



Fruit Selectivity in Anthropoid Primates: Size Matters

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Abstract

Certain features of both extant and fossil anthropoid primates have been interpreted as adaptations to ripe fruit foraging and feeding particularly spatulate incisors and trichromatic color vision. Here, we approach the question of anthropoid fruit foraging adaptations in light of the sensory and mechanical properties of anthropoid-consumed fruits in Kibale National Park, Uganda. We quantify the color, odor, size, and puncture resistance of fruits in Kibale that are consumed by anthropoid primates ($N = 44$) and compare these with the same traits of fruits that are not consumed by anthropoid primates ($N = 24$). Contrary to extant hypotheses, color and odor of anthropoid-consumed fruits do not differ from non-anthropoid-consumed fruits. However, we find that anthropoids in this system consume fruits that are significantly larger than non-anthropoid-consumed fruits, and with the exception of elephants that consume very large fruits, are the only dispersers of fruits with a surface area $<4032 \text{ mm}^2$, and a maximum diameter of 52 mm. While our findings do not support most extant hypotheses for the evolution of derived anthropoid primate traits as adaptations to ripe fruit foraging, we find some evidence to support the hypothesis that spatulate incisors may be an adaptation to foraging on large fruits, which tend to be harder.

Keywords Anthropoid evolution · Color vision · Frugivory · Olfaction · Puncture resistance · Spatulate incisor

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Introduction

Several derived features of anthropoid primates are hypothesized to be adaptations to foraging on plant foods, and characteristics of fossil primates are routinely employed to infer the feeding ecology of extinct species (Lucas *et al.* 2008; Williams *et al.* 2010). Adaptations to ripe fruit foraging and feeding have been invoked to explain myriad anthropoid traits, including aspects of skeletal morphology (Fleagle 1984; Venkataraman *et al.* 2013), dental morphology (Eaglen 1984; Hylander 1975; Kay 1975), sensory traits (Regan *et al.* 2001; Sumner and Mollon 2000a,b), and cognitive abilities (Janmaat *et al.* 2016). While methodologically and theoretically diverse, these studies hinge on the importance of fruit traits in driving a subset of derived anthropoid features, with implications for hominin evolution.

Of the putative anthropoid adaptations to frugivory, perhaps the best researched is the evolution of trichromatic color vision (Osorio and Vorobyev 1996; Regan *et al.* 2001; Valenta *et al.* 2018). While diurnal anthropoid color vision phenotypes are diverse, all diverge from the mammalian pattern of routine dichromacy—the presence of only two cone types (Jacobs 2008). Extant catarrhines possess three cone types (routine trichromacy), each maximally sensitive to different wavelengths of light (Jacobs 2008). Platyrrhines, with the exception of species of the genus *Alouatta*, which are routinely trichromatic, possess only two cone types, though an X chromosome-linked polymorphism permits trichromacy in polymorphic females of these species (Jacobs *et al.* 1996). Hypotheses for the selective force underlying the evolution of anthropoid trichromacy—both routine and polymorphic—have centered on its adaptiveness to ripe fruit foraging (Melin *et al.* 2017; Osorio and Vorobyev 1996; Sumner and Mollon 2000a, b;), though evidence for trichromacy as an adaptation to folivory is also compelling (Dominy and Lucas 2001; Dominy *et al.* 2002, 2003).

In addition to color vision, some aspects of anthropoid dentition have also been identified as ripe fruit foraging adaptations (Hylander 1975), in particular, the evolution of “spatulate” incisors. A derived feature of anthropoid primates, spatulate incisors are thought to aid in the removal of thick fruit husks by allowing anthropoid primates to control breaks in the husk–pulp interface (Lucas *et al.* 2008). A corollary argument is that the utility of incisors to achieve fruit peeling would be aided by greater mesiodistal breadth, though comparative examination of frugivore and folivore incisor morphology in platyrrhines and catarrhines has yielded conflicting results (Eaglen 1984; Hylander 1975).

The evolution of olfactory receptor gene repertoires of anthropoids has also been interpreted in light of frugivory. Relative to other mammals, many anthropoids show greatly reduced olfactory receptor gene function, though this reduction is particularly marked in catarrhines (Nei *et al.* 2008; Niimura and Nei 2007; Niimura *et al.* 2018; Rouquier *et al.* 2000). A recent genomic analysis revealed that the highest rate of olfactory receptor gene loss occurred at the ancestral branch of folivorous colobines, which the authors infer may have resulted from reduced selective pressure on olfactory discrimination resulting from a dietary transition from frugivory, in which odor information may be more essential (Niimura *et al.* 2018). Behavioral data corroborate the notion that folivores rely less on olfaction during foraging than do frugivores, as does the fact that the main olfactory bulb—the first station of olfactory processing in the brain—tends to be smaller relative to overall brain size in folivorous primates (Nevo

and Heymann 2015). Physiological studies of three frugivorous anthropoid species (spider monkeys, *Ateles geoffroyi*; squirrel monkeys, *Saimiri sciureus*; pigtail macaques, *Macaca nemestrina*) have also found both high olfactory sensitivity and discrimination capacity for volatile organic compounds that are common in ripe fruits (e.g., aliphatic esters, alcohols, aldehydes, aliphatic acids, and terpenoids), as well as mixtures mimicking ripe fruit scent (Laska and Hernandez Salazar 2015; Nevo and Valenta 2018). Thus, the main olfactory system of anthropoids can be useful in the context of frugivory, and mounting evidence suggests selection to fulfill this function (Nevo *et al.* 2015; Nevo and Valenta 2018).

Here, we approach the question of anthropoid fruit foraging adaptations in light of the sensory and mechanical properties of anthropoid-consumed (AC) fruits, and fruits that are not known to be consumed by extant anthropoids (NAC) in Kibale National Park, Uganda. Our goal is to determine whether the traits of AC fruits are (1) distinct from traits of NAC fruits in the same system and (2) whether traits of AC fruits support extant hypotheses for anthropoid fruit foraging adaptations. We compare the hardness (puncture resistance), color, odor, and size of AC and NAC fruits in the same system. Extant hypotheses for the adaptiveness of trichromacy, spatulate incisors, and olfaction to frugivory predict that AC fruits should have higher color contrasts against background leaves, harder husks, and invest more in the production of volatile organic compounds (VOCs)—particularly those associated with ripe fruits—than NAC fruits. We also predict that anthropoid-consumed fruits will be larger because of the large size of anthropoids in comparison to other potential consumers, such as birds. Body size alone facilitates access to large fruits given the likelihood that fruit meso- and exocarps become absolutely thicker with increased fruit volume. Such coatings are efficiently breached with the functional combination of large gape, spatulate incisors and absolutely large incisal bite forces. There is no requirement that the entire fruit mass be ingested for processing, in contrast to the situation for birds.

Another potential strategy for maintaining structural integrity of fruit is to alter mechanical properties of the exo- and/or mesocarps rather than their thickness. In such cases, one might predict scaling of one or more variables with fruit mass or volume, such as stiffness (elastic modulus), toughness, or hardness. Of course, it is also possible that the problem imposed by the scaling of mass to surface area could be resolved by a combination of structural and material compensation, in which case no positive correlation between fruit mass and fruit hardness will be observed.

Methods

The study took place in Kibale National Park, which sits near the foothills of the Rwenzori Mountains in southwestern Uganda covering 79,500 ha at 0°13′–0°41′N and 30°19′–30°32′E (Chapman and Lambert 2000; Chapman *et al.* 1994). The area is an evergreen, mid-altitude (1500 m) forest. Rainfall varies bimodally during the year, with an annual average of 1680 mm between 1990 and 2015 (CAC, *unpubl. data*). The mean annual temperature ranges between 19.1 and 21.4°C. The Kanyawara and Sebitoli research areas are home to six diurnal nonhuman anthropoid species that are known to consume ripe fruits and disperse seeds intact: common chimpanzees (*Pan troglodytes*), graycheeked mangabeys (*Lophocebus albigena*), red-tailed guenons

(*Cercopithecus ascanius*), blue monkeys (*Cercopithecus mitis*), l'Hoest's monkeys (*Cercopithecus lhoesti*), and olive baboons (*Papio hamadryas anubis*) (Onderdonk and Chapman 2000).

We opportunistically collected ripe fruits of fleshy, zoochoric species and mature leaves from the area of the Kanyawara and Sebitoli Research Stations in Kibale National Park January 2015–May 2017. We took between 5 and 10 ripe fruit samples and mature leaves of each species to the field laboratory and analyzed them within 4 h of collection. We collected fruits and leaves from the same individual plant. We measured fruit size in three dimensions using sliding calipers, and calculated fruit surface area and volume for each fruit using the formula for calculating the surface area of an ovoid (Thomsen and Michon 2004). This necessarily assumes a regular geometry in the estimation of volume and entails an unknown but likely acceptably small error given the large range of fruit sizes sampled. Because we measured diameters independently in three mutually perpendicular planes, and because none of the fruits exhibited reentrant surfaces that comprised a significant fraction of the measured dimensions, the method used was reasonably accurate for our purposes. We measured fruit puncture resistance using a modified force gauge (Shimpo MF 50) inserted into fruit exocarps at a 90° angle. We recorded the mean force in pounds (to a maximum of 50 lbs) required to puncture fruit exocarp for between 5 and 10 ripe fruits of each species, and calculated hardness values to represent kilograms of force per square millimeter after (Valenta et al. 2015).

We measured fruit and leaf color using a Jaz portable spectrometer, relative to a Spectralon white reflectance standard (Ocean Optics). To quantify whether the ripe fruit was chromatically distinct from the background of mature leaves (upper side) to anthropoids, we used Just Noticeable Difference (JND) modeling for the visual system of the common chimpanzee (*Pan troglodytes*), as this is likely shared by the monkeys in our system (Osorio et al. 2004). It is possible that in some cases, primates (e.g., baboons) assess fruit species from below the canopy, and that the difference between leaf undersides and fruits might be more relevant in these cases. However, since most of the anthropoids in this system are arboreal, or at least partially arboreal, we elected to calculate JND values based on fruits' contrast against the upper surface of leaves. We defined a fruit as chromatically distinguishable if it differed by at least 1 JND from leaves, which is the minimum chromatic distance at which two objects can be differentiated by a given visual system. A caveat of this approach is that it is based on human performance under conditions of ideal lighting; objects with increasingly higher JND scores are presumed to be visible under deteriorating (darker) conditions (Osorio et al. 2004).

Chimpanzees have three distinct photopigments, short-wavelength sensitive (S, λ_{\max} 420), mid-wavelength sensitive (M, λ_{\max} 430), and long-wavelength sensitive (L, λ_{\max} 560). First, we estimated for each target (ripe fruit) and background (mature leaves) the chromaticity by calculating the quantum catch of each photoreceptor (Eq. 1):

$$Q_i = \int_{400}^{700} R(\lambda) I(\lambda) S_i(\lambda) d\lambda \quad (1)$$

The quantum catch (Q) for photoreceptor “i” (S, M, or L cone) is calculated by summing for each wavelength (λ) within the range of the chimpanzee visual system

(400–700 nm), the product of an object's reflectance $R(\lambda)$, by the irradiance spectrum $I(\lambda)$, and the spectral sensitivity of the photoreceptor $S_i(\lambda)$. For spectrum $I(\lambda)$, we used an absolute irradiance spectrum measured under forest shade (Hiramatsu *et al.* 2008). We then calculated the chromatic distance between each ripe fruit and each background leaf of the same species. We defined the contrast for each cone channel as $\Delta f_i = |\ln(Q_i^F) - \ln(Q_i^B)|$, where Q_i^F and Q_i^B denote the quantum catches of the receptor "i" for fruit and background, respectively (Vorobyev *et al.* 1998, 2001). Finally, to calculate JND we followed the "dim-light" model of Osorio *et al.* (2004).

We sampled fruit odor using a dynamic headspace procedure. We placed 2–10 ripe fruits of each species in plastic oven bags (Reynold's large oven bags). We drew emitted VOCs onto a sorbent probe containing two XAD traps (Amberlite XAD-2, 200–400 mg, Sigma-Aldrich) at 1 L/min for 4 h using a pump. We filtered incoming air using activated carbon. We extracted VOCs from the probes using 3 ml of *n*-hexane (Sigma-Aldrich) and gently shaking them for 5 min. We mixed 190 μ l of the extract with 10 μ l of an internal standard solution (*n*-heptadecane; 200 ng/ml) and then concentrated the solution to 20 μ l using a gentle nitrogen stream.

We analyzed samples using an Agilent 7890B gas chromatograph equipped with a DB144 5 column (Agilent; 30 m \times 0.25 mm \times 0.25 μ m) and coupled with an Agilent 5977A inert mass spectrometer operating in electron ionization (EI) mode. We injected 2 μ l of each sample using a cold injection system. The starting inlet temperature was 10°C. We then heated the inlet at a rate of 12°C/min until it reached 300°C and then held for 4 min at this temperature. Then, we opened the split valve. Initial oven temperature was 45°C. Carrier gas was helium at a constant flow rate of 1 ml/min. The oven program consisted of an initial hold at 45°C for 1 min, followed by a 7°C/min ramp to 310°C and then a 15-min hold on this temperature. We held the transfer line temperature at 250°C. We monitored analytes in full scan mode using a selected mass range of 40–300 Da. We analyzed samples on Amdis 2.71. We identified and removed contaminants identified by analyzing control samples (empty oven bags) using the same procedure, as well as the solvent used for extraction. We identified VOCs based on their retention indices and the NIST 11 mass spectra library. We determined total VOC emission intensity for each fruit species by extracting overall VOC peaks and summing the area under the gas chromatography-mass spectrometry (GC-MS) chromatograms. In each case, we divided total VOC emission based on the surface area and the number of fruits sampled. To determine whether qualitative odorant classes, as opposed to overall odor emissions, were important in predicting whether or not a fruit is consumed by anthropoids, we additionally pooled odorants to five classes: esters/alcohols/carboxylic acids/ethers, ketones/aldehydes, aromatic compounds, terpenoids, and other hydrocarbons. We opted for a more functional (and less biosynthetic) classification because the study focuses on animal preference rather than plant evolution. We calculated the relative amount of each VOC class in the odor profile of each plant species by dividing its amount by the sum of the seven VOC classes.

We identified fruits as AC or NAC based on published literature and 20 years of researcher records maintained by CAC in Kanyawara, and field assistant knowledge of chimpanzee fruit consumption at the Sebitoli research site. In most cases, fruits were consumed by a subset of the six frugivorous species; however, because our goal was to understand anthropoid adaptations to fruit traits, and not species-specific responses, we defined all fruits as either consumed by anthropoids or not known to be consumed by

anthropoids. In all cases of NAC fruits, birds are known dispersers of these fruits (Electronic Supplementary Material [ESM] Table SI). However, because of the potential for NAC fruits to also be dispersed by myriad other taxa, including elephants, terrestrial mammals, bats, amphibians, and reptiles, we do not suggest that NAC fruits are necessarily bird adapted.

We compared all trait values of AC and NAC fruits using a Mann–Whitney U test for each variable. We chose a nonparametric model, as sample sizes are unequal and results were not normally distributed (Shapiro–Wilks values <0.05). We conducted a series of bivariate analyses and not a single multivariate analysis because our primary goal was not to identify differences between AC and NAC in a multivariate space, but rather to test individual hypotheses regarding several anthropoid adaptations. We additionally calculated a Pearson’s product moment correlation to test for correlation between fruit size and fruit puncture resistance, after removing outliers. Analyses were completed in R (CoreTeam, 2014). All P -values are two-tailed.

Ethical Note

All research complied with the laws of the Government of Uganda and the Uganda Wildlife Authority (Permit #EC 361). All authors declare that they have no conflict of interest.

Data Availability All data generated or analyzed during this study are included in this published article.

Results

In total, we sampled ripe fruit traits of 68 species. Of these, 24 species are not known to be consumed by anthropoids (NAC), and the remaining 44 species are consumed by anthropoids (AC) while ripe (ESM Table SI).

Overall, 79% of both AC species (31 of 39) and NAC species (15 of 19) for which reflectance data were available had JND values >1 , and the difference between the two groups is not significant (Mann–Whitney: $W = 361$, $P = 0.87$). The puncture resistance of AC fruits (median = 0.1164 kg/mm^2) is slightly higher than the puncture resistance of NAC fruits (median = 0.0835 kg/mm^2), but the difference is not significant (Mann–Whitney: $W = 483.5$, $P = 0.43$).

None of the qualitative or quantitative measures of fruit odor differed significantly between AC and NAC fruits. Overall median surface-area-scaled odor was slightly higher in AC fruits (median = 0.005) than in NAC fruits (median = 0.002), but the difference was not significant (Mann–Whitney: $W = 504$, $P = 0.67$). Median differences in qualitative odor categories were also not significantly different: esters/alcohols/carboxylic acids/ethers (Mann–Whitney: $W = 394$, $P = 0.27$), aromatic compounds ($W = 490.5$, $P = 0.81$), ketones/aldehydes ($W = 556$, $P = 0.15$), terpenoids ($W = 556.5$, $P = 0.25$), and other hydrocarbons ($W = 432.5$, $P = 0.58$).

The only significant difference between AC and NAC species is fruit surface area. AC fruits (median = 623.98 mm^2) have significantly higher surface area than NAC

fruits (median = 220.96 mm², Mann–Whitney: $W = 343$, $P = 0.03$), and aside from elephants, anthropoids are the only animals in this system that consume fruits with a surface area >4032 mm², and a maximum diameter of 52 mm. Additionally, removing the three exclusively elephant-consumed species, we found that fruit volume is positively correlated with fruit puncture resistance (Pearson's: $r = 0.46$, $P < 0.01$, Fig. 1).

Discussion

While the anthropoid primates in Kibale National Park, Uganda, feed on only a subset of available fruits, there are no differences in the properties of these fruits across any of the fruit traits measured here, with the exception of fruit size: anthropoid primates feed on larger fruits, and with the exception of elephants, are the only animals known in this system to feed on fruits with a surface area >4032 mm² (Fig. 1). These findings contradict several hypotheses that identify fruit foraging and feeding as selective loci for several anthropoid sensory traits. However, the finding that anthropoids feed on larger fruits and fruits above a certain size threshold indicates the potential importance of fruit size, anthropoid gape width, and the utility of spatulate incisors during large-fruit feeding.

Spatulate incisors have been considered a key anthropoid adaptation linked to the exploitation of a frugivorous niche (Williams *et al.* 2010). However, previous analyses of the feeding ecology of four species of Sumatran primates found that incisor size was not correlated with either degree of frugivory or degree of incisor use (Ungar 1995). Similarly, a previous examination of incisor breadth in great apes found no major differences between folivorous western lowland gorillas and frugivorous chimpanzees (McCollum 2007). Our results are consistent with these findings.

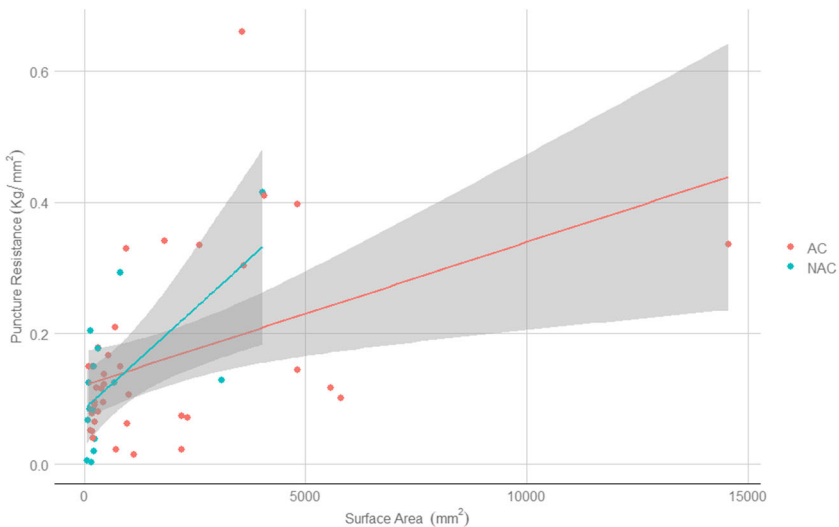


Fig. 1 The surface area and puncture resistance of non-anthropoid-consumed (NAC) and anthropoid-consumed (AC) fruits, excluding elephant-obligate species (Pearson's: $r = 0.46$, $P < 0.01$), collected from Kanyawara and Sebitoli Research Stations in Kibale National Park, January 2015–May 2017. The shaded areas represent 95% confidence intervals

Alternatively, our results may indicate that the evolution of spatulate incisors was driven by some aspect of food mechanical properties other than puncture resistance. For example, Lucas *et al.* (2008) suggest that broad incisors may have been selected during anthropoid evolution to increase the rate of large fruit husk removal. Because feeding time increases with dietary toughness (Coiner-Collier *et al.* 2016), fracture toughness may therefore be the most relevant property when considering the evolution of broad and spatulate incisors. Indeed, access to exceedingly tough fallback foods may have been a key evolutionary strategy that influenced craniodental evolution in frugivorous platyrrhines (Wright 2005; Wright *et al.* 2009).

While the overall odor and relative amounts of odor categories do not differ between AC and NAC fruits, this does not preclude the potential importance of odor in anthropoid fruit selection. Behavioral studies have demonstrated that both anthropoid and strepsirrhine primates use fruit scent for fruit selection (Hiramatsu *et al.* 2009; Nevo *et al.* 2015, 2018; Valenta *et al.* 2015). Fruit scent includes compounds which serve other functions such as defense (Nevo *et al.* 2017), and crucially, the attractants often belong to chemical classes such as terpenoids, whose members can fulfill other functions (Nevo *et al.* 2015, 2018). It has been suggested that the relevant olfactory signal is the chemical difference between ripe and unripe fruits (Nevo and Valenta 2018; Nevo *et al.* 2016, 2018). Thus, it is possible that while ripe AC fruits are not distinguishable from ripe NAC fruits in the broad categories examined here, a combination of greater shift in chemical profile from unripe fruits and increased sensitivity among anthropoids to these compounds would render fruit scent informative for anthropoids. High sensitivity to specific compounds is well documented in flower-pollinator mutualisms (Schiestl and Dötterl 2012), and relatively less well known in fruit–frugivore mutualisms, though this likely results at least partially from the relative novelty of chemical applications in studies of frugivory (Valenta *et al.* 2017). Further research into fruit odorants may yield new insights into the relative importance of specific odorant compounds—either attractants or deterrents—in anthropoid fruit selection and consumption.

The lack of concordance between anthropoid-consumed fruits and fruit properties may also reflect other characteristics of anthropoids, namely dietary flexibility and social learning. Previous studies of wild anthropoid diets have documented remarkable dietary flexibility, even within species (Chapman *et al.* 2004; Lambert 2004; Soligo and Smaers 2016). As well, anthropoids have demonstrated an ability to learn to both manipulate and consume novel food items (Lefebvre 1995; Pal *et al.* 2018; Visalberghi and Fragaszy 1990).

It is also possible that anthropoids in this system choose fruits based on traits not measured here. For example, a previous study of chimpanzees in Uganda documented a positive, linear relationship between fruit availability and chimpanzee fruit consumption (Kagoro-Rugunda and Hashimoto 2015). The link between fruit phenology and species-specific fruit consumption has also been observed in other mammalian and bird species (Fredriksson and Wich 2006; Noma and Yumoto 1997). Variation in nutritional content has also been proposed as an important predictor of fruit choice and consumption in multiple species (Felton *et al.* 2009; Matsumoto-Oda and Hayashi 1999; Moermond and Denslow 1985; Norconk and Conklin 2004; Stevenson 2004), as has taste (Nicklasson *et al.* 2017; Rowland *et al.* 2015; Simmen and Charlot 2003; Sorensen 1983). While quantifying fruit availability, nutrition, and taste were beyond the scope of the current study, it is

possible that anthropoids in this system choose fruits based on one or more of these variables. However, if these additional variables—and not color, odor, or hardness—drive variation in anthropoid fruit selection, extant hypotheses for anthropoid adaptations to frugivory are not supported by our results.

The hypothesis that exploitation of large fruits underlies anthropoid foraging and feeding strategies deserves additional scrutiny. Our data indicate that while larger fruits have harder husks (Fig. 1), anthropoids do not eat harder fruits overall. The correlation between fruit hardness and fruit volume may indicate that fruit hardness—or a mechanical property that covaries positively with it—represents a functional response to fruit volume. The logic here is that scaling of volume in larger fruits means that these fruits must increase husk thickness, hardness, or toughness to contain the pulp mass within. We measured only one of these variables (hardness, estimated by puncture resistance) here. Puncture resistance is a fairly coarse proxy for hardness, especially when compared to conventional indentation tests where load and surface conditions are more carefully controlled. In turn, hardness may have a predictable relationship with elastic modulus (i.e., material stiffness) for particular biomaterials [e.g., bone (Rapoff *et al.* 2008)], but across a class of materials such as fruit husks, this relationship is largely unexplored. Puncture resistance might be informative about the strength of fruit husks in an allometric context, but given the heterogeneity and anisotropy inherent to fruit, hardness is as much a product of particular testing conditions as it is a reliable predictor of other properties (Berthume 2016).

Regardless of scaling of husk thickness or strength, the apparent biological role of spatulate incisors is that they are useful for peeling husks away efficiently in large fruits (Hylander 1975). They are not particularly useful for penetrating hard or tough husks because their large surface area distributes the load such that the stress imparted to the fruit is relatively low: this is suboptimal for inducing plastic deformation (solving the hardness problem) or for propagating cracks (solving the toughness problem). There is no obvious advantage of spatulate incisors for ingesting small fruits.

Overall, the results of our study do not support hypotheses that posit that ripe fruit foraging drives selection for several derived features of anthropoid primates (Lucas *et al.* 2008), though future research into anthropoid and fruit phenotypes in other systems may yield this support. Further studies of the utility of derived anthropoid features—including color vision and spatulate incisors—would also do well to evaluate other possible selective forces, for example, the role of derived anthropoid traits in the detection of young leaves (Dominy and Lucas 2001), invertebrate prey (Melin *et al.* 2007), or fallback foods (Wright *et al.* 2009). Additionally, future studies that focus on the interaction between fruit size, and different metrics of fruit husk hardness and toughness are warranted to establish the spectrum of spatulate incisor utility.

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Author Contributions KV designed the study, collected, and analyzed data, and wrote the manuscript. ON, JL, UK, SB, PO, MA, CAC, RK, and BW contributed data and wrote the manuscript. DJD and DS analyzed data and wrote the manuscript.

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