical tester, or using bony or muscle-force-derived estimates, only captures part of an animal's ability to produce bite forces and break down food.

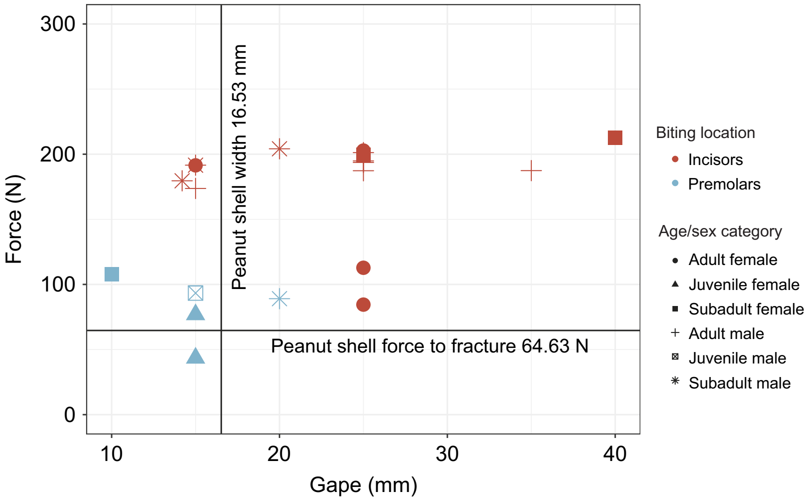

Fig. 4. Maximum *in vivo* bite forces and gapes for each animal colored by initial fracture location for peanut shell. Point shape indicates age/sex category. The plot includes lines for average width and force to fracture for the nut shell. Tufted capuchins used postcanine dentition to initially fracture peanut shells until their maximum *in vivo* bite forces and gape exceeded the width and force needed to initially fracture peanuts shells using an FLS-II tester by 30–40%.

Differences between *in vivo* bite forces, bite force derived from PCSA estimates combined with lever/load arm estimates, and food force to fracture measurements highlight the complexities of relating morphology to feeding behavior. The *in vivo* bite forces and gapes recorded in these experiments reflect performance ranges of normal feeding that are almost certainly below the animal's maximum force capacities, stimulated bite force and gape capacity. But maximum and *in vivo* bite forces and gapes are likely related, as *in vivo* bite forces were strongly correlated with measurements of muscle architecture in bats and rodents (Herrel et al., 2008; Ginot et al., 2018). However, unlike static forces estimated from muscle architecture and bony leverage, *in vivo* bite forces ultimately reflect a combination of muscles; their patterns of activation, timing and amplitude and are moderated by dynamic changes in the muscles during activation. Dynamic muscle architecture data from the capuchin temporalis suggest changes in architectural gearing in relation to food properties that allow primates to produce bite forces beyond those captured through traditional muscle architecture (Azizi et al., 2008; Laird et al., 2020a, in press). Santana and Dumont (2009) suggest both behavior and performance metrics change with differences in diet, which is supported by our data. The results presented here offer a first glimpse at bite force–gape curve variation in non-human primates.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.F.L.; Methodology: M.F.L., C.M.K., C.B.Y.; Software: M.F.L.; Validation: M.F.L.; Formal analysis: M.F.L.; Investigation: M.F.L.; Resources: M.F.L., C.M.K., J.A.d.O.; Data curation: M.F.L., J.C.-W.; Writing - original draft: M.F.L.; Writing - review & editing: M.F.L., C.M.K., C.B.Y., M.D.F., A.B.T., C.F.R., J.C.-W., M.A.H., C.E.T., J.A.d.O.; Visualization: M.F.L., J.C.-W.; Supervision: M.F.L., J.A.d.O.; Project administration: M.F.L., C.M.K., J.A.d.O.; Funding acquisition: M.F.L., J.C.-W., M.A.H., C.E.T.

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Data availability
All relevant data can be found within the article and its supplementary information.

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