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Chewing performance and the structure of primate communities

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Ecomorphological theory predicts a relationship between the morphology of a given trait and its ecological performance. In turn, variation in ecomorphology is viewed as integral to the structuring of animal communities. This reasoning is practically axiomatic, but the full logic chain is seldom integrated into a single study. We tested the functional relationship between premolar tooth size and chewing performance across a diverse community of wild primates, including chimpanzees and seven monkey species. We found that relatively large premolars were associated with improved food fracture, and that the chewing performance of granivores (seed predators) exceeded that of sympatric folivores and frugivores by 51–56% and 64–68%, respectively. This finding is robust when controlling for variation in chewing effort and seasonal grit ingestion. Evidence of convergent evolution speaks to the fitness advantages of enlarged premolars among granivorous species, and we show that premolar-mediated seed-eating shapes the composition of primate communities across nine African forest sites. Our findings are relevant to palaeoanthropology and the puzzling megadontia of some fossil hominin lineages, as our data favour a diet of stress-limited brittle foods, not ductile foods, as the principal selective pressure favouring the performance benefits of enlarged premolars.

1. Introduction

Morphological variation shapes the structure of animal communities, which Giller [1] defined as the number and relative abundance of species, and their ecological interactions. For example, functional anatomical differences in the limbs, jaws and teeth of animals can influence foraging preferences and habitat use [2–5], factors that determine niche partitioning and community structure [6–10]. The referenced studies are either foundational or destined to become so, but there are two persistent problems. First, the effects of morphological variation on performance are often inferred and seldom quantified, and second, the presumed link is almost never investigated at the community level [11,12].

Performance is defined as the capacity for a morphological trait to execute a relevant task [11], and it represents the pivotal nexus between morphology and resource use. Arnold [13] furthered this connection by linking performance directly to fitness and the adaptive origins of traits. He developed a ‘performance paradigm’ and called on researchers to measure (i) the effects of morphology on performance—its ‘biological role’ *sensu* Bock [14]; and (ii) the effects of performance on fitness. Wainwright [15,16] and others [17–19] heeded this call by measuring the performance of wild-caught animals in laboratory settings, mainly invertebrates and small vertebrates. Similar experimental conditions are seldom practical for larger mammals, especially primates. Given that many externalities can influence the interactions between morphology, performance and community structure, there is mounting interest in measuring the performance of animals under natural conditions [20–23].

To explore the effects of morphology on performance, we quantified variation in chewing performance across a diverse community of wild primates, including chimpanzees and seven species of monkey. We combined long-term foraging data with measures of premolar tooth size because fracture theory predicts a form–functional relationship between these variables [24–28] and because premolar enlargement is a topic of enduring interest in palaeoanthropology [28–30]. The prevailing thought is that relatively larger premolars improve chewing performance by withstanding higher bite forces and enabling greater food fracture [31], factors that are expected to enhance digestive efficiency [32–36]. In addition, we predicted significant covariation between diet, tooth size and chewing performance, as some foods (e.g. leaves) require greater levels of microbial fermentation in the gut, a process that benefits from smaller particles of digesta [37–39].

To test these predictions, we estimated chewing performance by calculating the size distributions of food particles that survive digestion, a measurement known as faecal particulate size (FPS) [40–42]. FPS is a non-invasive proxy for quantifying chewing performance because none of the ensuing digestive activities—acidic, enzymatic, bacterial—have an appreciable effect on the sizes of food particles ingested by terrestrial herbivores [43]. Thus, lower FPS values indicate better dental performance [41] and, potentially, higher rates of fermentation during digestion [38]. Still, other factors may affect FPS, such as variation in masticatory effort [44,45] and the seasonal consumption of exogenous quartz [46,47]. The present paper accounts for both of these confounding variables.

Our intent is to draw a throughline from tooth morphology to ecological performance and the structure of primate communities in Africa. We fulfil this aim below, but an unexpected finding concerning seed eating (granivory) motivated a validation analysis. To verify the inferred fitness benefits of larger premolars, we used the comparative method and fit two models of evolution—Brownian motion (BM) versus a multiple-optima Ornstein–Uhlenbeck (OU) model—to test for adaptive convergence.

2. Material and methods

(a) Study site and species

Our sample consists of eight sympatric catarrhine species inhabiting Taï Forest, Côte d'Ivoire: four cercopithecine monkeys, three colobine monkeys and chimpanzees (electronic supplementary material, figure S1). This community of primates is well-habituated to human observers from decades of research by the Taï Chimpanzee Project and Taï Monkey Project (TMP). Rainfall is variable over the course of the year, with two distinct wet (September–November; March–May) and dry (December–February; June–August) seasons [48].

(b) Tooth size

We focused on premolars because fracture theory predicts their sensitivity to the selective pressures of food material properties [31]. This rationale can be extended to the molar row too [49], and we verified a weaker trend with molars in our dataset (electronic supplementary material, figure S2), but it is the premolar that commands attention in hominin palaeobiology. Premolar size is often linked to adaptive shifts in human dietary evolution [29,30], even though its predicted effects on the chewing performance of wild primates are untested. We calculated tooth areas using two shape ratios—i.e. total upper premolar (UP) area relative to (i) maxillary M1 area (UP.M1) and (ii) palate area (UP.PA)—from the skulls of naturally deceased monkeys recovered from the primary study grid of the TMP, a narrow scope that controls for potential differences in tooth size driven by population-level variation [50]. The sample is composed of adults (n = 77 individuals) housed in the Department of Anthropology, Ohio State University. We supplemented this dataset with measurements from adult chimpanzees accessioned in the Museum of Comparative Zoology, Harvard University (n = 10; electronic supplementary material, table S1). This latter sample is mixed geographically, including West and Central African-sourced individuals. Pooling these data is justified given the negligible differences between subspecies or populations of chimpanzees [51].

We used digital callipers to measure the mesiodistal and buccolingual dimensions of the maxillary premolars, summing the areas. We body size-adjusted the total premolar area by scaling it to the maxillary M1 area and palate area, calculated as the product of palate length (distance from staphylion to intradentale superior) and palate width (distance between the mesiolingual root surfaces of the maxillary M1s). We generated premolar shape ratios by dividing each premolar area by its corresponding scalar after taking the square root of each measurement. Our rationale for these steps follows Scott *et al.* [31], who viewed these shape ratios as conducive to detecting disproportionate premolar enlargement relative to the oral cavity and first molar, respectively.

(c) Chewing performance

Freshly voided dung samples were collected opportunistically during full-day focal follows of adult monkeys over the course of an annual cycle, storing them in 96% ethanol (n = 362; electronic supplementary material, tables S2 and S3). Sub-samples were taken from the interior to avoid exogenous soil contamination. In the laboratory, we placed 5–10 g of wet faecal material in glass beakers, suspending them with a stir bar overnight [52]. We poured the faecal slurry over a sieving machine (AS 200 Controls Retsch, Haan, Germany) with a sieve cascade of 11 pore sizes: nos. 1 (0.025 mm); 2 (0.04 mm); 3 (0.063 mm); 4 (0.125 mm); 5 (0.25 mm); 6 (0.5 mm); 7 (1 mm); 8 (2 mm); 9 (4 mm); 10 (8 mm); 11 (16 mm). We sieved each sample for 10 min using a vibration amplitude of 2 mm and a water throughput of 2 l min^{-1}. We transferred the contents of each sieve to pre-weighed petri dishes, dried them at 103°C overnight and weighed them after cooling to room temperature in a desiccator.

Using the mass of dried faecal matter on each sieve, we calculated chewing performance as the discrete mean particle size (dMEAN; mm), i.e. the weighted average faecal particle size per unit mass on each sieve in each sample [52]. We excluded intact seeds on sieve nos. 8–11 (>2 mm) from our calculations because this unchewed matter can skew dMEAN values [42]. The dMEAN values of chimpanzees (n = 35) were sourced from Schulz-Kornas *et al.* [46], who followed a similar protocol. Absolute faecal particle size can be influenced by body mass [40]; thus, we divided each dMEAN by the average body mass of a species [53] raised to one-third power. If sex was known, we used a sex-specific body mass for the species. If not, then we used a sex-averaged species body mass. We report chewing performances as body mass-scaled dMEAN values, with a smaller relative FPS (rel.FPS) indicative of better performance.

(d) Faecal exogenous quartz

Following Fannin *et al.* [54], a subset of dung samples (n = 277) was dried at 103°C for 12 h to quantify ingested exogenous quartz. We combusted each sample in a muffle furnace for 4 h at 500°C to remove organic carbon. A subsample (10–20 mg) of each ashed sample was placed in a pre-weighed 1.5 ml conical tube. We added 200 µl of 6N HCL to dissolve acid-soluble carbonates. After two rinses with distilled water—including 3 s of vortexing and 10 min of centrifugation after each rinse—we added 200 µl of 30% H_2O_2 and placed the tubes in a water bath at 50°C for several hours to remove residual organic matter. At the end of the reaction, we rinsed and centrifuged each sample twice more before adding 1.4 ml of 5% sodium hexametaphosphate solution (Calgon) to the tube. We placed the tubes on an orbital shaker for 8 h to disaggregate clay particles.

Next, we removed small silt and clays (2–20 µm) from the supernatant [55] using a 2 min gravity sedimentation step after vortexing. The duration was calculated from Lentfer *et al.* [56], using a minimum particle diameter of 20 µm and a particle specific gravity of 2.3 g ml^{-1} at a solution depth of 3.2 cm. This step maximizes quartz retention—prioritizing particles >25 µm because they disrupt comminution [47]—and the removal of clay, which is far less damaging to enamel [57]. This sedimentation step was repeated with distilled water, and the supernatant was removed. We added 500 µl of a 2.26 g ml^{-1} sodium polytungstate solution (Sometu, Berlin, Germany), vortexed the sample for 3 s and sonicated it for 10 min. We vortexed the sample again (3 s) and centrifuged the tube at 2320 g (5000 rpm) for 10 min. Centrifugation separates phytoliths, which aggregate at the top of the solution, from exogenous quartz, which pellets at the bottom. We withdrew the supernatant and added distilled water, performing three washing cycles of vortexing (3 s) and centrifugation at 2320 g (5000 rpm). We dried extracted quartz in a drying oven at 60°C for 8–10 h, after which each tube was re-weighed to calculate the remaining mass. We expressed ingested grit as the per cent mass of quartz in each gram of dry dung matter (% grit DM).

(e) Feeding behaviour

We sourced feeding behavioural data from the literature [58–61], including chewing effort, defined as the number of postcanine chews per ingestive event [62–66]. This latter dataset is drawn from 5 min focal follows of adult Taï monkeys and is based on the number of times a food item was introduced into the oral cavity. Each new introduction was classified as a separate feeding action. For each action, the number of postcanine chews was recorded before the introduction of a new food item. The average number of masticatory chewing cycles per action was calculated across all focal periods for each species, resulting in a sample of 57 444 chew cycles distributed across 5133 focal bouts (table 1). Postcanine chews were unavailable for Taï chimpanzees.

(f) Data analysis

(i) Ecological analyses

To determine whether variation in chewing performance (rel.FPS) can be explained by variation in (i) relative premolar area and/or (ii) percentage folivory, we performed ordinary least squares (OLS) regressions in JMP 18 ([67]) and phylogenetic independent contrasts (PIC) using the phylogeny from 10kTrees [68] and the *ape* package for R [69]. We used ANOVA to compare rel.FPS across three dietary classifications: (i) granivory; (ii) folivory–frugivory; and (iii) frugivory. These simplified categories reflect common foods (electronic supplementary material, table S4); however, granivory was considered separately because seeds are hypothesized to have an outsized impact on the evolution of premolar morphology [31]. We controlled for the tandem effects of (i) chewing effort and (ii) % faecal grit in DM on variation in chewing performance and relative UP area using multiple regressions, followed by plotting model residuals with OLS and PIC. We included separate regressions for wet- and dry-season dung samples, when quartz loads are often greater [46].

(ii) Evolutionary analyses

We modelled the effects of diet on the evolution of UP areas across two consensus phylogenies, those of a single community (Taï) and another based on 61 catarrhine species from the dataset of Scott *et al.* [31]. Using the R package *OUwie* [70], we

Table 1. Feeding behaviour, morphological and performance data and sample sizes for the Taï Forest primate community. Dietary data sourced from [58–61]; body mass data sourced from [50,53]; chewing effort data sourced from [62–66]; and *Pan troglodytes verus* FPS data sourced from [46].

species	diet	% leaves in diet	relative FPS ± SE (*n*)	UP.PA ± SE (*n*)	UP.M1 ± SE (*n*)	chewing effort (mastications/ingestive event)
Cercocebus atys	granivore	1	0.58 ± 0.04 (59)	0.239 ± 0.004 (15)	1.128 ± 0.011 (15)	7.1
Cercopithecus campbelli	frugivore	8	1.22 ± 0.14 (47)	0.183 ± 0.006 (3)	1.036 ± 0.059 (3)	9.6
Cercopithecus diana	frugivore	6	1.29 ± 0.09 (52)	0.173 ± 0.005 (8)	1.093 ± 0.024 (8)	8.8
Cercopithecus petaurista	folivore–frugivore	40	0.79 ± 0.06 (45)	0.202 ± 0.027 (3)	1.098 ± 0.091 (3)	14.4
Colobus polykomos	granivore	48	0.61 ± 0.03 (71)	0.216 ± 0.003 (21)	1.175 ± 0.013 (21)	20.4
Piliocolobus badius	folivore–frugivore	50	1.08 ± 0.06 (59)	0.231 ± 0.003 (22)	1.079 ± 0.009 (22)	17.5
Procolobus verus	folivore–frugivore	91	1.22 ± 0.10 (29)	0.198 ± 0.006 (5)	1.041 ± 0.026 (5)	24.6
Pan troglodytes verus	frugivore	11	1.02 ± 0.09 (35)	0.201 ± 0.004 (10)	1.069 ± 0.029 (10)	N/A

compared two models: BM and a multiple-optima OU process. BM models stochastic diffusion, with phenotypic similarity proportional to shared evolutionary history. OU models adaptation, where phenotypic traits evolve deterministically towards several optima (selective regimes) represented by θ [71]. We fit our OU models with the same three dietary categories as above (electronic supplementary material, table S5), holding the parameters σ^2 and a constant [72]. We compared fits with Akaike information criterion (AIC) and corrected Akaike information criterion for small sample sizes (AICc). Our OU models required the assignment of internal node states. Thus, we mapped discrete dietary regimes across the edges of each tree using stochastic character mapping in the *phytools* package [73].

(iii) Community analyses

We assembled data on the estimated biomass (kg km^{-2}) of cercopithecoid monkeys in nine African forest sites [74,75] (see electronic supplementary material, table S6) and summed the biomasses of selected taxa at each site, differentiating between eastern and western Africa. We chose this geographic dichotomy because granivory is far more common among the cercopithecoids of West Africa [76], a pattern attributed to lower-quality leaves [74]. To narrowly assess the effects of premolar-mediated granivory on species abundance, we calculated an index of relative biomass—derived from the biomass of *Colobus* (black-and-white colobus) and its ratio to the combined biomasses of two well-studied baseline genera, *Cercopithecus* (guenons) and *Piliocolobus* (red colobus)—and regressed it against the degree of granivory at each site [77].

3. Results

(a) Variation in chewing performance

Variation in the chewing performance (rel.FPS) of Taï primates is readily explained by variation in UP area, regardless of whether it was calculated relative to M1 (figure 1*a*) or palate area (figure 1*b*). When this variation was parsed into dietary categories, we found no relationship with folivory (OLS: $r^2 = 0.01$; $p = 0.81$; PIC: $r^2 = 0.001$; $p = 0.93$), contrary to our *a priori* prediction. Instead, we found that chewing performance (rel.FPS) was greatest among the granivorous (seed-eating) species, followed by those classified as folivore–frugivores and frugivores, in descending order (figure 1*c*).

(b) Confounding effects

Ingestion of exogenous grit varied widely across all samples, ranging from 0.6% DM in the dung of *Colobus polykomos* to as much as 3.4% DM in the dung of *Cercocebus atys* (table 2). We controlled for this variation across seasons, together with species-level variation in chewing effort, and found that UP.PA and UP.M1 explain a significant amount of variation in seasonal chewing performance (rel.FPS; figure 2), although the PIC of residual FPS versus residual UP.M1 failed to replicate the significant relationship detected with OLS in the dry season.

(c) Evolutionary modelling

We found that larger premolars enhance chewing performance (rel.FPS) and that this functional (ecomorphological) relationship evolved convergently in Taï primate species with similar feeding behaviours today (electronic supplementary material,

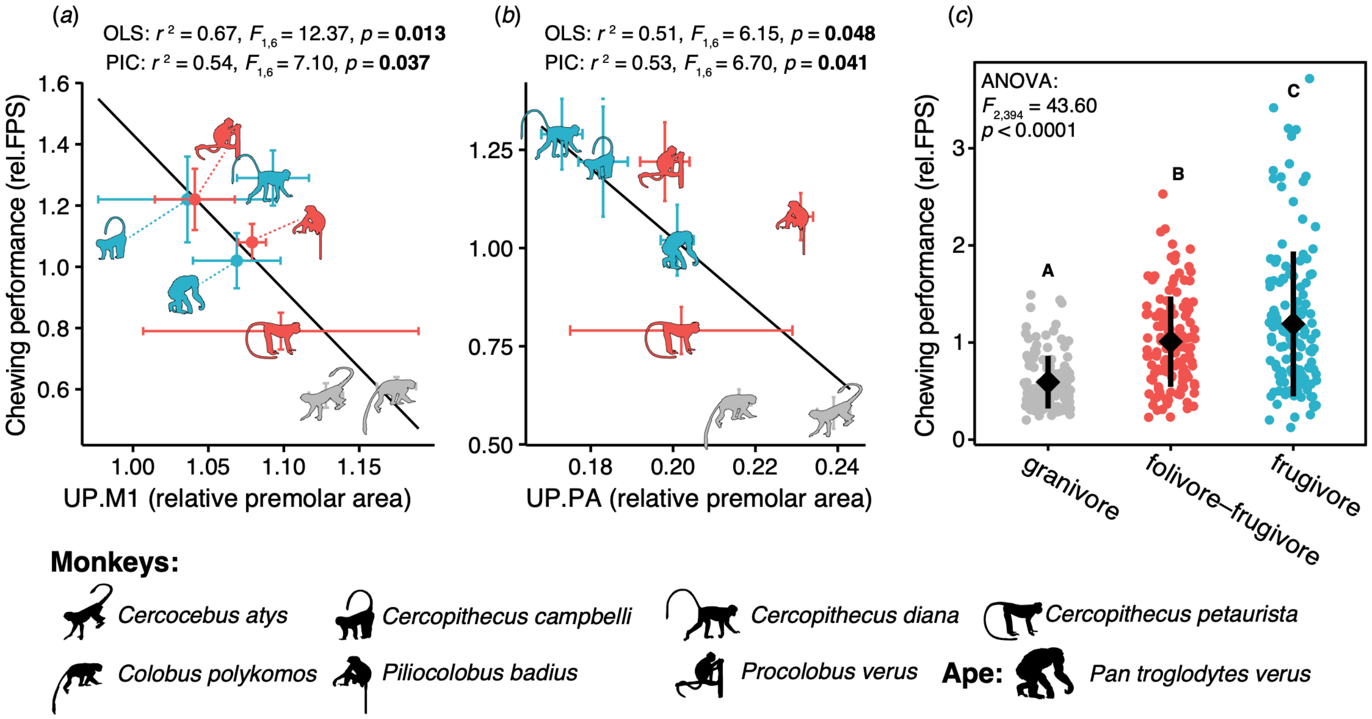

Figure 1. Scatter plots illustrate variation in the chewing performance of eight primate species, as measured by rel.FPS, as a function of UP area relative to (*a*) maxillary M1 area and (*b*) palate area (PA). Species are colour-coded per panel (*c*), and the regressions represent OLS fits. OLS and PIC results are reported. Whiskers represent ± 1 SE. (*c*) Jitter plot illustrating variation in chewing performance within broad dietary categories. Whiskers represent ± 1 SD.

figure S3). However, our evolutionary modelling found mixed support for the underlying process, with AIC supporting the OU process in all cases, but AICc supporting BM. This equivocal outcome is almost certainly a consequence of our small community sample (electronic supplementary material, tables S7–S9). Accordingly, we expanded this analysis to a larger dataset of 61 catarrhine species, finding strong support for OU, with granivores evolving towards optima with the largest premolar teeth, followed by folivore–frugivores and frugivores, respectively (figure 3*a,b*; electronic supplementary material, figures S4 and S5 and tables S10 and S11).

(d) Community structure

Turning to relative species abundances, we found that the biomass of granivorous primates is much greater in western Africa than eastern Africa (figure 3*c*), and we found that premolar-mediated granivory explains a striking proportion of variance in community biomass (figure 3*d*).

4. Discussion

Our study of eight primate species in Taï National Park, Côte d'Ivoire, finds a strong functional relationship between premolar tooth size and chewing performance, upholding ecomorphological predictions. This outcome was robust to seasonal variation in chewing effort and the prevalence of exogenous quartz (grit) in the diet. Furthermore, and contrary to predictions, we show that the chewing performance of seed-eating species exceeded that of leaf-eating species. This finding hints at the adaptive benefit of larger premolars for chewing and digesting seeds, but there is a need for additional data. For example, comprehensive data on food mechanical properties (FMPs) could prove instructive [78]. Interactions between FMPs and chewing effort may shape the relationship between diet, chewing performance and the evolution of tooth size in some species [44], but not others [79]. Furthermore, FMPs can influence individual chewing behaviours across seasons [41], a possibility that invites further investigation. In the absence of FMPs, we validated our findings with comparative evolutionary modelling, verifying the adaptive benefits of larger premolars in lineages with a greater reliance on seeds. Finally, we show that premolar-mediated seed-eating shapes the relative species abundance of primate communities across Africa. These findings are important for corroborating the influential predictions of Arnold [13] and others [14–19], who argued that performance is the crucial factor that connects the morphologies of animals to the structure of their communities.

(a) Why seeds?

Previous research focused on the chewing performance of folivorous and frugivorous primates because leaf-eating is expected to require greater digestive efficiency [37]. Our findings uphold this basic principle by replicating previous folivore–frugivore comparisons [37], but they also implicate seed eating as the outstanding driver of enhanced chewing performance across primates. This outcome complements the *in vitro* analyses of He *et al.* [39], who found that decreasing particle sizes increases

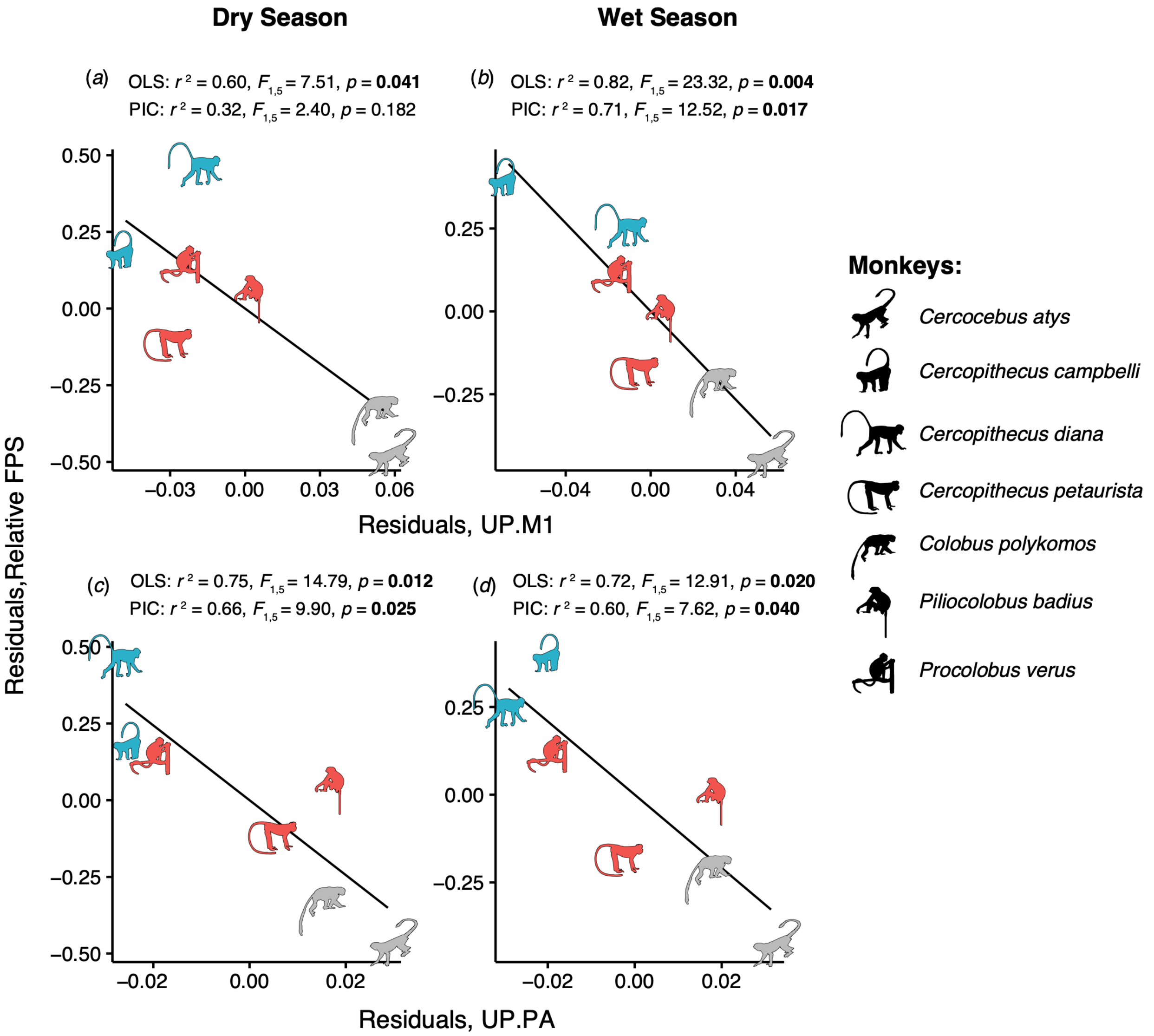

Figure 2. Scatter plots illustrate variation in residual chewing performance—and controlling for variation in chewing effort and exogenous grit ingestion—for residual UP area relative to maxillary M1 area during the (*a*) dry and (*b*) wet seasons, and relative to palate area (PA) during the (*c*) dry and (*d*) wet seasons. Species icons and colour-coding follow figure 1, and the regressions represent OLS fits. OLS and PIC statistics are reported above each panel.

Table 2. Seasonal chewing performance and dietary silica in the Taï Forest monkey community.

species	relative FPS ± SE, wet season (*n*)	relative FPS ± SE, dry season (*n*)	faecal grit, % DM ± SE, wet season (*n*)	faecal grit, % DM ± SE, dry season (*n*)	faecal grit, % DM ± SE, all seasons (*n*)
Cercocebus atys	0.65 ± 0.05 (33)	0.49 ± 0.04 (26)	3.14 ± 0.40 (20)	3.66 ± 0.65 (23)	3.42 ± 0.39 (43)
Cercopithecus campbelli	1.33 ± 0.24 (19)	1.14 ± 0.16 (28)	2.00 ± 0.27 (11)	2.92 ± 0.50 (25)	2.64 ± 0.36 (36)
Cercopithecus diana	1.20 ± 0.14 (28)	1.38 ± 0.11 (24)	2.06 ± 0.42 (16)	1.91 ± 0.35 (18)	1.98 ± 0.26 (34)
Cercopithecus petaurista	0.76 ± 0.07 (21)	0.81 ± 0.09 (24)	1.97 ± 0.52 (23)	0.79 ± 0.13 (13)	1.54 ± 0.35 (36)
Colobus polykomos	0.53 ± 0.05 (25)	0.64 ± 0.04 (46)	0.48 ± 0.16 (29)	0.62 ± 0.15 (39)	0.56 ± 0.11 (68)
Piliocolobus badius	1.07 ± 0.08 (31)	1.08 ± 0.08 (28)	3.04 ± 0.34 (21)	2.73 ± 0.29 (15)	2.91 ± 0.23 (36)
Procolobus verus	1.22 ± 0.15 (15)	1.22 ± 0.14 (14)	3.39 ± 0.64 (13)	2.55 ± 0.63 (11)	3.01 ± 0.45 (24)

the digestibility of seeds to a greater extent than for either young leaves or fruit pulp. In Taï Forest, *Piliocolobus* and *Procolobus* are dedicated folivores with a diet based on young leaves [50], and they possess an additional fourth stomach chamber (presaccus) with the putative function of increasing digestive retention time [80]. The intermediate chewing performances of these colobines puzzled us initially, but they are consistent with a masticatory–digestive complex that privileges gastric retention and fermentation over chewing performance, a pattern that invites direct comparison with black-and-white colobus monkeys (*Colobus*).

Linking the exceptional chewing performance of *Colobus* to a diet of seeds may surprise those familiar with the feeding habits of *Colobus guereza*, an East African species with a pre-occupation for leaves and flowers. In West Africa, however, seed

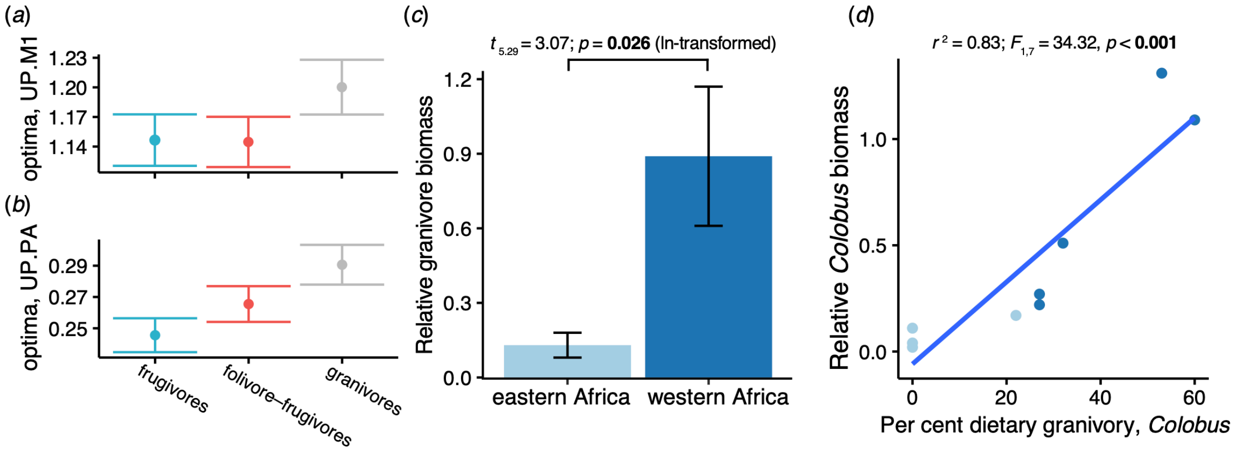

Figure 3. Evolutionary optima values for (*a*) relative premolar area scaled to maxillary M1 area and (*b*) relative premolar area scaled to palate area across a phylogeny of 61 catarrhine species. (*c*) Variation in the biomass ratios of granivorous and non-granivorous primate species in eastern and western Africa. (*d*) Variation in the biomass ratios of *Colobus* species and non-*Colobus* species (*Cercopithecus* spp. + *Piliocolobus* spp.) in nine African forest sites as a function of per cent granivory in *Colobus*. Bars represent ± 1 SE.

eating accounts for 30–60% of the feeding time of each *Colobus* species (electronic supplementary material, table S6). This dietary distinction has been attributed to the lower nutritional quality of foliage in West Africa and a relatively high density of leguminous trees and seeds [74], an argument that treats seed eating as a derived behaviour. This perspective is useful for explaining the unusual intensity of female-led agonism when groups of *C. polykomos* encounter leguminous seeds [81]. Such costly behaviour is a testament to the nutritional value of these seeds [82], a feature that underscores the fitness benefits of enhanced seed-chewing—and the evolution of enlarged premolars in *C. polykomos*—and why some *Colobus* species enjoy a competitive ecological advantage in the seed-dense forests of West Africa.

The seed eating of sooty mangabeys (*C. atys*) is quite different. These monkeys spend 76% of their day on the ground [58] and allocate 49% of their annual feeding time to the seeds of a single species, *Sacoglottis gabonensis*, which they find buried in the leaf litter of the forest floor [78]. The woody casing of these seeds is exceedingly hard, requiring extraordinary bite forces to induce fracture [83]. As a point of reference, these seeds are twice as hard as the average cherry pit [83,84] and 28 times harder than the seed pods of *Pentaclethra macrophylla*, a staple food of *C. polykomos* [63]. Despite these differences in mechanical properties (and molar teeth, as those of *C. polykomos* are thinly enamelled and high-crested [85]), both monkeys evinced comparable levels of premolar-mediated chewing performance, a result rooted in different forms of oral processing. Mangabeys fracture the brittle seeds of *S. gabonensis* using isometric biting, inducing catastrophic failure [50]—in other words, they shatter the seeds—whereas *C. polykomos* uses prolonged repetitive chewing to access the tough seed pods of *P. macrophylla* [63]. Only the former kind of granivory is expected to favour large bunodont premolars equipped with thickened enamel—tandem traits that protect against tooth fracture [86–89]. It is an instructive ecomorphological complex for informing our understanding of hominin evolution [83].

(b) Megadontia

The evolution of massive postcanine dentition, or megadontia, is an enduring puzzle in palaeoanthropology [90,91]. In the extreme case of *Paranthropus*, the premolars resemble molars—they are 'molarized'—and are three times larger than expected relative to body mass. The selective pressures that favoured such large teeth are a subject of spirited debate [92], with most arguments focused on food-mediated differences in chewing behaviour [84]; i.e. repetitive grinding of tough, ductile foods versus forceful shattering of stiff, stress-limited foods [93,94]. Our data on the chewing performances of wild primates are germane to this debate, as only one food type—seeds—is associated with performance-driven selection for premolar enlargement. This result is compatible with the hypothesis that a diet premised on grass seeds shaped the craniodental robusticity of *Australopithecus* [29,30] and *Paranthropus* [94], in part because this food resource can explain the high C_4 input of some species [84]. Yet, seeds have similar mechanical properties to corms [95], a type of plant underground storage organ and another putative food item in the diets of hominins [96]. A diet premised on grass seeds and/or corms is therefore expected to favour large, thickly enamelled premolars, a functional interpretation that corroborates recent efforts [97,98] to reconcile the dental morphological evolution of hominins with variation in carbon and oxygen stable isotopes.

Ethics. Our protocol for collecting observational data followed the American Society of Primatologists' principles for the ethical treatment of non-human primates, and it was approved by the Institutional Animal Care and Use Committee, Ohio State University (protocol 2008A0051-R4). Research in Taï Forest was approved by the residents of Poule Oula, the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, Direction Générale de la Recherche Scientifique et de l'Innovation Technologie, the Ministère de l'Environment, des Eaux et Forêts and the Office Ivorien de Parcs et Reserves (permit nos. 029-2019, 198-2022 and 003-2024 to L.D.F.). Sample exportation authorization was approved by Le Directeur General de l'Office Ivoirien des Parcs et Reserves (permit nos. 198-2022 and 0083-2024). Sample importation to the United States was approved by the Centers for Disease Control (permit nos. 20220916-3373A and 20231007-3691A) and sample import into Switzerland was approved by the Swiss Federal Food Safety and Veterinary Office (permit nos. 22EB001177-DS and 24EB001673-DS).

Data accessibility. All data and code used to generate the findings of this article are publicly available on Zenodo [99].

Supplementary material is available online [100].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. L.D.F.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; D.G.-S.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, writing—review and editing; J.A.-G.: data curation, formal analysis, investigation, methodology; M.C.: conceptualization, investigation, methodology, project administration, resources, software, supervision, validation, writing—review and editing; N.J.D.: conceptualization, funding acquisition, investigation, supervision, visualization, writing—review and editing; W.S.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests. We declare we have no competing interests.

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