Binturong (Arctictis binturong) and Kinkajou (Potos flavus) Digestive Strategy: Implications for Interpreting Frugivory in Carnivora and Primates

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Abstract

Exclusive frugivory is rare. As a food resource, fruit is temporally and spatially patchy, low in protein, and variable in terms of energy yield from different carbohydrate types. Here, we evaluate the digestive physiology of two frugivorous Carnivora species (Potos flavus, Arctictis binturong) that converge with primates in a diversity of ecological and anatomical traits related to fruit consumption. We conducted feeding trials to determine mean digestive retention times (MRT) on captive animals at the Carnivore Preservation Trust (now Carolina Tiger Rescue), Pittsboro, NC. Fecal samples were collected on study subjects for in vitro analysis to determine methane, pH, and short chain fatty acid profiles; fiber was assayed using standard neutral detergent (NDF) and acid detergent (ADF) fiber methods. Results indicate that both carnivoran species have rapid digestive passage for mammals that consume a predominantly plant-based diet: A. binturong MRT = 6.5 hrs (0.3); P. flavus MRT = 2.5 hrs (1.6). In vitro experiments revealed no fermentation of structural polysaccharides – methane levels did not shift from 0 h to either 24 or 48 hours and no short chain fatty acids were detected. In both species, however, pH declined from one incubation period to another suggesting acidification and bacterial activity of microbes using soluble carbohydrates. A comparison with primates indicates that the study species are most similar in digestive retention times to Ateles – the most frugivorous anthropoid primate taxon.

Introduction

Most specialist mammalian frugivores are found in the tropics where fruit is more likely to be available year-round compared to regions with more extreme seasons. Exclusive frugivory is rare even in the tropics, however, as fruit is a temporally and spatially patchy resource, generally low in protein (<1% N or <6% crude protein dry mass), and variable in terms of energy yield from carbohydrates [1–4]. Thus, while often described as a “high-quality” food [5–7], fruit is not without its limitations and frugivorous mammals must have adaptations for balancing macronutrient intake, modulating physiology to offset deficiencies, or switching foods altogether to cope with limiting availability and nutrient density [8–17]. While some adaptations for offsetting deficiencies or switching foods can be constrained by a species’ phylogeny and anatomical bauplane [18], others, particularly digestive, are more plastic [19,20]. Among arboreal (non-voIant) placental mammals, only a few carnivorans (e.g., procyonid, viverrid) and some primate species (e.g., Ateles, Pan) come close to exhibiting almost exclusive frugivory [1,13,21–24]. Recent macronutrient analyses have demonstrated that highly frugivorous primate species (e.g., Ateles spp) target ideal protein to energy ratios by maintaining a fairly constant protein intake as measured by dietary nitrogen; N) while allowing non-protein energy (carbohydrates + lipids) to vary as a function of nutritional composition of available foods [13,14]. Other highly frugivorous mammal species (e.g., didelphid marsupials, pteropodid bats) maintain nitrogen balance by increasing total fruit intake (thereby increasing total dietary N intake) and decreasing retention times [3,23]. However, increasing intake is done at the expense of digestive efficiency – i.e., extraction and uptake of macronutrients, especially carbohydrates. Moreover, rapid through-put can result in a “washing out” phenomenon in which endogenous (non-diet) protein sources such as gut epithelial cells, enzyme products, and bacterial cells are defecated and lost [23,25,26]. Hence, if nitrogen is limited in availability, rapid digestive passage is predicted as it facilitates higher intake of low N foods. However, the type of carbohydrates consumed by an animal – and how efficiently energy is extracted and utilized – will limit just how fast digestive passage can be.

Consumers utilizing monosaccharides (such as highly frugivorous birds) tend to have high intake and rapid digestive passage [8,20,27]. The longest digestive retention times in mammals are found in herbivores that rely on either fore- or hindgut microbial fermentation of polysaccharides, but even catalytic digesters that consume less refractory, shorter-chain carbohydrate molecules...
Digestion in Arctictis binturong and Potos flavus

Methods

Ethics Statement

The research was reviewed and approved by the University of Texas at San Antonio Institutional Animal Care and Use Committee (IACUC protocol #MS005). The laboratory in which all fermentation experiments occurred was inspected and approved by the Biosafety Committee of Environmental Health and Safety Division (BC – EH&S) at North Carolina State University (NCSU). The NCSU BC - EH&S certified that the laboratory met their stated safety criteria and that all personnel involved were trained in appropriate microbiological techniques and laboratory safety procedures.

Study subjects and their husbandry

We studied the digestive retention times (15 trials) and in vitro fermentation profiles (16 experiments) of two P. flavus and four A. binturong September 2008 – March 2010. All animals were housed at the non-profit institution Carnivore Preservation Trust (CPT) in Pittsboro, North Carolina (now known as Carolina Tiger Rescue). Only two P. flavus (one male, one female) were available for study (male: 17.9 yrs, 3.9 kg; female: 22 yrs, 4.6 kg). Of the 12 A. binturong housed at CPT, 4 (all male) were chosen for study based on health status and similarity in age (X age: 13.75 yrs, range: 12.7–15.6 yrs) and weight (X weight: 18.9 kg, range: 16.4–23 kg). The two P. flavus were housed individually in indoor enclosures measuring 3.6 × 2.1 × 3.1 m at an average ambient temperature of 23.3–26.6°C and under a 12L:12D light regime. The four A. binturong were housed individually in large (3.5 × 3 × 4.5 m) outdoor enclosures with sleep boxes; because they were outside, day length and temperature varied across the four trial periods (e.g., 75 minute difference between September and March). All animals were fed standardized diets to which they were habituated for three days prior to each digestive retention and in vitro fermentation profile trial period (Table 1). The diet was based on regular zoo diet to avoid disruption of normal feeding routine.

Digestive retention trials

The digestive retention trials involved feeding (at 1730 h) each study subject ten markers (each marker: 4 × 2 × 1 mm) concealed in a banana, following methods described by Lambert [42,43] and replicated by several authors [44,45]. Each individual was assigned its own marker color per trial, and the duration of time between marker ingestion and marker defecation was measured. Marker size was chosen based on the naturalistic observations of size of seeds swallowed by wild arboreal, frugivorous mammals in Africa and Asia [39,46]. The markers were made of Pepperell Plastic Craft Cord - an inert, non-toxic plastic material known commonly as Gimp that has been approved by the Food and Drug Administration for use by young children.

We undertook four digestive passage trials on the male P. flavus, and four on the female. We conducted one digestive trial on two of the four male A. binturong; on male 3 we conducted two trials and on male 4 we conducted three trials.

After the animals consumed the marker-loaded bananas, the study subjects were fed their normal daily ration. We monitored all defecations until the markers were recovered, then screened all fecal material to determine whether the sample contained colored markers. Defecated markers were highly visible and readily identified and quantified. We recorded the time of defecation, the number and color(s) of markers per fecal sample, and assessed mean retention time of markers (MRT). MRT is the best estimate of digesta movement through mammalian gastrointestinal tracts [47], and is a measure of the average time of retention of all elements of the focal digesta (in this case, colored markers). MRT is calculated as the following in which \( m_i \) = the number of markers excreted at the \( i \)th defecation at time \( t_i \), after dosing:
Sample collection and laboratory analysis of in vitro bacterial fermentation profiles

We evaluated bacterial fermentation using standard in vitro methods on fecal samples collected from study subjects collected December 2008 – February 2010. A preliminary experiment (December 2008) in which only methane was analyzed indicated no fermentation activity; this initial run was terminated and the decision made to run three further experiments. Availability of staff and enclosure locations meant that we could not monitor all study subjects simultaneously. We were thus unable to collect sufficient fecal samples for A. binturong in the subsequent three experiments; we also only had sufficient fecal inoculum to undertake gas chromatography on culture samples at two time periods for each experiment (i.e., rather than three). After the preliminary experiment, we ultimately ran 3 P. flavus and 1 A. binturong in vitro experiments. The P. flavus analysis from the March 2009 collection was incubated for 0 and 48 h, and the September 2009 for 0 and 24 h. In the February 2010 binturong and P. flavus analysis, there was only enough fecal substrate to incubate for a 24 h period.

Following previously described methods [48,49], we used controlled anaerobic methods to minimize exposure to air during fecal sample collection, transportation, manipulation, and maintenance. However, we cannot rule out that some aerobic exposure occurred, thereby lowering the reduction-oxidation potential of samples. Nonetheless, we have successfully employed these methods in previous experiments [49] and note, too, that anaerobic bacteria can have some ability to thrive after minimal oxygen exposure [50].

We used a sample of standardized diet of plant material and extruded food pellets to provide an appropriate growth medium in the fermentation tubes (Table 1). Samples were processed immediately upon arrival to the laboratory and within one hour of collection. Gas chromatography was undertaken for the by-products of bacterial fermentation of polysaccharides: short-chain fatty acids (SCFA) and methane; pH was also measured.

To monitor fermentation profiles, we used a batch system in which fecal inoculum was prepared to inoculate culture bottles [51,52]. We replicated the methods we used previously for primates [49], with one exception: due to insufficient fecal sample quantity, the dilution of inoculum for P. flavus was 1:6.5 instead of 1:5. Following incubation, gas samples were withdrawn and analyzed for methane by gas chromatography. A pH measurement was taken following methane analysis, and 4-mL aliquots of unstirred fluid were sampled from each bottle and prepared for SCFA analysis.

Dry matter (DM) was determined following protocol outlined by the Association of Official Analytical Chemists (AOAC, method 945.15) [53]. Neutral detergent fiber (NDF) and acid detergent fiber (ADF; determined sequentially to NDF) were calculated according to the method of Van Soest and colleagues [54] using the Ankom 200 fiber apparatus (ANKOM Technology Corporation, Fairport, NY). Disappearance of DM, NDF and ADF was calculated using data from culture bottles at 0 and 24 or 48 h incubation periods.

Results

Digestive Passage Trials

The subjects readily consumed the marker-dosed bananas. All study subjects reached for the bananas manually and then immediately ingested them. The total recovery rate of markers swallowed by P. flavus was 97.5% (78/80), and by A. binturong was 91.4% (64/70). The fate of the unrecovered markers is not
clear. Although unlikely, it is possible that the markers were overlooked in the fecal sample screening process or that they were spat out by the animals, but not found on the enclosure floor. It is also possible that the markers adhered to intestinal villi and were not detected with the other markers. A lack of 100% recovery of markers is common in mammal digestion trials [47,55].

The mean retention time (MRT) of markers in A. binturong was 6.5 h (SD 0.3; range 3.3–9.5 h) and in P. flavus 2.5 h (SD 1.6; range 0.7–5.6 h). Defecation patterns of markers were consistent with the short digestive passage times in the two species: markers were defecated in either one (84/142, 59.2%) or two (58/142, 40.8%) fecal samples.

Fermentation Parameters

As with the preliminary experiment for methane detection (see Table S1), we found no evidence of bacterial fermentation activity in any of the in vitro fermentation experiments; culture samples were processed and run on gas chromatography at 0 h, 24 h, and 48 h (depending on experiment), but no peaks were detected for any short chain fatty acid (acetate, propionate, isobutyrate, butyrate, isovalerate, valerate) (Table 2).

In the March 2009 P. flavus analysis, methane was similar at both 0 and 48 hours (24.56 versus 24.54 nmol/ml). In the September 2009 P. flavus experiment, methane levels decreased (23.70 versus 17.81 nmol/ml). In the February 2010 experiment on P. flavus and A. binturong, methane levels for both species were similar to the blanks (P. flavus versus blank: 26.35, 24.20 nmol/ml; A. binturong versus blank: 21.28, 20.47 nmol/ml).

In all three experiments, for both species, pH level decreased from the start of the trial to either the 24 h or 48 hour time periods. In the March 2009 P. flavus analysis, pH declined from 6.8 at 0 h to 4.48 at 48 h. The September 2009 P. flavus experiment revealed a similar pattern: 7.87 at 0 h to 3.92 at 24 h. For the February 2010 experiment, comparisons between the blank and the fecal inoculum are consistent with this acidification: pH for the P. flavus blank at 24 h is 6.73 compared to 4.50, while the A. binturong blank at 24 h is 6.5 compared to 4.33.

The diet of A. binturong comprised 17.5% NDF and 6.7% ADF, and of P. flavus 11.9% NDF and 3.1% ADF. P. flavus fecal fiber comprised 35.8% NDF and 13.8% ADF. In vitro DM disappearance (IVDMD) and fiber disappearance are indicative of the amount of substrate used by microbes during fermentation. Across all experiments, at 0 h the IVDMD values ranged from 54.6–58.6%. Incubation of fecal cultures from either species, irrespective of incubation times (i.e., 24 h or 48 h) resulted in similar DM and fiber disappearance. In estimating dry matter disappearance, the soluble components are not accounted for in the analysis. The absence of DM or fiber disappearance is consistent with the lack of fermentation reported in all experiments.

Discussion

Important caveats need to be noted regarding methods and research design. Unquestionably, our sample sizes are small; this was unavoidable because of the scarcity of the study species in captivity and difficulties of fecal sample collection. In addition, captive mammals can have decreased intestinal wall area and are less active than wild animals – both differences in gut area and energy expenditure can influence retention times [47,56–58]. In addition, because the animals were born in captivity, intestinal microbial communities no doubt differ from those of their wild counterparts. Indeed, previously we documented a “captivity effect” on in vitro carbohydrate fermentation in fecal samples from captive Gorilla gorilla gorilla [49]. While inherent limitations with the in vitro assay may be a potential issue (variability increases when incubation times are short), we view this as unlikely for two important reasons. First, the fermentation experiments were run on P. flavus fecal samples on three separate occasions with all experiments yielding the same result. In addition, previously we employed the same laboratory protocol and equipment on five primate species; this earlier work revealed extensive bacterial fermentation and methane production [49]. In short, it is our perspective that methodological concerns are mitigated by the facts that our research design and sample sizes are consistent with other studies [23,28,43,44,48], that no data exist on the digestive physiology of the study species (one of which is endangered: A. binturong), and that even a small data set can help substantially to clarify the influence of digestion on feeding biology [1,28,59,60].

Carnivoran solutions to the challenge of frugivory

That we found no evidence of polysaccharide fermentation was unexpected given the study species’ predominantly plant-based diets (both in the wild and captivity) and that other carnivoran species produce short chain fatty acids [29,61,62]. The digestive retention times are somewhat more in line with what we expected given their simple, carnivoran gut structure [55], but still shorter than predicted for mammals of their body mass and diet. Indeed, long passage times are certainly not precluded by carnivoran gut anatomy and can be under natural selection pressure in response to a plant-based diet; the omnivorous arctic fox (Alopex lagopus; 2.7–4.5 kg), for example, is reported to have passage times of up to 52 h [63].

The digestive passage times documented in the study animals may serve to maintain nitrogen levels by facilitating continuous and high intake of low-N plant foods, although this clearly remains to be tested. Fast passage also certainly influences patterns of carbohydrate extraction [8,9], and it is noteworthy that the pH dropped appreciably in all experiments between 0, 24, and 48 hours. These results are suggestive of the presence of bacteria that use soluble sugars and less refractory carbohydrates; Bifidobacteria spp, for example, use plant-derived fructo-oligosaccharides and thereby produce both lactic and acetic acids that acidify intestinal environments [64]. Both enzymatic digestion and microbial fermentation take time, and even catalytic digesters require sufficient time for enzyme production and nutrient transporter uptake as intestinal rates of hydrolysis and absorption is rate limiting [20]. This explains why other similarly-sized frugivorous mammals have gut passage times that, while rapid compared to hind- or foregut fermenting mammals, are still greater than 10 hours long (e.g., 16 h in Caluromys philander) [23]. The mean digestive retention times of P. flavus and A. binturong were 2.5 and 6.5 hours, respectively – considerably shorter than predicted by the retention times of the similarly-sized, sympatric, nocturnal and highly frugivorous Caluromys philander [23,37].

Such fast digestive passage can be useful for ensuring intake of nutrients in low concentration (e.g., nitrogen), but can leave a mammal of the sizes seen in the study species in a potential ‘energy crisis’ when very ripe fruit is not available in sufficient quantities to maintain high soluble carbohydrate intake. However, these shortfalls may be offset metabolically in the study species [32]. Indeed, while most Carnivora are hypermetabolic, both P. flavus and A. binturong exhibit hypometabolic adaptations [21,32,65,66]. Potos flavus has a lower basal metabolic rate and r_max values than would be predicted for its mass, lowers its body temperature while it sleeps, and shivers as it wakes up each
evening in order to return its temperature to an active level. *Arctictis binturong* is the largest endotherm with the ability to reduce their peripheral circulation so that the body becomes divided into a warm “core” and a cool “shell” by reducing thermal conductance without permitting core body temperatures to fall [32]. The reduction in metabolism is often so great at low ambient temperatures that it may be below basal rate [21,32]. Captive *A. binturong* specimens also have large subcutaneous fat deposits throughout their bodies — but especially around the base of their muscular tails (Hartstone-Rose, unpublished data). It is not clear whether this is a result of a captive diet; indeed, no anatomical description of a wild specimen of these rare animals has referred to this detail of anatomy, but we suggest that subcutaneous fat may be an energy

### Table 2. Results of in vitro experiments, including pH, methane, fiber disappearance, and short chain fatty acid (SCFA) profiles.

| In vitro variable | Potos flavus September 2009 | Potos flavus February 2010 | Potos flavus February 2010 | Arctictis binturong February 2010 |
|-------------------|-----------------------------|---------------------------|---------------------------|-------------------------------|
| pH                | 6.80 (0.1)                  | 7.87 (0.03)               | –                         | –                             |
|                   | 24 h                         | 3.92 (0.06)               | 4.50 (0.00)               | 4.33 (0.06)                   |
|                   | 48 h                         | 4.48 (0.03)               | –                         | –                             |
| pH (blank)        | 6.63 (0.04)*                | 9.23 (0.06)               | –                         | –                             |
|                   | 24 h                         | 8.43 (0.21)               | 6.73 (0.04)*              | 6.50 (0.00)*                  |
|                   | 48 h                         | 6.55 (0.07)*              | –                         | –                             |
| Methane nmol/ml   | 24.56 (3.5)                 | 23.70 (1.37)              | –                         | –                             |
|                   | 24 h                         | 17.81 (0.42)              | 26.35 (1.34)              | 21.28 (2.72)                  |
|                   | 48 h                         | 24.54 (0.35)              | –                         | –                             |
| Methane nmol/ml (blank) | 20.82 (9.74)              | 24.81 (3.02)              | –                         | –                             |
|                   | 24 h                         | 26.90 (10.35)             | 24.20 (3.75)*             | 20.47 (3.08)*                 |
|                   | 48 h                         | 25.94 (0.66)              | –                         | –                             |
| In vitro DM disappearance, % | 58.32 (1.30)              | 58.61 (2.90)              | –                         | –                             |
|                   | 24 h                         | 57.59 (6.72)              | 54.84 (4.93)              | 36.09 (1.48)                  |
|                   | 48 h                         | 54.61 (4.97)              | –                         | –                             |
| Fiber disappearance, % | NDF 0 h                | 28.16 (6.50)              | –                         | –                             |
|                   | 24 h                         | –                         | –                         | –                             |
|                   | 48 h                         | 14.22 (6.87)              | –                         | –                             |
| ADF               | 0 h                          | 25.54 (3.46)              | –                         | –                             |
|                   | 24 h                         | –                         | –                         | –                             |
|                   | 48 h                         | 28.82 (6.03)              | –                         | –                             |
| Fecal fiber, %    | NDF 0 h                     | 35.78 (1.57)              | –                         | –                             |
|                   | 24 h                         | 13.87 (0.67)              | –                         | –                             |
| Total SCFA (mM)   | None Detected               | None Detected             | None Detected             | None Detected                 |
| Individual SCFA (mM) | None Detected               | None Detected             | None Detected             | None Detected                 |
| Acetate           | None Detected               | None Detected             | None Detected             | None Detected                 |
| Propionate        | None Detected               | None Detected             | None Detected             | None Detected                 |
| Isobutyrate       | None Detected               | None Detected             | None Detected             | None Detected                 |
| Butyrate          | None Detected               | None Detected             | None Detected             | None Detected                 |
| Isovalerate       | None Detected               | None Detected             | None Detected             | None Detected                 |
| Valerate          | None Detected               | None Detected             | None Detected             | None Detected                 |

Culture samples were processed and run on gas chromatography at 0, 24, and 48 hours. Standard deviations reported in parentheses. DM = Dry Matter; NDF = Neutral detergent fiber; ADF = Acid detergent fiber; “–” = lack of data due to insufficient fecal substrate. * = n = 2 fermentation bottles due to insufficient fecal substrate, all others n = 3.

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storage adaptation that could allow A. binturong to adjust their metabolic demands in response to shifts in fruit availability.

In sum, although sample sizes are small and further research is required, we hypothesize that P. flavus and A. binturong offset limiting N in their fruit diets by maintaining high intake and rapid digestive passage, and offset limiting availability of carbohydrate energy (derived largely from monosaccharides) via metabolic shifts and subcutaneous fat deposits. These digestive and metabolic solutions indicate adaptation to diet independent of carnivoran phylogenetic inertia on gut structure.

Implications for understanding primate frugivory

Among non-volant, arboreal placental mammals, only a few species of Carnivora (e.g., Potos flavus, Arctictis binturong, Ateles geoffroyi, Nandinia binotata) and primates can have diets that are almost exclusively frugivorous – at least during some seasons. Some primate species stand out in particular – Pan spp and Ateles spp, for example, are commonly noted for their specialized frugivory and are called ripe fruit specialists [1,13,22,24,67]. A comparative understanding of digestive physiology can contribute to a more complete picture of how different taxa have adapted to high levels of fruit-consumption and manage the potential challenges of nitrogen (protein) and energy limitations. Ateles spp (spider monkeys) in this instance are particularly heuristic because of their sympathy with Potos. Kays [22], for example, has documented 100% dietary overlap in the fruits consumed by spider monkeys and P. flavus on Barro Colorado Island, Panama; he notes, too, extensive similarity in social organization and foraging behavior.

In absolute terms, Ateles spp have among the fastest digestive passage times documented in primates [1,28,42,68,69]. Data from Ateles paniscus, A. geoffroyi and A. belzebuth indicate digestive passage times (2.5–5.25 h) that are almost identical to those reported here for P. flavus and Arctictis binturong (2.5–6.5 h). This is contrast to other similarly-sized primate species (e.g., Cercopithecus spp) that have digestive passage times ranging from 38.9–48.8 [42,45]. In absolute terms, the digestive passage times of P. troglodytes are longer than those of Ateles, Potos and Arctictis [43,70]. However, after controlling for body mass differences, P. troglodytes exhibits similarly (i.e., relative to body mass) rapid digestive passage times [42,43]. Clearly, evaluations of gut passage times in mammals are complicated by the many physiological and anatomical variables that influence digestion [42,47]. However, digestive passage times to body mass ratios can provide a quick and rough means by which to evaluate digestive retention times among very differently-sized taxa [15,42]. Ateles spp (species average body mass: 7.7 kg) and P. troglodytes (species average body mass: 45.0 kg), have the lowest ratios of all primates (0.54 and 0.52, respectively) and are similar to P. flavus (0.61) and A. binturong (0.34), but different from other primate taxa (e.g., Cercopithecus spp ratios: 4.3–11.2) [42,43,45,67,69].

In the case of the two carnivorans, the energetic costs of digesting fruit so quickly may be offset metabolically. Anthropoid primates, however, are not hypometabolic, suggesting that frugivorous taxa such as Ateles spp may be particularly efficient at quickly digesting mono- and di-saccharides. Recent research also suggests that Ateles spp leverage protein intake over total daily energy intake [13]. In contrast to large-bodied, folivorous Gorilla beringei that prioritizes consumption of non-protein energy[14], Ateles chamack regulates dietary intake to maintain a consistent daily protein and energy gain [13]. Digestive retention times are consistent with these differences (G. g. gorilla: 72 h; Ateles spp: 4.2 h) [28,42,44,68,69].

Do the digestive strategies of the study species converge on strategies exhibited in similarly-sized, omnivorous/frugivorous primate species? We would argue not generally. Overall, digestive strategies among primates exhibit more flexibility in microbial fermentation, anatomy and digestive retention times than in Carnivora [11,19,42]. Thus, while P. flavus and A. binturong emphasize soluble carbohydrates and do not have the digestive efficiency to take advantage of structural polysaccharides, all primate species studied to date, regardless of gut structure or diet, exhibit high net production of short chain fatty acids from fiber fermentation [29,49,70–74]. Having the ability to access the energy yielded from soluble carbohydrates and structural polysaccharides increases feeding flexibility and total trophic niche space, even in fruit specialists such as Ateles and Pan [70]. For example, A. geoffroyi can consume a diet seasonally predominated by leaves and leaf buds, and the annual diet of highly frugivorous P. troglodytes can comprise high levels of terrestrial herbaceous vegetation during some seasons [67,73,76]. The comparative data suggest that fermentation and energy yield from short chain fatty acids facilitates dietary breadth for primates – they can handle structural polysaccharides without compromising ability to consume other carbohydrate types.

Supporting Information

Table S1 Methane concentration in culture bottles incubated with Potos flavus and Arctictis binturong feces as substrate (December 2008). This was a preliminary run and methane was the only measurement analyzed to determine presence of fermentation activity. The experiment was terminated based on the absence of any methane production at 24 h. (DOCX)

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Author Contributions

Conceived and designed the experiments: JEL, VF AH. Performed the experiments: JEL, EM VF AH. Analyzed the data: JEL, VF AH. Contributed reagents/materials/analysis tools: JEL, VF AH. Wrote the paper: JEL, VF AH.

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