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Gross intestinal morphometry and allometry in primates

Running title: Primate intestinal length

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Abstract

Although it is generally assumed that among mammals and within mammal groups, those species that rely on diets consisting of greater amounts of plant fiber have larger gastrointestinal tracts (GIT), statistical evidence for this simple claim is largely lacking. We compiled a dataset on the length of the small intestine, caecum and colon in 42 strepsirrhine, platyrrhine and catarrhine primate species, using specimens with known body mass (BM). We tested the scaling of intestine length with body mass, and whether dietary proxies (percentage of leaves and the diet quality index) were significant covariates in these scaling relationships, using two sets of models: one that did not account for the phylogenetic structure of the data, and one that did. Intestine length mainly scaled geometrically at exponents that included 0.33 in the confidence interval; Strepsirrhini exhibited particularly long caeca, while those of Catarrhini were comparatively short. Diet proxies were only significant for the colon and the total large intestine (but not for the small intestine or the caecum), and only in conventional statistics (but not when accounting for phylogeny), indicating the pattern occurred across but not within clades. Compared to terrestrial Carnivora, primates have similar small intestine lengths, but longer large intestines. The data on intestine lengths presented here corroborate recent results on GIT complexity, suggesting that diet, as currently described, does not exhaustively explain GIT anatomy within primate clades.

Keywords primate, anatomy, digestive tract, diet, phylogeny

Introduction

Of the various aspects of mammalian biology where a link between form and function has been investigated, the connection between diet and the morphology of the digestive tract has received considerable attention (Chivers and Langer, 1994). Illustrations of the digestive tracts of herbivores and carnivores make it evident that the digestive tracts of herbivores are more complex (Stevens and Hume, 1998) due to the less digestible nature of their natural diets. Though statistical evidence is lacking (Lavin, Karasov, Ives, Middleton and Garland, 2008; Smith, Parker, Kotzé and Laurin, 2017), it is usually thought that the intestines of herbivorous mammals are longer than those of carnivores (Orr, 1976). When considering gastrointestinal complexity across all eutherian mammal clades, however, there is a less clear-cut relationship between intestine morphology and diet. In particular, while complex hindguts are typically associated with (but not obligatory for) herbivores, complex stomachs are not necessarily linked with high-fiber herbivory, as evidenced by the morphology observed in whales and myomorph rodents (Langer and Clauss, 2018).

Among primates, the morphology of the gastrointestinal tract, both macro- and microscopically, has been suggested to be tightly linked to dietary ecology (Chivers and Hladik, 1980; Martin, Chivers, MacLarnon and Hladik, 1985; Lambert, 1998). Understanding aspects of the anatomy of primates' digestive systems is thought to provide information about the diet to which a particular taxon may be adapted (Ferrari and Lopes, 1995) or its dietary constraints, such as why a species may target or avoid certain food items (Lambert, 1998). Despite the value of broad anatomical comparisons across taxa, relatively few studies have taken an interspecific, phylogenetic approach to the gross anatomy of primate gastrointestinal tracts. Quantitative analyses of gut morphology frequently focus on a small range of taxa (e.g., Ferrari and Martins, 1992; Ferrari, Lopes and Krause, 1993 in callitrichines), and some studies (e.g., Hill, 1958) provide illustrations of primate gastrointestinal tracts, but do not provide measurements. The paucity of recent gross intestinal morphology research may be in part related to the fact that the proportions of different components of the gastrointestinal tract can vary intraspecifically with age (Langer, 1988) or with dietary shifts (Gross, Wang and Wunder, 1985). Nevertheless, the use of relative dimensions can provide information about the relative role of different portions of the tract in a particular subset of species (Chivers and Hladik, 1980; Caton, 1998) and can inform hypotheses about adaptations to different dietary regimes. The enlarged caecum and colon of some strepsirrhines, New World monkeys, cercopithecines, and hominoids (Hladik, Charles-Dominique, Valdebouze, Delort-Laval and Flanzy, 1971; Chivers, 1994), for example, act as fermentation chambers to aid in the digestion of plant foods.

On the other hand, it has also been recognized that gastrointestinal form alone is not sufficient to predict diet (Milton, 1987), even though general relationships between gross digestive morphology (e.g., relative gut proportions) and broad dietary categories are expected. Chivers and Hladik (1980) demonstrated an increase in the ratio of combined stomach, caecum, and colon volume to small intestine volume across a continuum of faunivores to frugivores to folivores, although there was substantial overlap between the groups. When Chivers and Hladik considered the surface area of the small intestine, however, no differences between trophic groups were evident. Notably, these analyses were performed prior to the arrival of statistical methods that account for phylogenetic non-independence. When controlling for phylogeny, Langer and Clauss (2018) did not find diet-associated differences in gut complexity among primates.

Despite these various lines of research, quantitative data on the digestive tracts of primates are scarce. In order to provide data on intestine length for a larger number of primates, we used the opportunity to take photographs of the digestive tracts of a number of specimens during dissections performed for a study on mammalian body composition

(Navarrete, van Schaik and Isler, 2011), and provide photographic evidence for the gross digestive tract morphology of 32 species. Because with any absolute measure, body size will be the main driver of the magnitude, we first investigate the allometric relationship of intestine length with body mass. Based on the general geometric relationship between a length and a volume measure, one would expect intestinal lengths to scale approximately with body mass to the power of 0.33. However, three previous data compilations – on mammals in general (Lavin et al., 2008), on mammalian carnivorans (McGrosky, Navarrete, Isler, Langer and Clauss, 2016) and on ruminants (McGrosky et al., 2019) – unexpectedly yielded higher exponents. The explanation for this phenomenon was, to our knowledge, first proposed by Woodall & Skinner (1993), who suggested that animals should evolve so that their intestinal surface retains a geometric or metabolic scaling (i.e., at an exponent between 0.67 and 0.75), but that the diameter of the intestine should scale less-than-geometrically to maintain short diffusion distances, and that hence, to compensate, intestinal length should scale more-than-geometrically. Therefore, a corresponding scaling was expected in primates as well.

As a second step, we tested whether proxies of the natural diet influenced the scaling relationships with body mass. Following broad mammalian trends and Chivers and Hladik (1980), we expect both small and large intestine length to increase along a dietary continuum from insectivores to frugivores to folivores.

Methods

During the data collection for a different study (Navarrete et al., 2011), a large number of mammalian specimens originating from various sources were dissected by AN; some additional specimens were contributed by MC. Most specimens derived from zoological collections. The specimens were either dissected directly after death or, in the majority of cases, after storage by deep-freezing and thawing. Body mass (BM) was recorded, and the gastrointestinal tracts were dissected by removing mesenteries. The intestinal tract was laid out according to common practice for anatomical documentation (Stevens and Hume, 1995), placing the intestine as a straight line without stretching, and photographs (with scale) were taken for later measurement. For measurements, the caecum served as the defining border between the small and the large intestine. Length of the different sections was determined using the polyline VOI tool of the MIPAV biomedical imaging software (version 14.0, National Institutes of Health), which facilitated tracing the length of the intestine directly on the digital photo and converting pixel length into centimeters.

For some large-sized specimens, the intestine was cut into several pieces prior to photography. Photographs of these specimens were not manipulated to create the impression of an uninterrupted intestine. The only photo manipulations included the deletion of background and, in some cases, adjustment of the brightness and color of the images and a mirroring to achieve a consistent position of the stomach.

Additional data were collected from the literature, but only if the original BMs of the specimens investigated were reported together with the length measurements; this led to the exclusion of many published intestine length measurements. When several specimens were available for a species, averages for both BM and the respective measurements were calculated; in doing so, we always ensured the averaged BM matched the averaged gut section measure.

Data on the natural diet of the investigated species, as the percentage of leaves in the overall diet (as generally the diet items most requiring microbial fermentation) and the diet quality index (to account not just for one but the range of diet items), were taken from a literature collection based on three publications (Van Woerden, van Schaik and Isler, 2010, 2014; Van Woerden, Willems, van Schaik and Isler, 2012), supplemented with additional information (for a full set of sources, see Table S1). The diet quality index represents a sum of each dietary item, multiplied by a factor that is higher for more digestible diet items (8 for insects, 5 for fruits/seeds/flowers, 3 for young leaves, 1 for mature leaves) and is weighted for the proportion of these items in the diet (Van Woerden et al. , 2010). All species-specific data are given in Table 1.

Allometric relationships were investigated using linear regressions on log-transformed data according to Length = *a* BM^b, with 95% confidence intervals for parameter estimates, for the whole dataset and for individual clades. Additionally, the same analysis was performed with clades as cofactors, and the clade x BM interactions, to directly test for differences between the clades. Proxies of the natural diet were added to the linear regressions on log-transformed data as covariates (only one proxy per model, i.e. either the percentage of leaves, or the diet quality index). Initially, models including the BM x diet proxy interaction were also included, but because there were no significant interactions, results are only presented here for models without interactions. Analyses were performed using Generalized Least Squares (GLS) and Phylogenetic Generalized Least Squares (PGLS), using a consensus phylogenetic tree downloaded from the 10kTrees Project (version 3; Arnold, Matthews and Nunn, 2010). The phylogenetic signal (Pagel's λ) was estimated using maximum likelihood (Revell, 2010). λ can vary between 0, indicating no phylogenetic signal, and 1, indicating a strong phylogenetic signal and that similarity among species scales in proportion to their shared evolutionary time (Pagel, 1999; Freckleton, Harvey and Pagel, 2002). Statistical tests were performed using the package caper (Orme et al., 2010) in *R* 2.15.0 (Team, 2011). The significance level was set to 0.05.

Finally, the data of primates were compared visually to data from terrestrial Carnivora including canids, mustelids, ursids, mephitids, procyonids, felids, hyenids, herpestids and viverrids, but excluding pinnipeds (McGrosky et al., 2016).

Results

Among the Strepsirrhini, lemurs appear to have particularly long caeca (Fig. 1) compared to the gummivorous cheirogalids (Fig. 2). The latter have smaller caeca, although their caeca still appear proportionally larger than those of the gummivorous callitrichids (Fig. 3). The non-gummivorous cebids studied here all have similar digestive tracts (Fig. 4). Atelids have an unremarkable caecum that appears part of a large proximal colon (Fig. 5), whereas the caecum of the pitheciids is more distinct (Fig. 5). Among the Catarrhini, colobines have a voluminous forestomach, as well as a distinct caecum and an enlarged proximal colon (Fig. 6). The hindgut of many non-colobine Catarrhini is voluminous and haustrated, with a short, broad caecum (Fig. 7-10). In the apes, the caecum bears a clearly visible, vermiform appendix (Fig. 10).

When using the complete gastrointestinal morphology dataset, as well as Strepsirrhini- and Platyrrhini-specific datasets, there was a strong, significant phylogenetic signal, indicating that the data scatter is guided by the phylogenetic structure in the datasets. However, this strong phylogenetic signal was generally not observed within Catarrhini (Table 2). Across all species, the scaling exponent typically included 0.33 in the 95% confidence interval, indicating geometric scaling (Table 2). The 95% confidence intervals for the allometric factors (*a*) and scaling exponents (*b*) generally overlapped between the clades, with the exception of both the factor and exponent of the caecum, which were higher in the Strepsirrhini (Table 2). This observation was corroborated by the models that tested the scaling including the clade and clade x BM interactions, where the Strepsirrhini x BM interaction was significant both in GLS ($P = 0.009$) and PGLS ($\lambda = 0.73$; $P = 0.017$), indicating a steeper scaling of the caecum with BM for this clade (Fig. 11). Additionally, although the corresponding 95% confidence intervals for *a* overlapped, the analyses for small intestine length and total intestine length indicated significantly smaller values for Platyrrhini (small intestine: GLS $P = 0.015$; PGLS $\lambda = 0.73$, $P = 0.018$; total intestine: GLS $P = 0.032$; PGLS $\lambda = 0.80$, $P = 0.035$; in all cases, with non-significant interaction terms; Fig. 11).

While the scaling exponent of GLS models was generally very similar to that of PGLS models (Table 2 and S2), the GLS scaling exponent for the caecum in the complete dataset was very low (due to the long caeca of small-bodied strepsirrhines) and excluded geometric scaling in the confidence interval (0.16; 95%CI 0.04-0.29; Fig. 11). However, PGLS analyses indicated a generally geometric scaling of the caecum (0.41; 95%CI 0.25-0.56; Table 2).

Neither the percentage of leaves in the diet nor diet quality index exhibited a significant effect on intestinal length in any of the models, including models of caecum length (P always > 0.05). The only exceptions to this trend included significant GLS models of colon and total large intestine length for the percentage of leaves dataset and the diet quality index (GLS: colon – leaves $P = 0.045$; colon – diet index $P = 0.008$; large intestine – leaves $P = 0.066$; large intestine – diet index $P = 0.011$). In PGLS, these dietary effects were no longer significant, indicating that variation in large intestine length with diet occurred mainly across and not within clades (PGLS: colon – leaves $P = 0.402$; colon – diet index $P = 0.075$; large intestine – leaves $P = 0.648$; large intestine – diet index $P = 0.231$). Using the diet quality index and the relative colon length (in cm/BM$^{0.33}$), Figure 12 illustrates how the phylogenetic structure of the dataset explains the colon – diet index relationship: within clades, there is little correlation between the measurements, and any trend within Strespirrhini or Platyrrhini is due to a particular genus, not due to similar variation in several genera; the position of the clades, however, suggests the expected negative relationship. For a more detailed graph including the phylogenetic tree and the distribution of these two measures across it, see Fig. S1.

When compared to terrestrial Carnivora, the total intestines of primates are generally slightly longer (Fig. 11). This holds particularly true for the colon, and the caecum of the Strepsirrhini. By contrast, the caecum of the Catarrhini was of a magnitude also observed in many terrestrial Carnivora.

Discussion

Using what is to our knowledge the most comprehensive dataset on primate intestine lengths directly linked to the body mass of the same specimens, the present study largely corroborates well-known features of different primate groups and in part confirms broad macroanatomical concepts about differences in intestinal length between carnivores and herbivores. However, it also demonstrates that, in primates, correlations of length measures of the different intestinal sections with the natural diet may not be as clear-cut as is often assumed.

The photographic evidence provided can be compared to drawings and reports from the literature. While we do not want to dwell on this in detail here, some points of interest shall be mentioned. Fisher (2000) explained a reliable classification of species with respect to whether they have a true ‘appendix’ or not requires more than visual inspection, including histology, and ontogenetic series. Several species that have been classified as having an appendix in comparative datasets (e.g., Smith et al., 2017), including *Eulemur* spp. (Fig. 1) and *Callithrix* spp. (Fig. 3), did not have a vermiform structure that was clearly distinguishable. For *Papio hamadryas*, a variable disposition with respect to the presence of an appendix has been assumed (Smith et al., 2017), with our specimen not showing macroscopic evidence of a vermiform structure (Fig. 9). With respect to *Varecia* spp. or *Lemur catta*, it is evident that the macroscopic appearance could be interpreted both ways

(Fig. 1), and that further investigations as recommended by Fisher (2000) would be required for a reliable assessment.

A series of limitations applies to the present study. Our own and the literature data represent a mixture of measurements taken from freshly dissected specimens and specimens dissected after frozen storage and thawing. While we do not think that this has a relevant effect on macroscopic length measurements, readers that question this assumption should therefore consider the results with extra caution. In our view, it needs to be mentioned that length measurements of intestinal structures should rather be considered as indicating magnitudes, and not precise data (hence, we give no decimals in Table 1). When laying out intestines for length measurements, details such as the dryness of the organ and the smoothness of the surface used for measuring can influence whether an unintentionally stretched organ can contract again or retains the stretched disposition, for example. A further kind of caveat that needs to be mentioned refers to the use of a consensus tree (here, from the 10kTrees Project) rather than testing a whole distribution of trees. The standpoint, adopted intuitively in the present study, that absence of a signal when using the consensus tree is meaningful, could of course be questioned, and the data could be explored using the whole distribution of trees available.

However, the main limitations of the present study are its reliance on mainly captive specimens, and the low sample size for the majority of the included species that also precludes tests of ontogenetic changes. Freckleton, Harvey, & Pagel (2002) demonstrated that at lower species numbers below 20, a phylogenetic signal may not be always detected reliably, whereas a wrong detection of a phylogenetic signal is rare. In our analyses, this was also reflected in the finding that confidence intervals for λ could often not be calculated (Table 2). Among the Strepsirrhini (n=11) and Platyrrhini (n=14), the limited number of species might have been responsible for the finding that small intestine length and colon length (and hence also large intestine and total intestine length) showed a phylogenetic signal. This phylogenetic signal indicates that variation in these measures and clades was mainly an effect across, and not within, the included taxonomic subgroups. Notably, this did not apply to the Catarrhini, for which we obtained a larger sample size (n=17). In contrast, the fact that no phylogenetic signal was evident in strespirrhine caecum length suggests that a long caecum that increases in length with body mass is a common feature across various strepsirrhine subgroups. For more confidence in the phylogenetic signal of intestinal length measurements, a larger species sample would be required. This would also help to clarify if primates are really different from carnivores, ruminants or mammals in general (Lavin et al., 2008, McGrosky et al., 2016, 2019), which all show a more-than-geometrically scaling of intestine length, possibly to achieve geometrical constancy of absorptive intestinal surface while keeping diffusion distances in the instestine small by increasing the intestinal diameter at less-than-geometrically scaling (Woodall and Skinner, 1993). The large 95% confidence intervals for the scaling exponents in the present study do not allow a clear answer to this question.

Another limitation becomes evident given the absence of a clear dietary signal in intestinal length measurements, and is inherent to our study design: intestinal length is possibly poorly correlated with diet. Other measures, notably the volume or the actual gut fill (Clauss, Schwarm, Ortmann, Streich and Hummel, 2007; Müller et al., 2013), are most likely more meaningful correlates with diet, as mammalian herbivores generally have more voluminous (yet not necessarily longer) intestines. Chivers and Hladik (1980) addressed this fact by using intestinal surface area rather than length for some of their analyses. Notably, they did not find a significant difference in small intestine surface area between diet groups, and they did not report results for the large intestine or caecum in isolation, as done in the present study, where any dietary signal that derives from the anatomy of the stomach and forestomach was excluded. The often-cited patterns between gut morphology and diet described by Chivers and Hladik (1980) always represent a composite signal in which the volume or surface area of the (fore)stomach and the large intestine are summed up before evaluation. However, even using this composite signal, their study revealed substantial overlap between faunivores, frugivores and folivores. Additionally, affiliation to dietary groups varied, depending on whether anatomical surface or volume measurements were used; while colobine monkeys were exclusively grouped as folivores in terms of volume measures (Fig. 20 in Chivers and Hladik, 1980), they were also depicted within the range of frugivores in terms of surface measures (Fig. 18 of their study).

Nevertheless, the present study provides evidence for the functional relationship between colon or large intestine length and diet, as postulated previously (Hladik, 1978; Chivers, 1994). Similar to the findings on gastrointestinal complexity of Langer and Clauss (2018), GLS models revealed a significant relationship between diet and large intestine length. However, in both Langer and Clauss (2018) and the present study, these effects were not significant when accounting for the phylogenetic structure of the data using PGLS. This indicates that these effects do not occur within the different primate clades and therefore cannot be considered convergent between them in the respective datasets. Rather, the pattern occurs at deeper nodes of the phylogeny in each dataset, to the extent that clades as a whole differ in both, the GIT and the diet measure. The lack of significance in PGLS, or, in other words, the lack of evidence for dietary convergence, should not encourage the interpretation of a lack of a functional relationship. The relationship is just not evident *within* clades, but only *across* the clades included in this study. This could lead to the traditional interpretation often applied to non-significant findings when accounting for phylogeny, i.e. clade-specific characteristics other than diet (represented by ‘phylogeny’) led to the evolution of longer or more complex large intestines in those taxa that also ingest more leaves. Alternatively, it suggests that clade diversification in primates followed, to a large extent, dietary niche and concomitant intestinal adaptations, but that diet diversification within clades left less reliable marks on intestinal anatomy. Reporting only one result, such as – in the case of a significant phylogenetic signal – the PGLS result while ignoring the GLS result, as sometimes recommended in the biological literature (Freckleton, 2009), would leave this observation unrecognized.

With respect to length, primates do not appear to differ from terrestrial carnivores for the small intestine where auto-enzymatic digestion occurs. However, as also described by Martin (1990) and Lambert (1998), primates generally have a longer large intestine (a site of allo-enzymatic digestion), which coincides with their generally higher reliance on diets that contain plant cell walls compared to carnivores. The difference in the intestinal segment by which primates achieve a longer large intestine resembles the pattern observed between other large (e.g., perissodactyl) and small (e.g., rodents and lagomorphs) hindgut-fermenting herbivores (Stevens and Hume, 1998); while smaller species typically have particularly large caeca and are often called ‘caecum fermenters’, larger species also possess a voluminous colon for allo-enzymatic digestion. This pattern is reflected in the differences between the larger Catarrhini and the smaller Strepsirrhini and Platyrrhini, which both have larger caeca compared to the Catarrhini (Fig. 12D). The difference in caecum size and shape between these groups has been known for some time (Reider, 1936; Scott, 1980). One can only speculate that for smaller species, the retention times necessary for allo-enzymatic fiber digestion are more easily achieved by a larger dead-end structure such as the caecum rather than by a larger colon.

Ultimately, primate clades have a typical mammalian macroscopic appearance of their gastrointestinal tracts. The measure of intestinal length in primates matches broad statements about differences between carnivorous and herbivorous species mentioned in the

Introduction, and, in the case of the large intestine, about the effect of natural diets on primate intestinal length. Within primates, however, dietary effects are found only across but not within clades, as models of the effect of diet on intestine length are only significant if the phylogenetic structure of the dataset is not accounted for. Within primate clades, dietary specialization as measured in our dataset has little power to explain intestinal length measures.

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Table 1 Average (±S.D.) body mass (g) and intestinal length (cm) measurements of primate species

Species (Clade[a])	Source	n	Body mass	Small intestine	Caecum	Colon	Large intestine[b]	Total intestine	%leaves in natural diet[c]	Diet quality index[c]
Alouatta sara (P)	1	2	3950 (±636)	123 (±11)	6 (±5)	74 (±3)	80 (±1)	202 (±10)	50	NA
Alouatta seniculus (P)	2	1	635	239	12	58	70	309	48	328
Ateles paniscus (P)	1	1	8070	211	13	60	73	283	8	456
Callthrix argentata (P)	1	1	242	43	4	23	28	70	0	NA
Callithrix jacchus (P)	1,3	5	323 (±30)	58 (±14)	5 (±1)	25 (±13)	30 (±12)	88 (±27)	0	519
Cebuella pygmaea (P)	1	1	163	41	5	24	29	69	0	599
Cebus apella (P)	1	1	1750	145	5	34	39	184	16	543
Cheirogaleus medius (S)	1	2	197 (±49)	114 (±0)	5 (±0)	16 (±3)	21 (±3)	135 (±3)	4	549
Chiropotes satanas (P)	2	1	3130	282	19	48	67	349	1	504
Chlorocebus pygerythrus (C)	1	1	5300	176	7	67	74	250	10	526
Colobus guereza (C)	1	2	9750 (±354)	278 (±57)	8 (±0)	104 (±22)	112 (±22)	390 (±79)	61	348
Eulemur coronatus (S)	4	1	1580	99	14	55	69	168	3	493
Eulemur fulvus (S)	1	1	2500	91	16	57	73	164	25	396
Eulemur macaco (S)	1	2	1875 (±530)	125 (±20)	26 (±6)	66 (±1)	92 (±5)	217 (±15)	45	454
Gorilla gorilla (C)	1,5	2	154648 (±102032)	810 (±299)	18[d]	139[d]	162 (±8)	972 (±307)	61	359
Hapalemur griseus (S)	6	4	648 (±106)	86 (±16)	7 (±4)	50 (±6)	57 (N.R.)	144 (N.R.)	100	296
Homo sapiens (C)	9	6	65300 (±14471)	678 (±138)	8 (±2)	146 (±16)	154 (±15)	831 (±144)	30	NA
Lemur catta (S)	1	3	2117 (±144)	156 (±43)	24 (±7)	86 (± 24)	111 (±28)	267 (±71)	32	432
Leontopithecus chrysomelas (P)	1	3	642 (±98)	101 (±12)	5 (±1)	27 (±4)	32 (±4)	133 (±15)	0	490
Macaca arctoides (C)	1	4	14525 (±3495)	297 (±51)	7 (±2)	125 (±47)	132 (±45)	429 (±95)	40	NA
Macaca cyclopis (C)	7	6	119667 (±1783)	230 (±29)	6 (±1)	79 (±7)	85 (±7)	315 (±30)	23	470
Macaca fuscata (C)	1	1	11970	434	5	121	126	560	32	372
Macaca nigra (C)	1	1	5600	295	8	113	121	415	2	596
Macaca sylvanus (C)	1	1	9625	334	7	163	170	504	11	430
Mandrillus sphinx (C)	1	1	23000	515	8	189	197	713	8	482
Mirza zaza (S)	1	1	336	82	4	34	38	120	38	420
Nomascus leucogenys (C)	1	1	6550	449	13	83	96	545	59	356
Pan paniscus (C)	1	1	37730	527	12	234	245	773	24	415
Papio hamadryas (C)	1	2	23250 (±8132)	426 (±161)	10 (±2)	148 (±12)	158 (±10)	585 (±172)	28	401
Pithecia pithecia (P)	1,2	3	1467 (±339)	191 (±25)	11 (±4)	56 (±17)	67 (±21)	258 (±46)	9	492
Pongo pygmaeus (C)	9	1	56250	559	23	328	351	910	48	458
Propithecus tattersalli (S)	6	1	2760	362	37	252	289	651	39	378
Propithecus verreauxi (S)	6	2	3890 (±438)	365 (±38)	39 (±7)	364 (±42)	403 (N.R.)	767 (N.R.)	53	302
Saguinus fusicollis (P)	1	1	330	81	2	22	25	106	0	614
Saguinus oedipus (P)	1	4	460 (±211)	75 (±8)	5 (±1)	29 (±9)	33 (±10)	109 (±17)	0	NA
Saimiri boliviensis (P)	1	1	1003	144	5	18	22	166	0	500
Saimiri sciureus (P)	1,2,8	22	678 (±117)	104 (±17)	4 (±1)	12 (±4)	16 (±4)	120 (±21)	0	684
Symphalangus syndactylus (C)	1	1	8500	298	5	60	65	362.46	45	435
Theropithecus gelada (C)	1	1	11400	227	4	121	125	352	94	313
Trachypithecus vetulus (C)	1	1	5000	305	9	83	92	397	45	300
Varecia rubra (S)	1	1	4200	162	35	72	108	269	12	454
Varecia variegata (S)	1	1	3520	102	25	51	75	178	9	472

NA not available

[a] C Catarrhini, P Platyrrhini, S Strepsirrhini

[b] including caecum length

[c] for sources, see Table S1

[d] caecum & colon length only obtained from the present study

Sources: 1 present study; 2 Fooden (1964); 3 Caton, Hill, Hume and Crook (1996); 4 Schwitzer (2009); 5 Steiner (1954); 6 Campbell, Eisemann, Williams and Glenn (2000); 7 Makita et al. (1984); 8 Beischer and Furry (1964); 9 Chivers (pers. comm.): for a previous study on mammal body composition (Navarrete et al. 2011), handwritten notes of Dr. Chivers were obtained of files used in preparation of his publication on mammal digestive tract anatomy (Chivers and Hladik 1980); while these notes did not record the lengths of the intestines for the species included in that publication, they contained measurements of some additional specimens.

Table 2 Phylogenetic signal (λ) and allometric relationships between intestinal length measures (in cm) and body mass (BM, in kg) according to Length = a BM^b with 95% confidence intervals for parameter estimates from analyses using Phylogenetic Generalized Least Squares

Length of	n	λ (95%CI)	a (95%CI)	b (95%CI)
Total intestine	42	0.82 (0.47; 0.96)	187 (123; 287)	0.38 (0.30; 0.47)
Strepsirrhini	11	1.00 (0.40; NA)	217 (127; 371)	0.47 (0.15; 0.79)
Platyrrhini	14	0.72 (NA; NA)	156 (134; 181)	0.41 (0.30; 0.51)
Catarrhini	17	0 (NA; 0.46)	198 (146; 269)	0.34 (0.24; 0.45)
Small intestine	42	0.80 (0.37; 0.94)	130 (86; 198)	0.38 (0.29; 0.47)
Strepsirrhini	11	1.00 (0.57; NA)	141 (94; 213)	0.31 (0.07; 0.56)
Platyrrhini	14	0.66 (NA; 0.97)	115 (93; 142)	0.45 (0.30; 0.60)
Catarrhini	17	0 (NA; 0.58)	143 (101; 203)	0.34 (0.22; 0.46)
Caecum	42	0.92 (0.62; NA)	7.1 (3.2; 15.9)	0.41 (0.25; 0.56)
Strepsirrhini	11	0 (NA; 0.79)	12.3 (10.5; 14.5)	0.76 (0.61; 0.91)
Platyrrhini	14	0.77 (NA; NA)	6.2 (4.5; 8.4)	0.39 (0.18; 0.61)
Catarrhini	17	0 (NA; 0.69)	3.9 (2.1; 6.9)	0.29 (0.09; 0.48)
Colon	42	0.94 (0.76; 0.99)	46 (23; 93)	0.38 (0.25; 0.51)
Strepsirrhini	11	1.00 (0.77; NA)	61 (37; 100)	0.60 (0.30; 0.89)
Platyrrhini	14	0.75 (0.07; NA)	31 (23; 42)	0.29 (0.09; 0.49)
Catarrhini	17	0 (NA; 0.81)	49 (32; 76)	0.33 (0.19; 0.48)
Large intestine	42	0.94 (0.74; 1.00)	55 (28; 106)	0.38 (0.26; 0.50)
Strepsirrhini	11	1.00 (0.60; NA)	75 (47; 120)	0.64 (0.35; 0.92)
Platyrrhini	14	0.82 (0.20; NA)	38 (29; 49)	0.31 (0.13; 0.48)
Catarrhini	17	0 (NA; 0.76)	54 (36; 82)	0.33 (0.19; 0.47)

NA - no respective confidence limit available

for GLS results, see Table S1

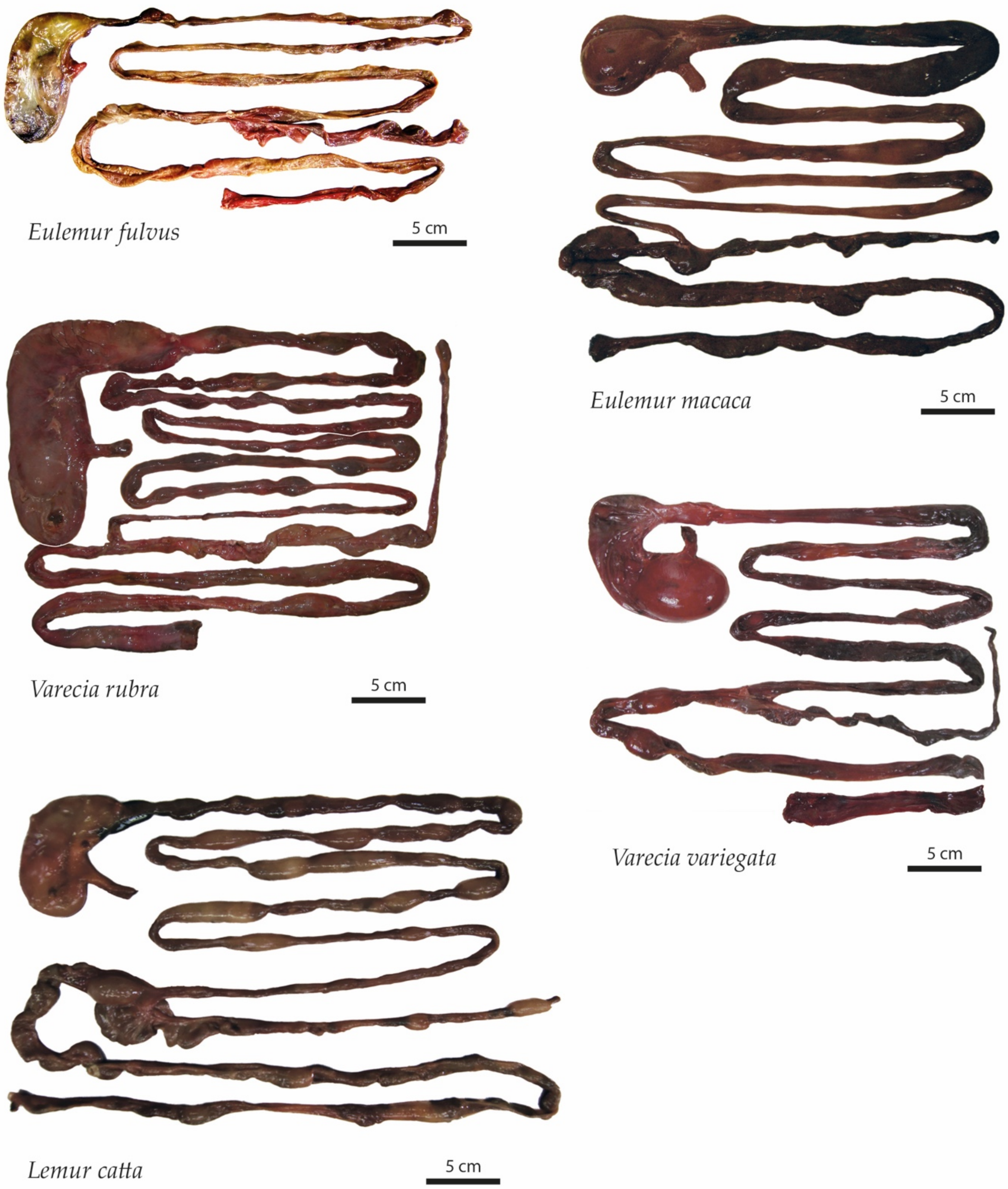
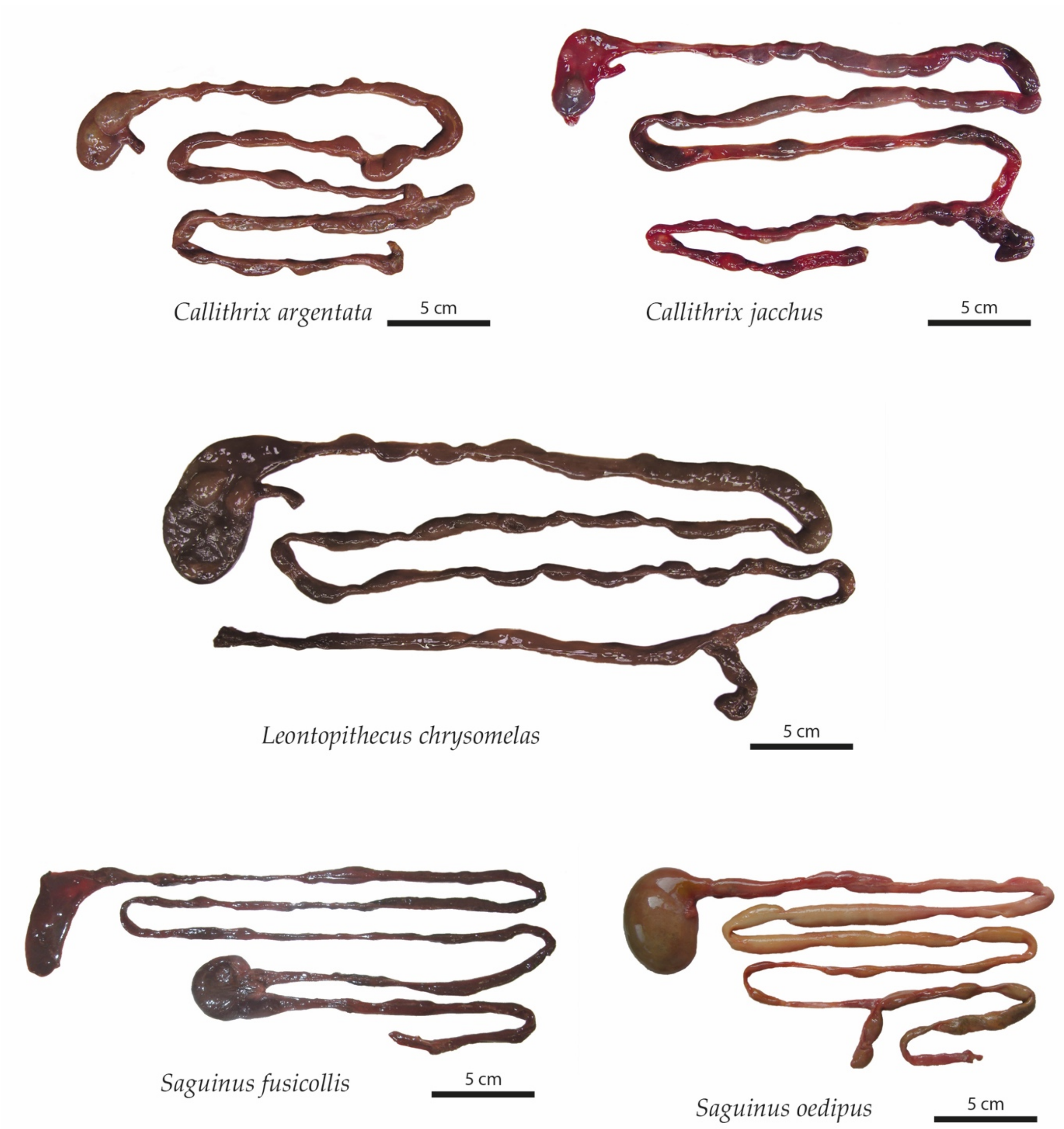


Figure 1 Digestive tracts of various lemur species. Note the long caecum in all species.

Figure 2 Digestive tracts of two cheirogalid species.


Callithrix argentata

Callithrix jacchus

Leontopithecus chrysomelas

Saguinus fusicollis

Saguinus oedipus

Figure 3 Digestive tracts of five callitrichid species.

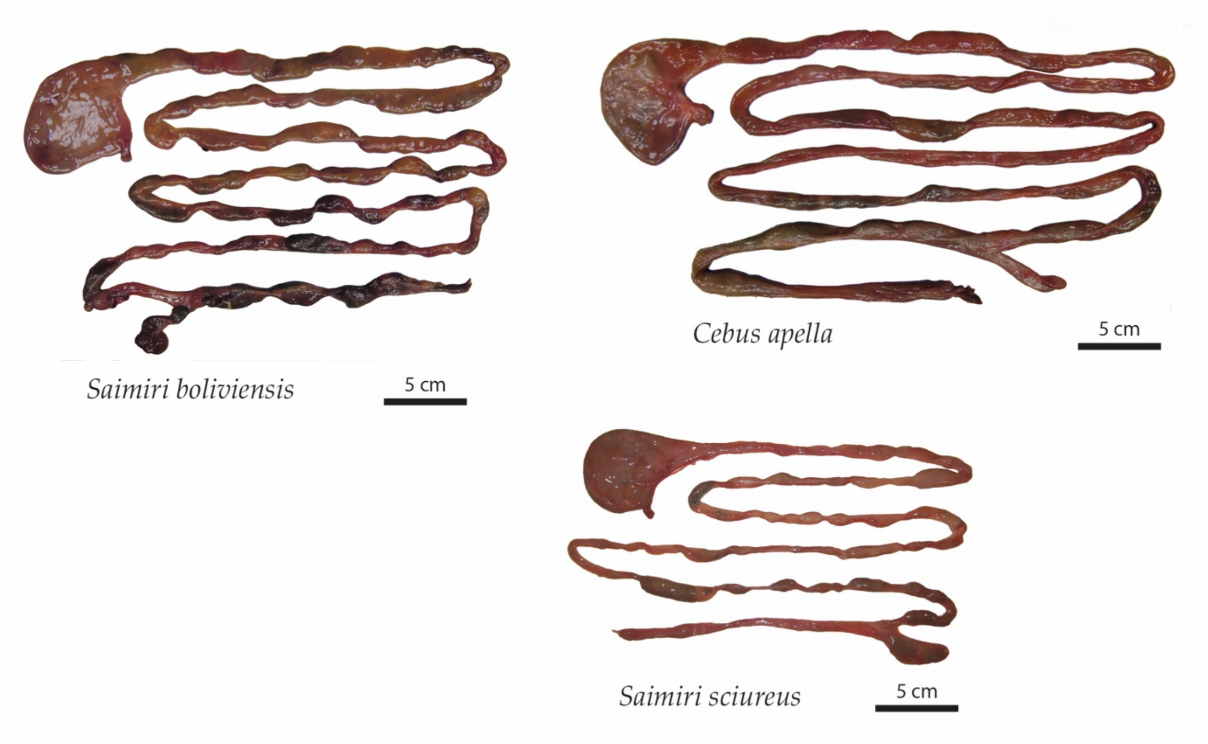


Figure 4 Digestive tracts of three cebid species.

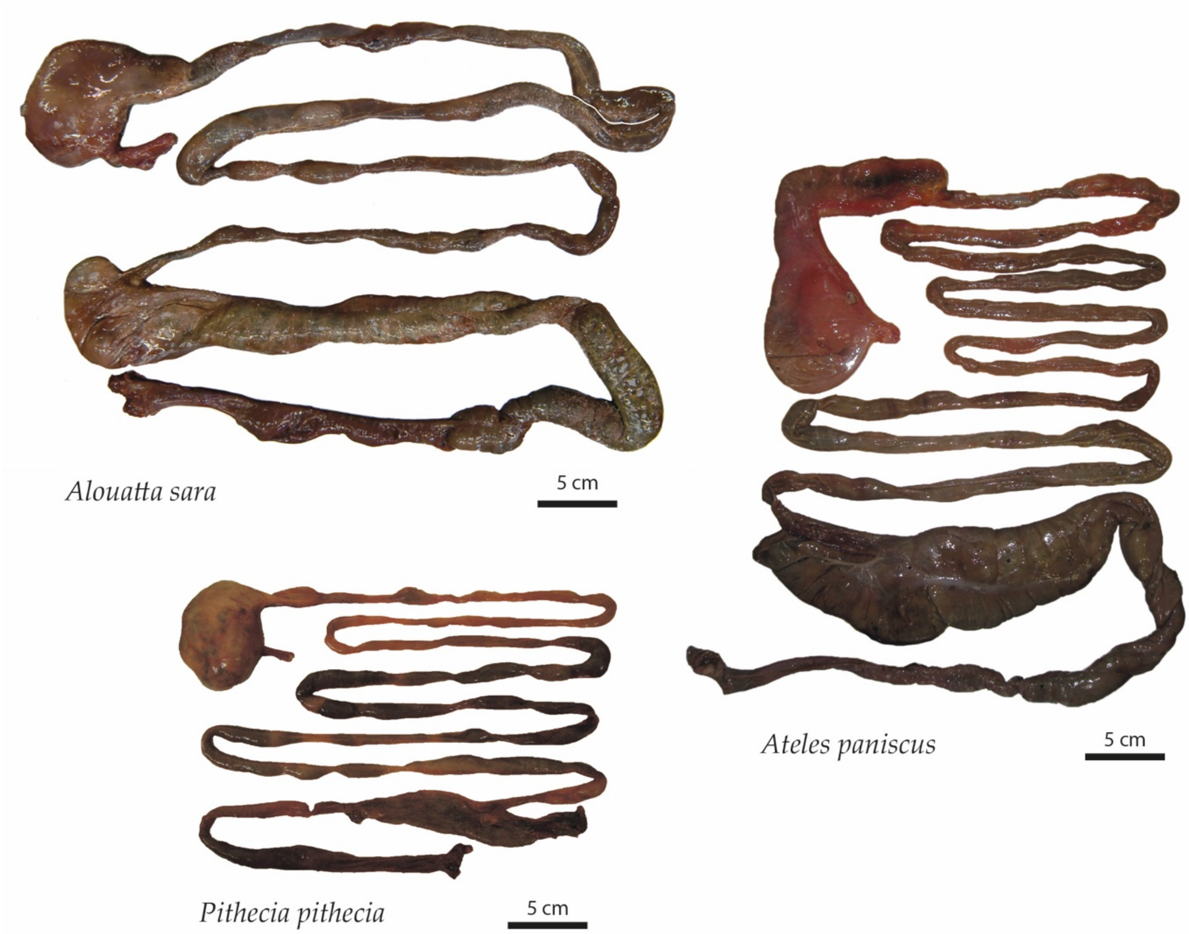


Figure 5 Digestive tracts of two atelid and one pitheciid species.

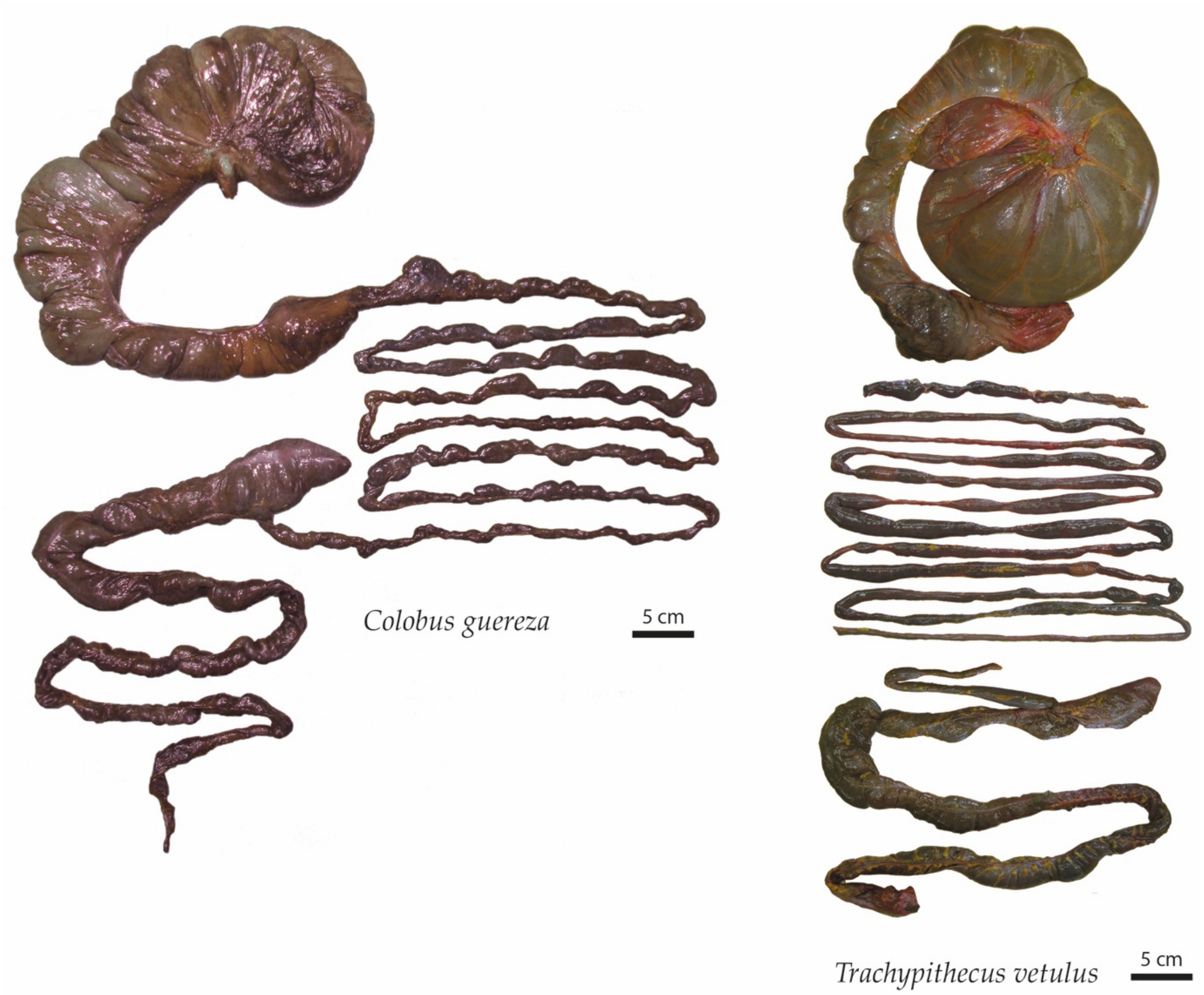


Figure 6 Digestive tracts of two colobine species.

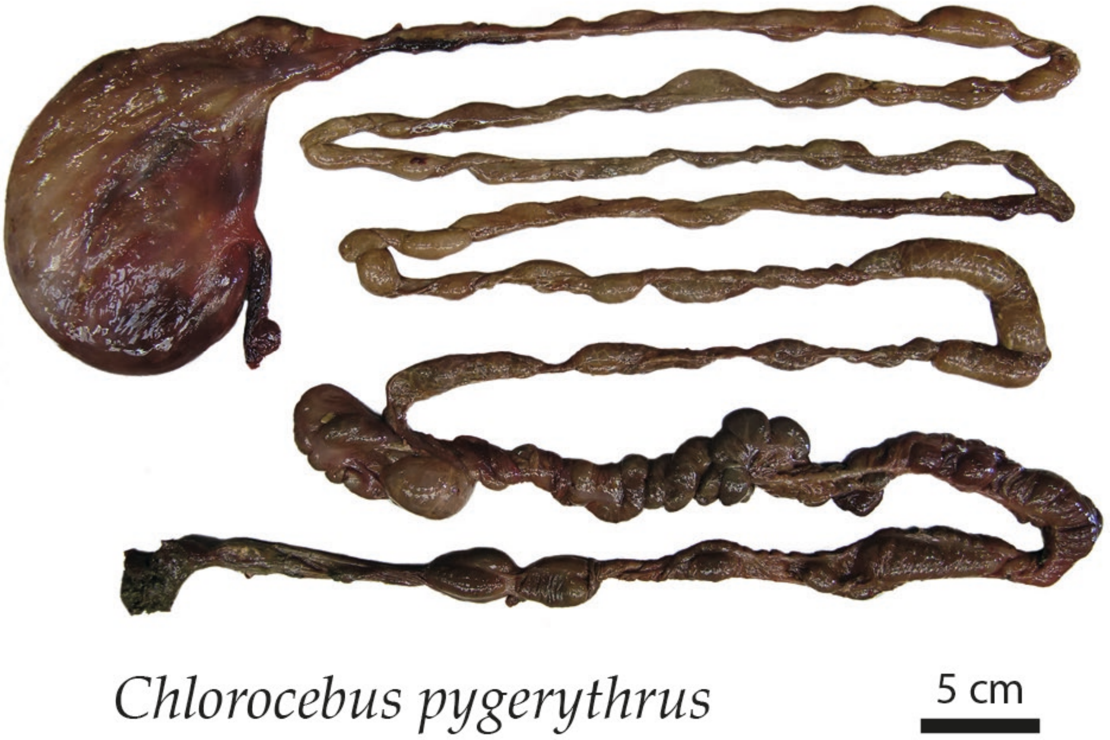


Figure 7 Digestive tract of *Chlorocebus*.

Figure 8 Digestive tracts of four macaque species. The * indicates where the small intestine was linked before dissection.

Figure 9 Digestive tracts of three baboon species. The * marks where the small intestine was linked before dissection.

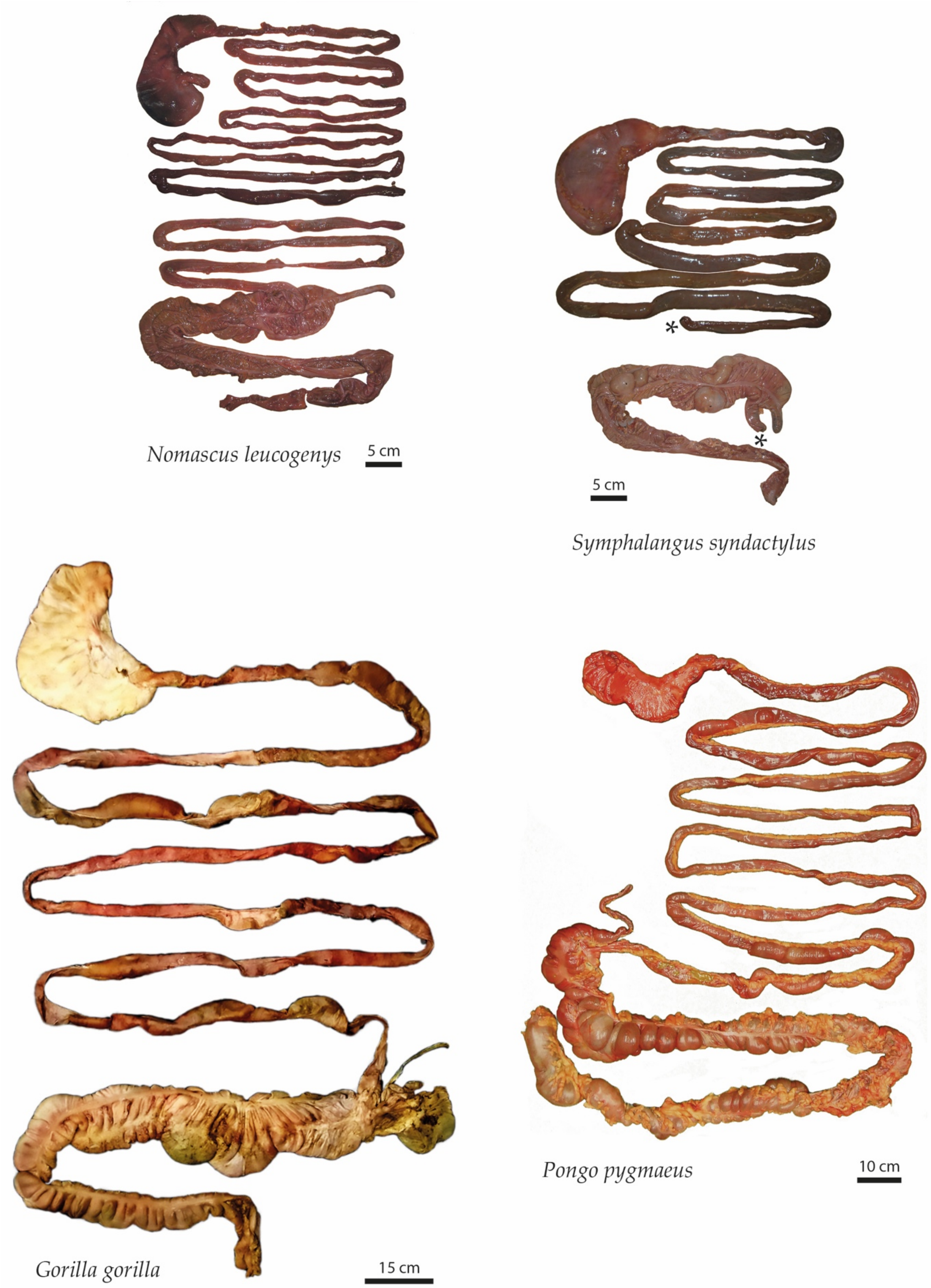


Figure 10 Digestive tracts in four ape species. The * marks where the small intestine was linked before dissection. Note the caecal appendix in all four species.

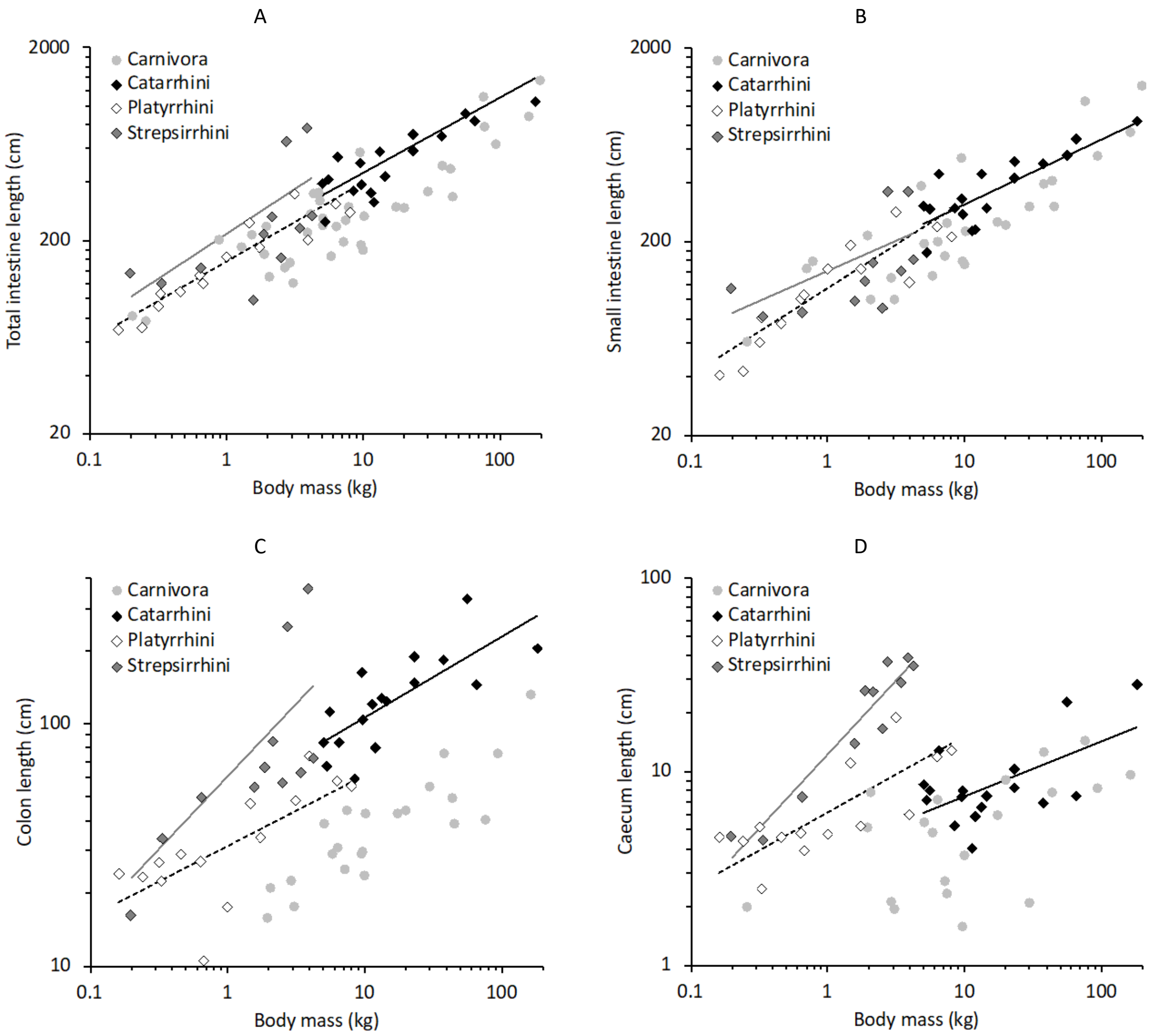


Figure 11 Relationship between body mass and A) total intestinal length, B) small intestinal length, C) colon length and D) caecum length in primates as compared to terrestrial carnivorans (from McGrosky et al., 2016). Regression lines from Phylogenetic Generalized Least Squares (Table 2). Straight black line = Catarrhini; black dotted line = Platyrrhini; grey line = Strepsirrhini. The two outlier lemurs in (A-C) are sifakas (*Propithecus* spp.).

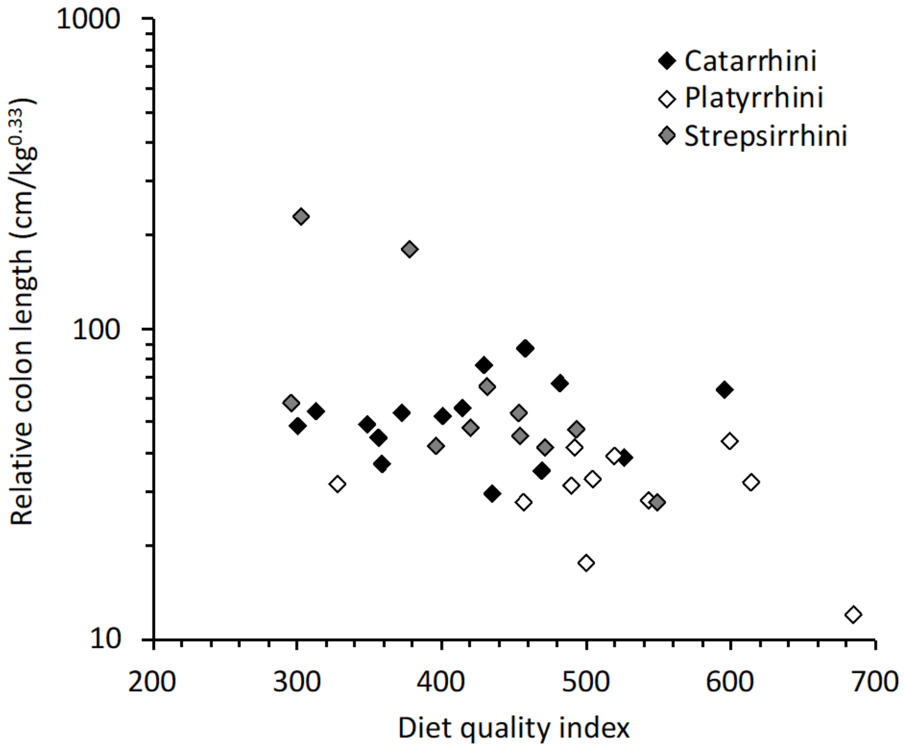


Figure 12 Relationship between the diet quality index and the relative length of the colon in species of three different primate clades. Note that while there is a negative relationship in the overall data, this is not the case in the individual clades, leading to a non-significant result when accouting for the phylogenetic structure of the data (see Results). The two outliers with a high relative colon length in the Strepsirrhini are from one genus (*Propithecus* spp.); the two outliers in the Platyrrhini with a low relative colon length are also from one genus (*Saimiri* spp.).

Supporting Information

Gross intestinal morphometry and allometry in primates

Amanda McGrosky • Carlo Meloro • Ana Navarrete • Sandra A. Heldstab • Andrew C. Kitchener • Karin Isler • Marcus Clauss

Table S1 Sources for diet information

ACHTUNG: alles normal ist aus den Van Woerden Papers bzw. aus der Excel-Tabelle; gelb = keine Ahnung, woher (incl. der Angabe im Excel); blau = Angabe aus Excel, obwohl Quelle in Van Woerden Papers; pink = all the worlds primates – kann man da die direkte quelle rausziehen?

Species (Clade[a])	Source
Alouatta sara (P)	Neville, M. K., Glander, K. E., Braza, F., & Rylands, A. B. (1988). The howling monkeys, genus *Alouatta*. In *Ecology and behavior of neotropical primates, vol 2* (ed. R. A. Mittermeier, A. B. Rylands, A. Coimbra-Filho, G. A. B. Fonseca). Washington DC: World Wildlife Fund.
Alouatta seniculus (P)	Julliot, C., & Sabatier, D. (1993). Diet of the red howler monkey (*Alouatta seniculus*) in French-Guiana. Int J Primatol 14:527-550. Di Fiore, A., & Campbell, C. J. (2007). The atelines: variation in ecology, behavior, and social organisation. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Ateles paniscus (P)	van Roosmalen, M. G. M. (1980). *Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (Ateles paniscus paniscus Linnaeus 1758) in Surinam*. PhD thesis. Landbouwhogeschool Wageningen: Leersum. Di Fiore, A., & Campbell, C. J. (2007). The atelines: variation in ecology, behavior, and social organisation. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Callthrix argentata (P)	xxx (Willems and van Schaik 2015?)
Callithrix jacchus (P)	de Castro, C. S. S., & Araújo, A. (2007). Diet and feeding behavior of marmoset, *Callithrix jacchus*. *Brazilian Journal of Ecology*, 7, 14-19. Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). Callitrichines: the role of competition in cooperatively breeding species. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Cebuella pygmaea (P)	xxx (Van Woerden 2010?)
Cebus apella (P)	Zhang, S. Y. (1995). Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French-Guiana. *International Journal of Primatology*, 16, 489-507.
Cheirogaleus medius (S)	Fietz, J., & Ganzhorn, J. U. (1999). Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? *Oecologia*, 121, 157-164.
Chiropotes satanas (P)	Norconk, M. A. (1996). Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In *Adaptive radiations of neotropical primates* (ed. M. A. Norconk, A. L. Rosenberger, P. A. Garber). New York: Plenum Press.
Chlorocebus pygerythrus (C)	Enstam, K. L., & Isbell, L. (2007). The guenons (*genus Cercopithecus*) and their allies: behavioral ecology of polyspecific associations. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Colobus guereza (C)	Plumptre, A. J. (2006). The diets, preferences, and overlap of the primate community in the Budongo Forest Reserve, Uganda. In *Primates of western Uganda* (ed. N. E. Newton-Fisher, H. Notman, J. D. Paterson & V. Reynolds). New York: Springer; Fashing, P. J. (2001). Feeding ecology of guerezas in the Kakamega Forest, Kenya: The importance of *Moraceae* fruit in their diet. *International Journal of Primatology*, 22, 579-609.
Eulemur coronatus (S)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Eulemur fulvus (S)	Rasmussen, M. A. (1999). *Ecological influences on activity cycle in two cathemeral primates, the mongoose lemur (Eulemur mongoz) and the common brown lemur (Eulemur fulvus fulvus)*. PhD diss. Duke University, Durham, NC; Tarnaud, L. (2006). Feeding behavior of lactating brown lemur females (*Eulemur fulvus*) in Mayotte: influence of infant age and plant phenology. *American Journal of Primatology*, 68, 966-977.
Eulemur macaco (S)	Andrews, J. R., & Birkinshaw, C. R. (1998). A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, *Eulemur macaco* (Primates: Lemuridae), in Lokobe forest, Madagascar. *Folia Primatologica*, 69, 175-182.
Gorilla gorilla (C)	Remis, M. J. (1997). Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology*, 43, 87-109; Doran, D., & Greer, D. (2002). The influence of swamp use and fruit consumption on western gorilla (*Gorilla gorilla gorilla*) ranging behavior at Mondika Research Center. *American Journal of Physical Anthropology*, 34, 64-65; Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National-Park, Congo. *Primates*, 36, 151-168.
Hapalemur griseus (S)	Overdorff, D. J., Strait, S. G., & Telo, A. (1997). Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in southeastern Madagascar. *American Journal of Primatology*, 43, 211-223.
Homo sapiens (C)	Wilman H., Belmaker J., Simpson J., de la Rosa C., Rivadeneira M. M., & Jetz W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027-2027.
Lemur catta (S)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Leontopithecus chrysomelas (P)	xxx (Willems and van Schaik 2015?)

Macaca arctoides (C)	Wilman H., Belmaker J., Simpson J., de la Rosa C., Rivadeneira M. M., & Jetz W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027-2027.
Macaca cyclopis (C)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Macaca fuscata (C)	Agetsuma, N. (1995). Dietary selection by Yakushima Macaques (*Macaca fuscata yakui*), the influence of food availability and temperature. *International Journal of Primatology*, 16, 611-627; Agetsuma, N., & Nakagawa, N. (1998). Effects of habitat differences on feeding behaviors of Japanese monkeys: Comparison between Yakushima and Kinkazan. *Primates*, 39, 275-289; Hanya, G. (2004). Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology*, 25, 55-71; Hill, D. A. (1997). Seasonal variation in the feeding behavior and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *American Journal of Primatology*, 43, 305-322.
Macaca nigra (C)	pers. comm. in van Woerden J. T., Willems E. P., van Schaik C. P., & Isler K. (2012). Large brains buffer energetic effects of seasonal habitats in catarrhine primates. *Evolution*, 66, 191-199.
Macaca sylvanus (C)	xxx (Thierry 2007?)
Mandrillus sphinx (C)	Hoshino, J. (1985). Feeding ecology of Mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. *Primates*, 26, 248-273.
Mirza zaza (S)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Nomascus leucogenys (C)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Pan paniscus (C)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Papio hamadryas (C)	Hill, R. A., & Dunbar, R. I. M. (2002). Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology*, 16, 579-593.
Pithecia pithecia (P)	Norconk, M. A. (1996). Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In *Adaptive radiations of neotropical primates* (ed. M. A. Norconk, A. L. Rosenberger, P. A. Garber). New York: Plenum Press.
Pongo pygmaeus (C)	Rodman, P. S. (1977). Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In P*rimate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. (ed. T. H. Clutten-Brock). London, New York: Academic Press; Galdikas, B. M. F. (1988). Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology*, 9, 1-35; and unpubl. data in van Woerden J. T., Willems E. P., van Schaik C. P., & Isler K. (2012). Large brains buffer energetic effects of seasonal habitats in catarrhine primates. *Evolution*, 66, 191-199.
Propithecus tattersalli (S)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Propithecus verreauxi (S)	Richard, A. F. (1978). *Behavioral variation: case study of a Malagasy lemur*. Bucknell University Press, Lewisburg, PA.
Saguinus fusicollis (P)	Porter, L. M. (2001). Dietary differences among sympatric Callitrichinae in Northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *International Journal of Primatology*, 22, 961-992; Peres, C. A. (1993). Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins in an Amazonian terra firma forest. *Journal of Zoology*, 230, 567-592. Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). Callitrichines: the role of competition in cooperatively breeding species. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Saguinus oedipus (P)	xxx (Willems and van Schaik 2015?)
Saimiri boliviensis (P)	xxx (Van Woerden 2010?)
Saimiri sciureus (P)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Symphalangus syndactylus (C)	Bartlett, T. Q. (2007) The hylobatidae. In *Primates in perspective* (ed. C. J. Campbell, A. Fuentes, K. C. McKinnon, M. Panger, S. K. Bearder). New York: Oxford University Press.
Theropithecus gelada (C)	Rowe N., & Myers M. (2011). *All the world's primates*. Rhode Island: Primate Conservation Inc.
Trachypithecus vetulus (C)	Hladik, C. M. (1977). A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In *Primate Ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes*. (ed. T. H. Clutten-Brock), London: Academic Press; Dela, J. D. S. (2007). Seasonal food use strategies of *Semnopithecus vetulus nestor*, at Panadura and Piliyandala, Sri Lanka. *International Journal of Primatology*, 28, 607-626
Varecia rubra (S)	Vasey, N. (2004). Circadian rhythms in diet and habitat use in red ruffed lemurs (*Varecia rubra*) and white-fronted brown lemurs (*Eulemur fulvus albifrons*). *American Journal of Physical Anthropology*, 124, 353-363.
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[a] C Catarrhini, P Platyrrhini, S Strepsirrhini

Table S2 Allometric relationships between intestinal length measures (in cm) and body mass (BM, in kg) according to Length = a BM^b with 95% confidence intervals for parameter estimates from analyses using Generalized Least Squares (i.e., not accounting for phylogeny)

Length of	n	a (95%CI)	b (95%CI)
Total intestine	42	168 (148; 190)	0.40 (0.34; 0.46)
Strepsirrhini	11	188 (133; 367)	0.40 (0.08; 0.73)
Platyrrhini	14	152 (137; 168)	0.40 (0.32; 0.49)
Catarrhini	17	198 (146; 269)	0.34 (0.24; 0.45)
Small intestine	42	117 (103; 132)	0.41 (0.35; 0.46)
Strepsirrhini	11	125 (93; 167)	0.29 (0.01; 0.56)
Platyrrhini	14	111 (96; 128)	0.44 (0.32; 0.56)
Catarrhini	17	143 (101; 203)	0.34 (0.22; 0.46)
Caecum	42	7.5 (5.7; 9.7)	0.16 (0.04; 0.29)
Strepsirrhini	11	12.3 (10.5; 14.5)	0.76 (0.61; 0.91)
Platyrrhini	14	6.1 (5.0; 7.4)	0.34 (0.18; 0.51)
Catarrhini	17	3.9 (2.1; 6.9)	0.29 (0.09; 0.48)
Colon	42	41 (34; 49)	0.41 (0.32; 0.50)
Strepsirrhini	11	54 (37; 79)	0.62 (0.26; 0.98)
Platyrrhini	14	31 (25; 38)	0.31 (0.14; 0.47)
Catarrhini	17	49 (32; 76)	0.33 (0.19; 0.48)
Large intestine	42	49 (41; 59)	0.38 (0.29; 0.47)
Strepsirrhini	11	69 (48; 98)	0.66 (0.34; 0.98)
Platyrrhini	14	38 (31; 45)	0.32 (0.17; 0.47)
Catarrhini	17	54 (36; 82)	0.33 (0.19; 0.47)