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The effects of feeding frequency on jaw loading in two lemur species

Nayuta Yamashita[1,2] | Nina Flowers[1] | Mariana Dutra Fogaça[1,3]

[1]Institute of Population Genetics, University of Veterinary Medicine, Vienna, Austria

[2]Austrian Academy of Sciences, Vienna, Austria

[3]Neotropical Primates Research Group-NeoPRego, São Paulo, Brazil

Correspondence
Nayuta Yamashita, Institute of Population Genetics, University of Veterinary Medicine, Vienna, Austria.
Email: nayuta.yamashita@vetmeduni.ac.at

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Abstract

Objectives: Studies on oral processing are often snapshots of behaviors that examine feeding through individual bouts. In this study, we expand on our previous work comparing bite/chew variables per feeding bout to summed daily biting, chewing, and food intake to interpret loading that could have potential morphological effects.

Materials and Methods: We observed sympatric *Lemur catta* and *Propithecus verreauxi* over two field seasons in the dry forest of Bezà Mahafaly Special Reserve in southwestern Madagascar. Bite and chew rates determined from videos filmed during observations were multiplied with time spent feeding on specific foods during focal follows to calculate daily values for each feeding bout. Food mechanical properties (FMPs) were tested on dietary items with a portable tester. We contrasted daily bite/chew numbers and intake with FMPs, species, season, and food shape.

Results: Daily bite and chew numbers increased with maximum, but not average, food toughness. Daily intake decreased with average and maximum toughness. Season had a strong effect on daily bites and chews, but not on intake. Food shape influenced intake and total bite and chew numbers. The lemur species did not differ in our models.

Discussion: Maximum food toughness impacted feeding behaviors and intake, which is consistent with higher loads having a greater effect on morphology. In contrast to feeding per bout, cumulative biting and chewing did not differ between species; taking feeding frequency into consideration affects interpretation of jaw loading. Finally, biting, as much as chewing, may generate strains that impact morphology.

KEYWORDS
diet, functional morphology, stiffness, toughness

1 | INTRODUCTION

Food mechanical properties (FMPs) testing provides insights into how primates access, prepare, and masticate foods (e.g., Chalk-Wilayto et al., 2022; Coiner-Collier et al., 2016; Laird et al., 2020; Laird et al., 2022; Lucas, 2004; McGraw et al., 2016; Van Casteren et al., 2016; Wright et al., 2008; Yamashita et al., 2009). FMPs interact with feeding behaviors (e.g., food placement and biting and chewing rates) to load the jaw (McGraw & Daegling, 2019; Ross et al., 2012). The resultant strains in the jaw presumably dictate how selection will act on jaw form to ensure adequate nutritional supply through efficient food processing, and, most fundamentally, prevent fatigue failure during the lifetime of the animal. FMPs have been linked to specific morphologies, such as the dentition (e.g., food toughness and crest lengths, Kay, 1975; Lucas & Teaford, 1995; Yamashita, 1998; durophagy and enamel thickness, Daegling et al., 2011; Lucas et al., 2008), greater masticatory muscle mass and cross-sectional area (e.g., Perry et al., 2011; Taylor & Vinyard, 2009), and greater robusticity in the oral/masticatory apparatus (e.g., Wright, 2005).

Despite these links between morphology and diet, functional morphology studies have often failed to establish direct relationships among the individual components of the oral masticatory system in taxa where habitual or seasonal feeding on certain food types could lead to a reasonable expectation of morphological specialization (e.g., McGraw & Daegling, 2019; Ross et al., 2012; Ross et al., 2016; Vinyard et al., 2011). For example, several studies have been unable to find corresponding differences in jaw morphology or mandibular symphyseal stiffness of hard-object feeding *Colobus* compared to the sympatric *Piliocolobus* (Daegling et al., 2009; Daegling & McGraw, 2001; Koyabu & Endo, 2009) or between durophagy and facial buttressing (Daegling et al., 2011). Vinyard et al. (2003) did not find the predicted robust skull and jaw morphologies corresponding to tree gouging in exudate-feeding primates. Wright et al. (2009) found that the more craniofacially robust *Cebus* (now *Sapajus) apella* ate a less tough diet than the more gracile capuchin *S. libidinosus*, which was related to stone tool use by *S. libidinosus* for opening the most obdurate foods. Taylor et al. (2018) compared hard-object feeding sooty mangabeys with three other papionin species and did not find clear morphological correlates to hard-object feeding in muscle fiber architecture and jaw leverage morphology as they had in their earlier study on capuchins (Taylor & Vinyard, 2009). The authors speculated that large body size among papionins by itself was sufficient to generate high bite forces without additional morphological buttressing.

Moreover, empirical studies linking morphology with FMPs have had mixed results (e.g., Daegling et al., 2009, 2011; McGraw & Daegling, 2019; Ross et al., 2012, 2016; Vinyard et al., 2011). Hylander (1979, 1985) described how the jaw experienced stresses and strains from activation of the chewing muscles (i.e., wishboning, dorsoventral shear) and where it would require buttressing to counteract the increased strain. Characterizing how initial loads translate into increased strain is complex and identifying the relevant variables (e.g., FMPs, location, and cycles) is not straightforward. For example, Ross et al. (2016) found oral processing behaviors in *Sapajus* monkeys, such as the position on the jaw where foods are initially bitten and chew number, had a greater effect on strain in the mandibular corpus than FMPs. The significance of chew number here lends some support to the idea of daily loading cycles having an effect on bone adaptation. However, biting in different positions across the toothrow produced higher strain magnitudes than chewing, which suggests that biting may be the more salient behavior in shaping jaw morphology. This dichotomy encapsulates a more general discussion on the effects of routine low impact, high frequency events versus high impact, low frequency events in maintaining or stimulating bone formation, respectively (e.g., Adams et al., 1997; Burr et al., 2002; Fritton et al., 2000).

Ravosa et al. (2015) found that chewing investment (i.e., chewing cycles per gram) increased with food stiffness in rabbits, and Ravosa et al. (2016) showed correlated differences in masseter fiber type and temporomandibular joint condyle size with FMPs. Their results support the idea that both challenging FMPs and loading frequency are necessary for specialized morphology to evolve. Whether a higher cycle number (in biting or chewing) translates into greater strain and concomitant changes in the mandible are questions that require further exploration in more taxa.

The studies above underscore the need for better characterization of jaw loading during feeding and food preparation. What is becoming ever clearer is that in-field behavioral observation and testing must be incorporated into biomechanical studies of jaw loading to accurately assess the location and magnitude of the stresses and consequent strains that impact morphology (e.g., Kane et al., 2020; Laird et al., 2020; McGraw et al., 2016; Ross et al., 2012; Vinyard et al., 2011; Wright et al., 2008; Yamashita et al., 2009). What is less clear are the combinations of variables that could load the jaw (as laid out in Ross et al., 2016), under what conditions, and whether different taxa find different morphological solutions to similar loading regimes (Daegling & McGraw, 2001).

In this study, we compare Verreaux's sifaka (*Propithecus verreauxi*, *Pv*) to the ring-tailed lemur (*Lemur catta; Lc*). *Pv* have a more robust mandible (e.g., deep mandibular corpus and ramus, expanded angle, and a partially-fused symphysis) than *Lc* that corresponds with their characterization with other indriids as morphological folivores (Ravosa, 1991; Ravosa & Vinyard, 2020; Tattersall & Schwartz, 1974). The obvious differences in the oral apparatus between the species, yet apparent similarity in the toughness of their foods (Yamashita, 2002), raise the question of how their loading regimes have produced such disparate morphologies. Hylander (1979) posited that deep jaws in primates were correlated with increased bending stresses on the balancing side during mastication. Repetitive loads introduce microcracks through bone strain that may be removed via remodeling or may ultimately cause fatigue failure at a fraction of the maximum strength of the bone (e.g., Bouvier & Hylander, 1981; Hylander, 1979; Lafferty et al., 1977; Lee et al., 2000; McGraw & Daegling, 2019). The relatively greater robusticity of the *Pv* jaw could, therefore, be related to distributing higher cumulative loads during chewing and countering the effects of increased strain.

Though we are primarily concerned with how loading in terms of food properties is related to the oral apparatus, other aspects of feeding could have an impact on morphology. For example, Yamashita (2003) found that food placement anteriorly in the mouth or on the postcanines by *Lc* and *Pv* depended on the size of the fruit or leaf and not on their toughness. Tree-gouging primates in Vinyard et al. (2003) did not show the expected skull morphologies associated with high force production, but exudate feeders did have very wide gapes enabled by low mandibular condyles. Jaw use in nonfeeding contexts in strepsirrhines, such as grooming with the toothcomb or its use in pheromonal communication (e.g., Asher, 1998; Rosenberger & Strasser, 1985), could also affect morphology.

1.1 | Hypotheses for daily oral processing and intake

Flowers et al. (2023) investigated whether biting and chewing during feeding bouts of the most frequently eaten foods were influenced by FMPs (average and maximum toughness [R_{av}, R_{max}] and membrane stiffness [E_{inst}]), lemur species, food shape, or season. Feeding behaviors were variably associated with FMPs. Although *Pv* maintained consistent biting and chewing behaviors (though chew numbers increased with R_{av} for both species), *Lc* adjusted its feeding behaviors with respect to FMPs. Specifically, *Lc* increased bite number and decreased bite rate with R_{max} and decreased chew numbers on stiffer leaves. *Lc* consistently chewed more and faster than *Pv*. *Pv* had a tougher maximum diet than *Lc* in the wet season.

Few studies consider feeding frequencies across daily or extended time scales, but many examine feeding behaviors per plant or per bout (e.g., Chalk-Wilayto et al., 2022; Coiner-Collier et al., 2016; Laird et al., 2022; Ross et al., 2016; Yamashita et al., 2009). Here, we extend the analysis from bites and chews for individual bouts per plant in Flowers et al. (2023) to cumulative effects of daily biting and chewing to address our broader interest in loading of the oral apparatus. Specifically, we investigate if food properties affect processing behaviors over daily and seasonal periods.

1. We initially expect that tougher foods will have higher bite/chew numbers because they require more processing to be fragmented (e.g., Lucas, 2004). This is related to the discussion on the relative effects of low impact, high frequency events or high impact, low frequency events with respect to bone formation (e.g., Adams et al., 1997; Burr et al., 2002; Fritton et al., 2000; Hylander, 1979). We had predicted, on a per bout basis, that tough foods may require more bites/chews to process specific foods (i.e., tough foods require more bites/chews per food), and we also expect the same relationships to be maintained when scaled up to daily numbers (i.e., repetitions of bites/chews for specific foods in each day). The relationship of processing via bite/chew numbers and food toughness is expected to be invariant with respect to per bout or daily feeding. Bite number increased with R_{max} for *Lc* in Flowers et al. (2023), and we expect the same trend to continue with tough foods requiring more processing on a daily scale.
2. We expect that as food toughness increases intake will decrease because of the higher processing time associated with tougher foods, as above. In addition, while bite number increased with R_{max} for *Lc*, bite rate decreased in Flowers et al. (2023). We do not examine rates explicitly here (the rate was used in the calculation of total numbers of daily bites/chews), but rate may possibly be related to intake in that slower bites/chews could lead to decreased intake. Therefore, we expect that intake will decrease with increasing toughness or membrane stiffness.
3. On a per bout basis, *Lc* chewed more and had a much faster chewing rate than *Pv* that could lead to differences in numbers of chews throughout the day (Flowers et al., 2023). We had also found that *Pv* spent more time feeding during the day in both seasons. In this paper, we examine if faster rates per plant part translate into greater numbers of chews (and bites) across the day. Put another way, are bite and chew rates per plant indicative of loading, or do longer feeding times across the day contribute more to bite/chew cycles?
4. *Pv* has a more robust jaw and a tougher diet overall than *Lc*. However, *Lc* has a higher chewing rate and chew numbers on a per plant basis, as above. Given the morphology, we expect that *Pv* will have a higher cumulative load (measured here as total daily bite and chew numbers) that results from potentially higher daily cycles and a tougher diet.

2 | MATERIALS AND METHODS

2.1 | Site and study species

Bezà Mahafaly Special Reserve (BMSR) is a highly seasonal, tropical dry forest in southwestern Madagascar. BMSR is comprised of several parcels of land with different management schemes (Axel & Maurer, 2011; Sussman & Rakotozafy, 1994). We confined our observations to Parcel 1 (P1), an 80-hectare area that grades from a gallery forest on its eastern edge to a xeric habitat on the west.

Southern Madagascar experienced a prolonged and devastating drought that reached its peak in the wet season of November 2020–February 2021 (Joint Research Centre Drought Observatory Analytical Report, 2021). Rainfall and vegetation declined in the four years preceding the peak of the drought (JRC GDO Analytical Report, 2021). Total precipitation during our wet season data collection was notably reduced compared with averaged 50-year wet season records in Richard et al. (2000) (259 mm compared to 430 mm).

We conducted all day focal follows of four groups of *Lc* (three per season) and four groups of *Pv*. Numbers of focal individuals were limited to three to four individuals per group to balance observations per individual and numbers of sexes across all groups (*Pv*, 7F, 7 M; *Lc*, 7F, 2 M). Practical considerations made it difficult to continuously follow males in *Lc* troops: males transfer between troops frequently, and, because *Lc* troops can be diffuse and the males peripheral, it can be difficult to assign group membership to specific individuals. Lemur individuals wore collars and pendants (all *Pv* individuals and some *Lc*) or had identifying marks.

2.2 | Data collection

2.2.1 | Observation protocol and food collection

Focal groups were followed six days a week by two teams. Groups and species were alternated to routinely collect data on all. Individuals were followed with continuous time focal animal sampling for 1 h at a time to ensure that all focal individuals were followed throughout the day. Start and stop times were taken for all basic activities (feed, move, rest, and social). During feeding bouts, additional data were taken on plant species, plant part, units of plant part ingested in a specific unit of time (e.g., 30 s, 1 min), and ingestive techniques (e.g., insert front or side of mouth, stripping). The outer coverings that primates remove are often more mechanically challenging than the harvested food part (e.g., Yamashita et al., 2009). For these plant parts, data were taken on the processing location on the jaw, harvesting behaviors (e.g., stripping, biting), and numbers of bites before being discarded.

Foods were collected just prior to processing and testing. Once in the field lab, plant parts were weighed (both wet and dry weights) and photographed with a scale bar prior to mechanical testing. Individual food parts (e.g., leaves, fruits, and stalks) were weighed to 0.01 g, dried in tea bags, then weighed again. A minimum of three individual parts per food item were weighed and the final values averaged. If individual parts were too light, multiple items were weighed together then divided by the numbers of items.

2.2.2 | Video feeding observations

Feeding bouts were filmed throughout the day with a camcorder. We later quantified biting and chewing from these videos because these behaviors occurred too quickly to count consistently during focal observations. We extracted and scored 10 min of feeding sequence time for approximately 10 of the most frequently eaten foods per lemur species per season. All videos were watched with VideoLoupe that enabled playback at 25 frames per second.

Feeding bouts began with an initial ingestive bite(s) and ended when chewing stopped on a particular plant part. Bites were defined as occurring during oral preparation up to and including bite off; chews (mastication) occurred after bite off and took place solely on the postcanines prior to swallowing. Associated bites and chews comprised a single bout. Biting and chewing variables collected included bite and chew numbers, start and stop times for biting and chewing in the format mm:ss.ms, and unit and numbers of foods eaten (e.g., single fruit or leaf). The unit eaten per bout had to be clearly defined since intake volume was based on this amount. In many cases, the unit was a single fruit or leaf. However, different measurements were used for plant parts that were large enough to require multiple bite-chew sequences to ingest (e.g., *Tamarindus indica* fruit) or were parts of a larger whole (e.g., segments of a compound leaf). For *T. indica* fruit, for example, an entire video clip can be related to a single fruit comprised of multiple bouts (bite-chew sequences). For compound leaves, the intake unit could vary from clip to clip so had to be carefully defined for each clip; e.g., individual leaflets of a compound leaf.

Bite numbers, bites per second, chew numbers, chews per second, time per bout, and numbers of units were averaged across all bouts in each clip to normalize among clips of different lengths. Once all clips were assembled from all three observers, every food item had multiple entries for each lemur species per season. Each food item was further identified by group and focal animal.

In addition to data on identifiable individuals, we also collected data on several uncollared individuals since the values for bites and chews were averaged across all individuals for each plant part.

2.2.3 | Food mechanical testing

FMPs (toughness, membrane stiffness of leaves were tested with a portable tester (FLS-1) on foods collected just prior to testing. These foods were usually directly adjacent to the parts observed to be eaten. In many cases, bite marks were present and guided selection of the parts for testing. These parts with bite marks were also collected to test the remnants.

The tester has interchangeable jigs for testing a number of material properties. This tester and a previous model have been used in numerous field studies of primate FMPs (e.g., Coiner-Collier et al., 2016; Lucas et al., 2001; Vogel et al., 2012). We primarily conducted two tests:

a. Toughness (R) describes how much work is required to fracture an object. Toughness was tested using a scissors-cutting test in J/m^2 and was subdivided for each plant part into average toughness (R_{av}; leaf lamina, fruit flesh) and maximum toughness (R_{max}; rachis, petiole, exocarp) datasets if all these parts were consumed. The different specific parts for each plant part (e.g., leaf lamina, rachis, exocarp) were individually tested;
b. Membrane stiffness (E_{inst}) measures the modulus of membranes/plates such as leaves (Talebi et al., 2016). In the test, a probe loads the surface of a membrane (e.g., leaf lamina) for 10 s (loading ramp), then is held in place for an additional 90 s (relaxation curve). The loading ramp is measured as the instantaneous modulus in megapascal (MPa) and relaxation as the infinite modulus as the material relaxes during the static phase. We used the instantaneous modulus values in our models. This test was limited to leaf material in the wet season.

If both lemur species ate a food part/species but the part was only tested for one lemur, the FMP values were copied over for the other lemur species. All tests per plant part were averaged, so that each plant part had one toughness value in the final dataset. Young and mature leaves of the same plant species were averaged separately when the lemurs ate them separately (either in different seasons or within a season).

2.3 | Dataset construction

2.3.1 | Intake calculations

Intake was calculated as total units consumed multiplied by wet weight in grams (g). The wet weight was an average of a minimum of three separate units to account for variation in the parts eaten. The total units consumed were calculated from unit counts taken from feeding bouts during focal follows that were converted to units per second, then multiplied by time in seconds for that feeding bout to obtain the total units consumed per bout.

Total intake was then calculated (1) per plant part per day for each lemur species (daily consumption) and (2) per plant part in each season for each lemur species (seasonal consumption). For daily consumption, all feeding bouts per plant were summed per day and the value multiplied by the averaged wet weight of the plant part. For seasonal consumption, all bouts per plant were multiplied by the averaged wet weight of the plant part and then summed per season to obtain the total intake in grams. We had to ensure that we used a common unit (e.g., one leaf, one whole fruit) across the different types of data used in calculating intake (i.e., bite/chew counts in the video clips, time spent feeding on each plant part during focal follows, weights of each plant part, and mechanical property tests).

2.3.2 | Total bites and chews

The focal follow feeding data for each day was matched with bites and chews per second to calculate bite/chew numbers for every feeding bout. Bites and chews per second were first averaged from the video observation data for each plant part per lemur species per season. These values were then multiplied by the total time spent feeding on that plant part (in seconds) derived from the focal animal follows. These values were summed per plant per day or per season to obtain total bites and chews per day or per season, respectively.

Only the most frequently eaten foods (approximately 10 foods per lemur species per season) were quantified for bites and chews. Therefore, models with bites and chews were more limited than that for intake, which included the entire range of foods eaten during the focal follows.

2.3.3 | Shape categories

We assigned each plant part to a shape/size category because shape and size may influence initial placement and bite off in the mouth when FMPs may not necessarily play a role (Table S1). Because some categories were unpopulated in some models (e.g., shapes specific to a lemur species or season) or had few cases, categories had to be consolidated on a per model basis to enable robust statistical analysis (see Tables S3, S4, and S7 for category assignments per model).

2.3.4 | Dataset assembly

For the daily dataset, each plant part eaten during each follow day was represented by summed intake (calculated as above in Section 2.3.1), bite and chew counts (calculated as above in Section 2.3.2), FMPs (derived from concurrent field tests), shape categories, lemur species, group identification, and season. Each focal follow day had multiple entries representing each food eaten on that day.

The seasonal dataset was similar except that the associated data for each plant part was summed per season so that each plant part was only represented once in the dataset.

2.4 | Analysis

We investigated the effects of FMPs on daily (and seasonal) intake, total bites, and total chews. The datasets were (1) plant part per day ("daily") and (2) plant part per season ("seasonal"). Linear and linear mixed models (LMM) were run in R (R Core Team, 2019) using packages car (Fox & Weisberg, 2019), lme4 (Bates et al., 2015), and lmerTest (Kuznetsova et al., 2017). Post hoc pairwise comparisons of estimated marginal means were conducted with the emmeans package (Lenth, 2019) for the different levels of "shape." ggplot2 (Wickham, 2016) was used for plotting with the ggeffects package (Lüdecke, 2018) to plot the predicted values.

In each dataset, intake and bites and chews were the dependent (response) variables. The independent (predictor) variables were FMP (average and maximum toughness and membrane stiffness, each modeled separately as covariates), lemur species, season, shape, and the interaction between FMP and species.

For the daily dataset, we ran LMMs and implemented a "maximal random slopes" model (Barr et al., 2013; Osuna-Mascaró et al., 2022, Schielzeth & Forstmeier, 2009) (see Supporting text for details). Plant part and lemur social group were modeled as random intercept effects. In addition, we included random slopes of FMPs, shape, and season within group. The variance inflation factor (VIF) was checked for each effect in each model. All VIFs were less than 3.0. (See Table S6 for complete models.)

The range of variation per plant and per day in the daily dataset is preferred for analysis because of the loss of information from summing by season for each plant part as in the seasonal dataset.

After calculating daily and seasonal values for total bites/chews and intake, all variables were divided by the number of follow days per lemur group in order to control for differences in follow days. Follow days ranged from 7 to 9 days for *Lc* and 6–9 days for *Pv* per season per group.

We also compared the degree of consumption of tough foods in the diets. We contrasted foods that were shared by the two lemur species to the foods that were eaten exclusively by each with Type III Anova and emmeans.

3 | RESULTS

The results of the mixed models (daily dataset) are in Table 1 and Figure 1. Pairwise emmeans contrasts and emmip plots for the different levels of "shape" are in Tables S3 and S4. The seasonal model results are in the Supporting text, Figure S2, and Table S2.

TABLE 1 Linear mixed model results for the daily dataset.

Model	Response Variable	*N*	Estimate	SE	Effect	*F*-value	*p*-value
A	intake	780	−0.3459	0.1100	R_{av}	9.8852	0.0018**
			0.0666	0.0796	species	0.6984	0.4136
			−0.0616	0.0725	season	0.7222	0.3958
					shape	4.6773	0.0002***
			0.2023	0.0908	R_{av} × species	4.9643	0.0262*
B	intake	683	−0.3950	0.1323	R_{max}	8.9185	0.0033**
			0.0520	0.1024	species	0.2582	0.6199
			0.0329	0.1245	season	0.0699	0.7966
					shape	1.5974	0.1926
			0.1205	0.1049	R_{max} × species	1.3201	0.2515
C	intake	294	−0.1317	0.2454	E_{inst}	0.2879	0.5924
			−0.0241	0.1368	species	0.0309	0.8618
			0.0678	0.1936	shape	0.1227	0.7281
			0.0531	0.2193	E_{inst} × species	0.0587	0.8088
D	total_bites	386	0.1066	0.1401	R_{av}	0.5789	0.4504
			0.0448	0.0795	species	0.3168	0.5753
			−0.2662	0.0773	season	11.8579	0.0143**
					shape	6.4005	0.0022**
			0.0884	0.1374	R_{av} × species	0.4137	0.5221
E	total_bites	365	0.2234	0.1022	R_{max}	4.7776	0.0295*
			−0.0559	0.0732	species	0.5844	0.4451
			−0.4314	0.0822	season	27.5320	p < 0.0001****
					shape	7.7078	0.0019**
			−0.0381	0.0832	R_{max} × species	0.2095	0.6475
F	total_bites	155	−0.1404	0.1725	E_{inst}	0.6622	0.4437
			−0.0028	0.1154	species	0.0006	0.9812
			−0.0692	0.1703	shape	0.1651	0.6958
			−0.0735	0.1192	E_{inst} × species	0.3794	0.5416
G	total_chews	386	0.1197	0.1538	R_{av}	0.6056	0.4385
			−0.0478	0.0862	species	0.3067	0.5809
			−0.2472	0.0844	season	8.5734	0.0214*
					shape	5.4729	0.0040**
			0.0515	0.1481	R_{av} × species	0.1209	0.7286
H	total_chews	365	0.2240	0.1142	R_{max}	3.8452	0.0570
			−0.1197	0.0777	species	2.3742	0.1257
			−0.4059	0.0908	season	19.9850	*p* < 0.0001****
					shape	7.1277	0.0033**
			−0.0256	0.0903	R_{max} × species	0.0806	0.7772
I	total_chews	155	−0.0318	0.2130	E_{inst}	0.0224	0.8849
			−0.1622	0.1226	species	1.7497	0.1903
			0.0884	0.2058	shape	0.1844	0.6778
			−0.1013	0.1237	E_{inst} × species	0.6701	0.4181

Note: Model outputs for maximal random slopes models. Model letters correspond to Figure 1. Values for each fixed effect are *F*-values from Type III Anova. Pairwise emmeans results for "shape" in the models with R_{av} and R_{max} are in Table S3. All response variables are logged and FMP variables are *Z*-transformed. See Table S6 for full models.

Abbreviations: N, numbers of observations; SE, standard error; R_{av}, average toughness; R_{max}, maximum toughness; E_{inst}, membrane stiffness (instantaneous membrane modulus).

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$.

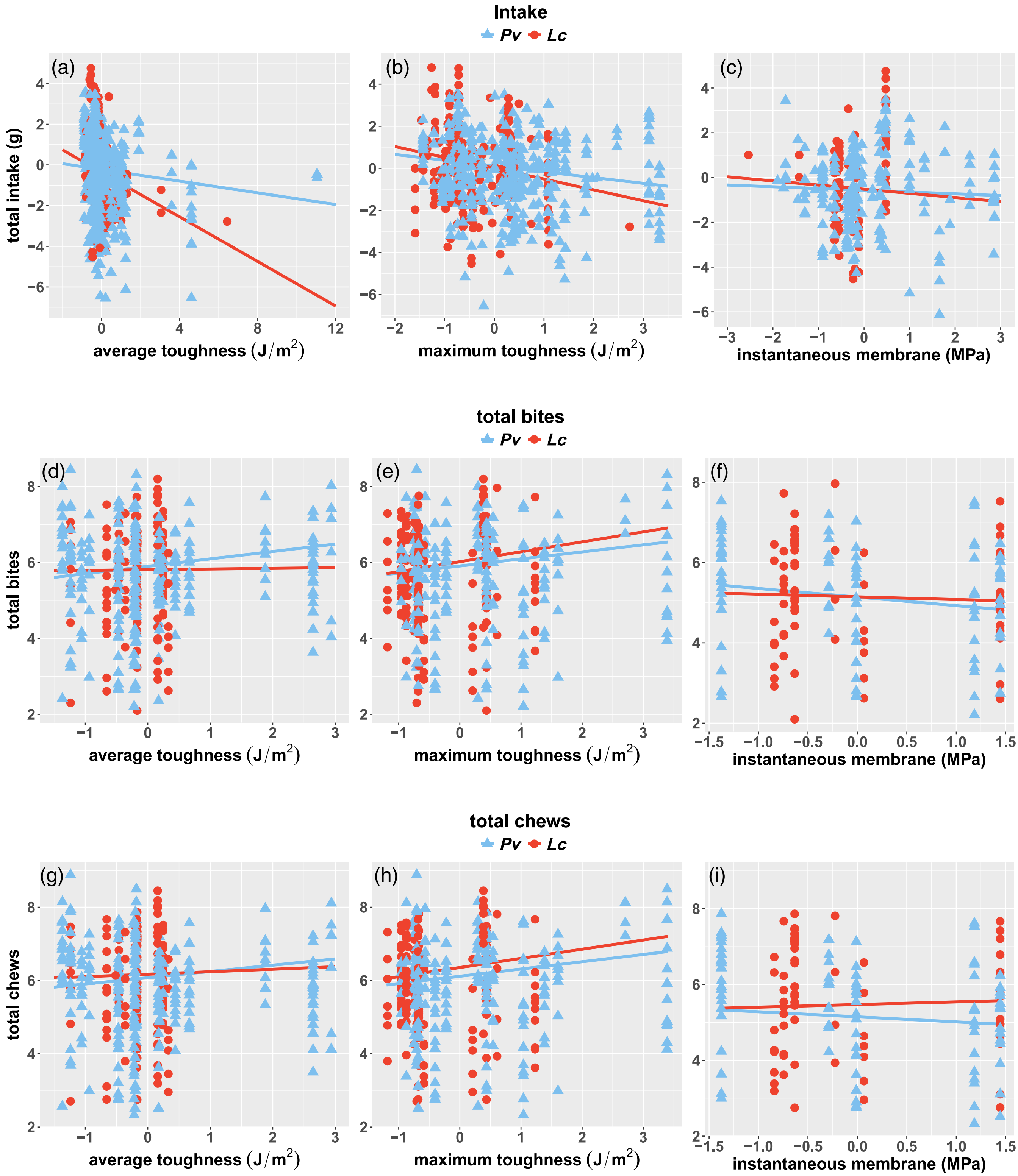

FIGURE 1 Daily intake (a–c), total daily bites (d–f), and total daily chews (g–i) regressed against each food mechanical property (FMP). Original data scatter with predicted value lines for species superimposed. Intake data includes the entire range of foods observed eaten; total bite and chew data are based on the most frequently eaten foods. All FMP values per plant part are averages; each plant part is represented by one value that is repeated for individual response variables. Model used is ~ z.FMP × species + season + shape + random effects. Lc, *Lemur catta*; Pv, *Propithecus verreauxi*.

3.1 | Daily dataset

3.1.1 | Intake

FMPs. R_{av} and R_{max} impacted daily intake; as both average and maximum toughness increased, intake decreased (Table 1, Figure 1). E_{inst} (membrane stiffness) did not have an effect.

Species. The two lemur species did not significantly differ in daily intake; however, the interaction between R_{av} and species was significant with *Lc* having a steeper negative slope than *Pv*. The lemur species are not significantly different in emmeans contrasts (p-value = 0.0725), but *Lc* have a non-zero slope (confidence interval: −0.952, −0.145). The trend for *Pv* is also negative, but the slope encompasses zero (CI: −0.895, 0.608).

Season. Daily intake did not differ between wet and dry seasons.

Shape. Shape did not significantly affect seasonal intake in models containing R_{max} and E_{inst}; however, shape had an effect in the model with R_{av}. The intake of large fruits (3D2—high intake) was distinct from large cylinders (3D5—low intake) and small- and medium-sized leaves (2D1, 2D2) (Table S3).

3.1.2 | Total bites

FMPs. Neither R_{av} nor E_{inst} affected total daily bites (Table 1, Figure 1). However, total daily bites increased with R_{max}.

Species. The two lemur species did not significantly differ in daily bites.

Season. The dry season had significantly more daily bites than the wet season.

Shape. Shape had a significant impact on the total number of daily bites (Table 1). With R_{av} as a covariate, small fruits (3D1) were associated with more bites than both medium-sized leaves (2D2) and large cylinders (3D5) (Table S3). With R_{max} as a covariate, more bites were taken for small fruits (3D1) than small- and medium-sized leaves (2D1, 2D2) and large fruits (3D2) (Table S3). No effect was found with E_{inst} as a covariate, in which case shapes were limited to flat leaf material.

3.1.3 | Total chews

FMPs. R_{av} and E_{inst} did not influence total daily chews. R_{max} had a marginally significant impact with chew number increasing with food toughness.

Species. The two lemur species did not significantly differ in their daily chews.

Season. The lemurs chewed more in the dry than in the wet season.

Shape. Shape had a significant impact on the total number of daily chews (Table 1). With R_{av} as a covariate, small fruits (3D1) were chewed more than medium-sized leaves (2D2) and large cylinders (3D5) (Table S3). With R_{max} as a covariate, small fruits (3D1) were chewed more than small- and medium-sized leaves (2D1, 2D2) and large fruits (3D2) (Table S3). No effect was found with E_{inst} as a covariate.

3.2 | Toughness comparisons of shared and exclusive foods

3.2.1 | Intraspecific comparisons

Lc had 18 overlapping foods between seasons that constituted 35.3% and 23.4% of the dry and wet season diets, respectively. *Pv* had 35 overlapping foods that comprised 63.6% and 31.5% of the diet (Figure S1). Since a greater number of plant parts are eaten in the wet season, we also calculated the time spent feeding on overlapping foods in each season. For *Lc*, these foods comprised 78.3% of total feeding time (dry season) and 51.8% (wet season), and for *Pv*, 78.2% (dry season) and 44.7% (wet season). The overlapping foods were not necessarily the most frequently eaten foods (these comprised >70% of the *Lc* diet and 56% on average for *Pv* in both seasons).

We next compared the within-species toughness values of these overlapping foods ("common") and those that were eaten exclusively in one season ("exclusive") using the seasonal dataset (Table S5; Figures S3 and S4). The average toughness of the overlapping and the exclusively eaten foods for each season did not significantly differ for either *Lc* or *Pv*. In terms of maximum toughness, the overlapping foods between seasons significantly differed for both species. In addition, the exclusive foods significantly differed between seasons for *Lc*. In each case, the wet season foods were tougher. Unlike *Lc*, the season-exclusive foods for *Pv* were not significantly different from one another. R_{max} of the overlapping foods in each season did not differ from the values of the exclusive foods in the same season for either lemur species (C1-E1 and C2-E2 comparisons); therefore, differences in R_{max} were related to seasonality.

3.2.2 | Interspecific comparisons

Comparing the lemur species directly, 13 plant species/parts were eaten by both lemur species in both seasons ("core" foods) (Figure S1), in addition to foods that were eaten in at least one season by both species ("shared"). These shared foods were contrasted with foods that were only eaten by one lemur species in both seasons (Table S6; Figure S5). (Time spent on the core foods was: *Lc*, 76.4% [dry season], 55.8% [wet]; *Pv*, 39.7% [dry]; 23.7% [wet].) For both R_{av} and R_{max}, the foods eaten by only *Lc* were less tough than foods shared with *Pv*, which were less tough than the *Pv* only foods (*Lc* only <shared <*Pv* only), though this was only significant for R_{max}. Contrasts of shared foods-*Lc* only foods and *Lc*–*Pv* only foods were significantly different for R_{max}.

4 | DISCUSSION

4.1 | Model effects

4.1.1 | Toughness FMPs are negatively correlated with intake and positively with total bites and chews

Average and maximum toughness are negatively correlated with intake in the daily dataset as expected. We previously found that bites per second are negatively correlated with R_{max} for *Lc* (Flowers et al., 2023); the lemurs take longer to bite as foods become tougher. This agrees with our finding here if we assume that lower rates are indicative of lower intake. In both these studies, the negative relationship is more pronounced for *Lc*. The negative correlation also indicates that the most commonly eaten foods are less tough, suggesting that one of the criteria for selecting them is that they are simply easier to eat, and tougher foods are eaten at lower volumes. This negative correlation between food toughness and food intake was also found when Perry and Hartstone-Rose (2010) conducted feeding trials on 17 species of captive strepsirrhines. They found that maximum food size (V_b) was negatively correlated with food toughness. Though their experimentally determined measure of food size differs from our measure of food unit per bite, we reach similar conclusions regarding intake volume and food toughness.

In the daily dataset, total bites are positively correlated with R_{max} and not with R_{av}; the lemurs bite more on the toughest foods per day. This is consistent with our prediction and previous result that *Lc* take more bites with the toughest foods (Flowers et al., 2023), but seems at odds with the previous finding that bite rate decreases with the toughest foods. When *Lc* eat the toughest foods, they bite more in a given feeding bout but spend more time on each bite. Individual tough foods may take longer to process, and the lemurs adjust by increasing feeding time or frequency, which agrees with the differences in feeding time in the activity budgets in Flowers et al. (2023). Coiner-Collier et al. (2016) similarly found that smaller-bodied primates, including lemurs, increased feeding time with increasing food toughness, whereas feeding time decreased with food toughness for larger primates.

Chew numbers are not strongly influenced by toughness in either daily or seasonal datasets, though the trends are positive as they were with bite number. Chew numbers in per bout feeding increased with R_{av} in Flowers et al. (2023), as do total chew numbers marginally with R_{max} here in the daily dataset. Reed and Ross (2010) found that chew numbers varied more than chew time (chew cycle duration) with respect to variance in sequence time, and Ross et al. (2009) did not find strong relationships between food toughness and chewing. We likewise found no correlation between chew rate and toughness in Flowers et al. (2023). If chew rate is relatively invariant with respect to FMPs, then the lemur must find alternative ways to control intake because intake is negatively correlated with the two toughness measures; in our data, this seems to occur by increasing feeding duration.

In Ross et al. (2007), increased strain magnitude in chewing is correlated with increased strain rate (rate of loading) rather than loading duration as we argue here (actually decreased bite rate). We did not measure strain rate; however, we can compare load time and strain magnitude if we approximate bite time as load time and R_{max} as strain magnitude. We found in Flowers et al. (2023) that for *Lc* bite number increased with R_{max} and bite rate decreased with R_{max}. In Ross et al. (2007), load time is positively correlated with strain magnitude in the few models that were significant. If we compare this with our data, then we come to a similar conclusion: that with increasing load, load time increases (or, in our case, bite rate decreases). However, our significant results are for biting and those in Ross et al. (2007) for chewing. Bites are less uniform in food placement and in size/geometry; therefore, biting strains are likely to differ from those generated during chewing. We found few differences with food toughness and chewing in our datasets.

E_{inst} is negatively correlated with total bites and chews in the seasonal dataset (Table S2), as is also the case for chew number for *Lc* in Flowers et al. (2023). As leaf membranes become stiffer, bites and chews decrease. Since stiff foods tend to be brittle, stiffer leaf laminae may require fewer bites and chews to break them apart. These results should be interpreted cautiously considering the small sample sizes.

In summary, the lemur response to increasing food toughness is to bite (and chew) more for a longer time (chewing did not have as significant a relationship with toughness). Taking longer to bite may be a behavioral means to decrease strain when eating tough foods; this approach may lead to an increase in bite number, which we also find. Although we do not know if decreased bite rates are directly responsible for the lower intake pattern we observe with increasing food toughness, it is consistent with that finding. Intake is calculated as the numbers of food units consumed and the time taken for their consumption. Increasing food toughness affects all of these variables: the numbers of units decrease as processing time goes up and processing effort increases (more bites and chews). With increasing food toughness, some combination of decreased numbers of units, increased effort, and increased time affect the actual amount taken in.

4.1.2 | R_{max} has an effect on the response variables; R_{av} does not

Given the response to R_{max}, especially for total bites and chews (Table 1), food toughness may not be a consideration in food selection or processing until toughness reaches a certain threshold, at which point the lemur responds by eating less, biting and chewing more, or presumably avoiding the food. This may be a seasonal effect, in which plant foods are generally tougher in one season and feeding on foods with greater toughness is unavoidable in that season. R_{max} in the wet season is unexpectedly higher than in the dry (see below for discussion on drought-related effects; Figure S4), and our modeling supports a strong seasonal effect in total bites and chews (Tables 1and S2). However, more bites and chews are taken in the dry season, which seems to be at odds with our findings that tougher foods require more processing and that R_{max} of the diet is higher in the wet season. Although the wet season diet has a higher R_{max} and that bites and chews increase with food toughness, the trend is the same in both seasons—tougher foods require more processing. The values for bite/chew numbers are slightly elevated in the dry season but the wet season has higher values for R_{max}. In any case, the greater impact of the toughest foods on intake and biting and chewing may have consequences for masticatory morphology (see below).

4.1.3 | Lemur species do not differ in daily intake, total bites, or total chews

Our results here are in marked contrast to our previous results in Flowers et al. (2023), in which species had a significant effect on chew number and chew rate. In all cases, *Lc* was elevated over *Pv*. *Lc* adjusted feeding behavior when eating mechanically challenging plant materials, whereas *Pv* showed little response in oral processing (Flowers et al., 2023). Here, there are few species differences.

The differences between our two studies in the effect of species are due to the level of comparison—feeding on a per plant basis compared to a summed daily or seasonal basis. If, as an example, *Lc* chew more per plant but less frequently over a day compared with *Pv*, then the differences between the lemur species largely disappear. Over the course of a day, *Pv* make up for its slower chewing rate by feeding for a longer time, resulting in total chews that do not differ from *Lc* (Tables 1and S2). This is consistent with the observation that *Pv* spend more time feeding than *Lc* in both seasons (Flowers et al., 2023). The distinction between per bout feeding and cumulative feeding underscores the necessity of accounting for feeding time when evaluating the impact of oral processing on the masticatory morphology. In this study, many of the species distinctions no longer apply when scaled to daily and seasonal feeding periods.

4.1.4 | Daily bites and chews are seasonal; intake is not

Interestingly, intake does not differ between seasons (Tables 1and S2). Even with seasonal differences in FMPs and food availability, both lemur species take in similar amounts of food in each season. This suggests that intake volume may be a target, and feeding time is adjusted seasonally to achieve this amount.

Total bites and chews do have a strong seasonal component, especially with respect to R_{max}. As discussed above in Section 4.1.2, bite/chew numbers increase with food toughness in both seasons, but the bite/chew numbers are elevated in the dry season. The higher bites/chews in the dry season are most likely a consequence of consumption of specific foods that require more processing while having lower R_{max} values than in the wet season (e.g., *Ipomoea batatas* leaves, *mamyaho* leaves, *Tamarindus indica* old fruit, *Acacia bellula* leaves; see Table S2 in Flowers et al. (2023)). These foods vary in shape and size, so they are not differentiated in the shape effect (see below). Within the dry season, these foods also show increased bites/chews with increasing food toughness. Feeding time could also be a factor, though this is equivocal. *Pv* do spend more time feeding in the dry season, though *Lc* spend more in the wet (Flowers et al., 2023).

4.1.5 | Food shape influences intake and bite and chew numbers

Food size and shape are significant with respect to intake with R_{av} as a covariate (Table 1). Table S3 shows specifically that large fruits have a higher intake than small and medium-sized leaves and large stalks and stems. The greater per unit volume of large fruits translates into a higher intake, though they may be eaten less frequently than smaller volume foods such as leaves. Consolidating the shape categories for the models with R_{max} resulted in less differentiation among the categories.

Both total bites and chews are impacted by food shape with both R_{av} and R_{max} as covariates (Tables 1and S3); small fruits especially have more bites and chews than leaves or large stalks and stems. Small objects can be consumed faster (higher bite and chew numbers) than larger foods; however, the faster processing of small fruits did not translate into higher intake as we saw above. We hypothesized that leaf material (e.g., flat shapes) would potentially have higher cumulative loads (repetitive loads) because they may require more chews to process and/or they are eaten for a longer time. Implicit in this is that leaf materials are tough foods. However, the leaf categories (2D1-3) did not have notably higher chews than other food shapes.

4.1.6 | Intraspecific and interspecific toughness comparisons

The number of common food plants within and between lemur species point to the relative importance of these foods to each lemur species, and the percentage time spent feeding on them indicates that they are not avoided (even if they are tough).

The within-species toughness comparisons of these common and seasonally exclusive foods in Table S5 and Figures S3 and S4 reinforce the results of the full model, that the maximum toughness of the overall diet is seasonal and higher in the wet season for both lemur species. Furthermore, combined with the degree of plant species overlap, food toughness is not a strict deterrent to consuming these common foods since they are eaten even if they are tougher in one season (C1-C2 comparisons), and the exclusive foods are not (E1-E2 comparisons).

When the lemur species are compared directly (Table S6, Figure S5), the shared foods appear to be more of a challenge for *Lc* than for *Pv* since the foods only eaten by *Lc* are less tough and the *Pv*-only foods are tougher. We saw a similar pattern in Flowers et al. (2023) for bite number and rate in models with R_{max}, in which *Lc* adjusted behaviorally whereas *Pv* did not. All this begs the question of why these tougher, shared foods are eaten by *Lc*. Most likely, they are nutrient-rich or contain other desirable compounds. In the context of our study, the consequences for *Lc* are greater loads relative to *Pv* due to feeding outside the range of their exclusive foods.

4.2 | Effect of drought

We had expected that more mechanically challenging foods would be eaten during periods of predictable resource shortages (e.g., the dry season) or unpredictable environmental events (e.g., droughts, cyclones). Although we did not set out to test the latter explicitly, our study coincided with the worst drought recorded in 40 years in southern Madagascar, which extended approximately from 2016 to 2021 (Joint Research Centre Drought Observatory Analytical Report, 2021; USAID Fact Sheet #4, 2022). As a result, the animals may have been feeding more on the edge, and the seasonal differences we found in FMPs, food types eaten, and amounts may be related to drought-related effects on food availability. Measurements of the photosynthetic activity of the vegetation cover (fAPAR) strongly agreed with other indices that measure drought conditions (e.g., precipitation, soil moisture), especially from November 2020 to February 2021 (JRC GDO Analytical Report, 2021). Plant species in this study would presumably have been affected, though the extent of drought-related effects compounded over several years on food availability and their mechanical properties is not clear. We did find strong seasonal effects for R_{max} that are unexpectedly higher in the wet season for both species (and additionally R_{av} for *Pv*) (Figures S3 and S4).

The effects of the drought were probably more pronounced in our wet season as it became an extension of the dry season. As we saw in the shared and exclusive foods comparisons above, the overlapping foods between seasons for each lemur species were tougher (R_{max}) in the wet season (Figure S4). In the 1991–1992 drought at BMSR, Gould et al. (1999) reported *Lc* eating less desirable foods, such as desiccated *Tamarindus indica* (kily) fruit pods. In contrast to previous years (Sauther, 1998; Yamashita, 2002; Yamashita et al., 2012), we also observed old kily fruit being consumed more than unripe or ripe fruit. Old kily fruit exocarp tends to be less tough than the other developmental fruit stages.

4.3 | Morphological considerations

Though we find no species effect with respect to our response variables, the greater robusticity of the sifaka masticatory apparatus nonetheless calls to mind Liem's paradox, in which seemingly overbuilt morphology is beneficial during periods of resource stress (Norconk & Veres, 2011; Robinson & Wilson, 1998; Ungar, 2010). We find that maximum food toughness is more highly correlated with daily intake and bite/chew numbers than average toughness. The drought may have brought existing differences in food choice into sharper relief, and the more robust *Pv* masticatory apparatus may have enabled easier access to the toughest foods. As we saw when comparing foods eaten in common between the lemur species, the shared foods between the species seem to be more challenging for *Lc* since they are tougher than their exclusive foods, whereas the shared foods for *Pv* do not differ in toughness from their exclusive foods. Furthermore, though the lemur species do not differ in our models, *Lc* consistently show a greater response between FMPs and the response variables (Figures 1and S2).

Hylander (1979) asked whether repetitive, low loads or less frequent, and high loads were morphologically more significant and whether it was possible to distinguish between them. Vinyard et al. (2011) echoed this question, hypothesizing that the lack of correlation between food toughness and EMG activity in howler monkeys may result from the distinction between everyday, repetitive loads versus extreme activities, which generate peak loads. The former corresponds to the low impact, high frequency events that maintain bone mass, whereas the latter initiates bone formation (e.g., Adams et al., 1997; Burr et al., 2002; Fritton et al., 2000). Turner and Robling (2003) found that a combination of load intensity, number, and timing interval between loading bouts determined bone formation. These mechanical signals in turn are conveyed to the bone cells that implement bone repair, growth, and resorption (e.g., Stewart et al., 2020). In terms of generating new bone, the magnitude of the loads and their frequency are both higher for *Pv* than *Lc* (Figure 1). Behavioral variation within and between species complicates assessing timing intervals between feeding bouts as these intervals can vary by social activities and season. Given the differences in load magnitude and frequency alone, *Pv*'s feeding activities are likely to stimulate bone growth.

Furthermore, our findings that maximum food toughness significantly affected total bites (and chews) and that the sifaka diet is tougher (higher R_{max}) are consistent with the idea that the more robust jaws of sifakas are related to the greater loading/strain that accompanies infrequent but intense events. However, we classified toughness in such a way that most food items have maximum and average values and both are regular properties of the diet throughout the year. The patterns in our data support the idea that both challenging FMPs and loading frequency produce strains that require a more specialized morphology and that these are not necessarily constrained to infrequent events or to specific periods of time—high values occur habitually. However, the higher R_{max} values in the wet season for both lemurs suggest potential drought-related effects on food properties that may have further amplified species' differences.

Perry et al.'s (2011) work comparing the jaw adductor muscles of strepsirrhines related greater bite force generation to smaller gape size in folivorous strepsirrhines compared with frugivores. The small gapes were attributed to the relatively shorter jaws and shorter fiber lengths of the adductor muscles in the folivores that, along with greater physiological cross-sectional area (PCSA), contributed to greater bite force (Perry et al., 2011). The relatively smaller gapes in folivores aligned with their earlier finding that folivorous lemurs took smaller bites (V_b; maximum food size) relative to the other strepsirrhines (Perry & Hartstone-Rose, 2010). The contrast between folivorous and frugivorous strepsirrhines parallels our comparisons of *Pv* and *Lc* (though *Lc* are as folivorous as they are frugivorous in our study). The relationship between small gape and greater bite force generation in folivores (Perry et al., 2011) may underlie our finding that *Pv* consumes a diet with a higher maximum toughness than *Lc*. The combination of the adductors and short jaw may even contribute to *Pv* generating higher bite forces anteriorly during biting (see below). As an interesting aside, *Lc* reached similar daily chew totals as *Pv* by chewing faster in a shorter amount of time. Fast chewing may be enabled by its own suite of specializations, including muscle attachment sites, muscle fiber type, associated neural control, and a longer jaw, the latter of which *Lc* possesses relative to *Pv*.

Finally, R_{max} affects both total bites and chews (Table 1). This is perhaps unsurprising given that the lemur has already chosen and ingested the food by the time it is chewing it, and toughness would affect both phases. What may be of immediate concern to the consumer with respect to FMPs is whether it can bite off the food rather than if it can chew it. Oral preparation (e.g., husking, peeling) of non-food parts, for example, may place higher loads on the jaw than ingestion of actual food parts (e.g., McGraw & Daegling, 2019; Wright, 2005; Yamashita et al., 2009). In the sympatric Taï monkeys studied by McGraw and Daegling (2019), the most gracile species, the Diana monkey (*Cercopithecus diana*), chewed more per ingestive event than the more robust, seed-eating sooty mangabey (*Cercocebus atys*). The hard work of ingestion occurred when the mangabeys bit and fractured the hard seed casing of their major food, followed by relatively minimal mastication. In terms of loading and strains during initial biting and food preparation, capuchins (*S. libidinosus*) processed stiffer and tougher foods anteriorly rather than on the postcanines (Laird et al., 2020). Biting cycles, therefore, may be as important to morphology as repetitions in chewing. From our study, the greater robusticity of the sifaka jaw is as likely to be a consequence of the combination of maximum food toughness compounded by the accumulated effects of daily numbers of bites as much as chews. The more gracile-jawed ring-tailed lemurs modified their behaviors more than the sifakas with respect to bite number and rate when eating their toughest foods (Flowers et al., 2023). A morphological interpretation of this is that jaw shape can be as closely allied to biting and oral preparation as chewing.

5 | CONCLUSIONS

In this paper, we modeled summed daily and seasonal intake, biting, and chewing with respect to dietary FMPs, lemur species, season, and food shape. Our major findings are that intake decreases with food toughness, total bites and chews are positively correlated with maximum toughness, and the two lemur species do not differ in our models. The contrast between our earlier results per plant and this study on cumulative daily and seasonal effects demonstrates that determining the effects of food processing on morphology should include some measure of feeding frequency. A per plant or per bout analysis is revealing for what a primate is capable of consuming (in terms of food properties); a daily or cumulative analysis is more informative in terms of jaw loading.

Future research will investigate initial food placement during oral preparation and the nutritional content of foods in relation to FMPs. We will also expand the biting and chewing data collection beyond the most frequently eaten foods in the diets of the lemur species. Extending data collection to less frequently eaten foods could increase the range of toughness values per season and sharpen the correlations among the response variables and different fixed effects.

AUTHOR CONTRIBUTIONS

Nayuta Yamashita: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (lead); investigation (equal); methodology (lead); project administration (lead); resources (lead); supervision (lead); validation (lead); visualization (lead); writing – original draft (lead). **Nina Flowers:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); investigation (equal); methodology (equal); visualization (equal); writing – review and editing (equal). **Mariana Dutra Fogaça:** Conceptualization (supporting); data curation (supporting); investigation (equal); methodology (equal); visualization (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data underlying this study are available on Zenodo at http://doi.org/10.5281/zenodo.10213314.

ORCID

Nayuta Yamashita https://orcid.org/0000-0003-2010-8513
Nina Flowers https://orcid.org/0000-0003-0562-9759
Mariana Dutra Fogaça https://orcid.org/0000-0002-6776-9389

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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