Testing Hypotheses About the Relationship Between Diet and Torso Morphology in Extant Primates: Implications for Human Evolution

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Dedication

This dissertation is dedicated to my mother, Sultana Rose Khan-Boyle, who always told me to take pride in my work.

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Abstract of Dissertation

Testing Hypotheses About the Relationship Between Diet and Torso Morphology in Extant Primates: Implications for Human Evolution

Torso differences between *Australopithecus* and *Homo* are often claimed to reflect a reduction in gut size following an increase in diet quality in the latter genus. This hypothesis emerges from the fact that animals that primarily eat green plants exhibit larger guts than animals that rely on prey, and the assumption that torso form reflects accommodations for differently sized guts. However, recent studies show that other factors might influence primate torso morphology (e.g., body mass, locomotion), and the existence and nature of any relationships between the torso and diet have not been demonstrated in living primates. This dissertation uses phylogenetic generalized least squares (PGLS) regressions and other analyses to test hypotheses relating diet to anthropoid primate torso morphology. Linear measurements and 3D torso volume were collected across a broad sample of primates and integrated with data on gut size, feeding observations, locomotion, and body size from the literature.

Chapter 1 introduces the background and research objectives. Chapter 2 tests hypotheses that have been laid forth in the paleoanthropological literature. I present the results of two analyses that use PGLS regressions and another that utilizes discriminant function analysis to test how torso form is related to diet and locomotion. Chapter 3 provides more narrow comparisons among a subsample of anthropoid species. Chapter 4 identifies if torso volume, calculated from the convex hulls of articulated torsos, is related to diet. Chapter 5 presents the conclusions of the dissertation and the significance of the results for describing and analyzing fossil hominin torso remains.

The analyses presented in this dissertation demonstrate that there is no consistent relationship between the extant primate torso and observed diets and gut sizes. Across the entire sample, torso features—considered both individually and together—are more closely related to body size and locomotion than to diet. Narrow comparisons among similarly-sized, closely-related species reveal that there is no reliable pattern in how torso dimensions vary among species with different or similar diets. Variation in torso volume is also driven by body size and phylogenetic relatedness and is not related to diet or gut size. Altogether, this research suggests there is no basis to support the practice of inferring diet from fossil hominin torso remains.

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Chapter 1: Introduction

Diet has important connections to several aspects of primate biology. Differences in the amount and types of food items primates consume have been linked to differences in body size (e.g., Sailer et al., 1985; Price & Hopkins, 2015; Pineda-Munoz et al., 2016) and brain size (e.g., Fish & Lockwood, 2003; DeCasien et al., 2017), while where and how primates forage is related to locomotor capabilities (e.g., Fleagle, 1984), habitat use (e.g., Milton and May, 1976), and social behavior (e.g., Clutton-Brock & Harvey, 1977). Diet has also featured in hypotheses that seek to explain important changes within hominin evolution, such as the emergence of *Homo* (Dart, 1953; Wrangham et al.,1999; Milton, 2003; Ungar et al., 2006; Bunn, 2007; Anton and Snodgrass, 2012; Thompson et al., 2019) and the subsequent enlargement of the brain (Aiello and Wheeler, 1995; Wrangham et al., 1999; Foley, 2001; Langdon, 2006; Leonard et al., 2007). Attempts to reconstruct the diet of early hominins have traditionally focused on analyses of craniodental form and/or function (e.g., Ungar, 2011; Eng et al., 2013; Berthaume et al., 2018) and behavioral signals from the archaeological record (e.g., Braun et al., 2010; Thompson et al., 2019), but more recently researchers have turned to chemical analyses of teeth (e.g., Sponheimer et al., 2013) and traces of ingested foods preserved in dental calculus (e.g., Henry et al., 2012) as indicators of the diets of extinct hominins.

One obvious source of direct evidence about dietary adaptations in living primates are the soft tissue remains of the gastrointestinal tract (GIT aka gut) and its associated organs (i.e., liver, pancreas and gall-bladder) that together form the gastrointestinal system (GIS), but with the exception of gastroliths, none of the GIS fossilizes. The bones of the torso which surround the gut—the lower ribcage, pelvis, and lumbar vertebrae—

have been recovered for several hominin species and appear to show changes over evolutionary time that have led researchers to speculate that significant diet-induced gut size changes have occurred within the hominin lineage (Aiello and Wheeler, 1995; Wrangham et al., 1999; Lovejoy et al., 2009). Specifically, researchers have argued that torso differences between *Australopithecus* and *Homo* signify a substantial change (or grade shift) in diet quality occurred between the two genera circa 3 to 2 million years ago (Ma) (Aiello and Wheeler, 1995; Wrangham et al., 1999). However, the existence and nature of any relationships between the size and shape of the lower torso and diet have *not* been tested in extant primates. Until we understand if, and how, differences in diet, are reflected in the shape and size of the bones of the torso of living primates, there is no comparative basis to suggest that torso morphology can be used as a proxy for the diet of extinct hominin taxa.

Research objectives

This project explores the relationships between dietary observations, gut size, torso volume, and specific morphological aspects of primate torso form (i.e., dimensions of the thorax, vertebral column, and pelvis). To do this I use phylogenetically-informed comparative methods to:

1. Test if the five features of the torso that have been linked to gut size, abdominal volume, and diet in the paleoanthropological literature carry a dietary signal in extant primates.
2. Determine whether lower torso volume, measured from convex hulls of articulated torsos, is related to diet.

3. Examine how torso form and lower torso volume relate to diet while taking into account the influences of body size and locomotion.

The results of this research will influence how we infer diet from fossil primate skeletons and how paleoanthropologists interpret the functional implications of the torso anatomy of fossil hominins.

Gut size and diet in extant primates

As mentioned above, differences in torso form among extinct hominins have been linked to potential gut size shifts related to the different digestive demands of animal tissues, fruits, and leaves (Aiello and Wheeler, 1995; Wrangham et al., 1999, Lovejoy et al., 2009; Schmid et al., 2013; Williams et al., 2017). In mammals, including primates, gut size and functional morphology broadly correlate with dietary categories (Mitchell, 1905; Le Gros Clark, 1971; Chivers and Hladik, 1980; Milton, 1987).

Chivers and Hladik (1980), which is one of the first publications to integrate data about diet with quantitative data on the primate digestive tract, provide the largest comparative sample of primate gut sizes. Working under the assumption that gut proportions—namely the relative length contributed by the components of the small and large intestine—reflect dietary adaptation, they compared the sizes and shapes of the primate stomach, small intestine, and large intestine—caecum and colon—to those of other mammals to find patterns that define diet categories. Most of their measurements come from fresh specimens that were opened and flattened under water in dissecting trays. The lengths and widths of the components were then used to calculate surface area and estimate volume. The authors acknowledge the plasticity of gut organ tissue and

claim that their methods are "the best compromise" for taking measurements (Chivers and Hladik, 1980, p. 356).

Overall, these authors found 1) overlap in gut size and organ proportions among faunivores, frugivores, and folivores, which they attributed to individuals with diets that straddle these categories, and 2) that larger species have absolutely larger guts (Chivers and Hladik 1980). However, there are some general patterns in gut size and proportions that characterize primate diet groups. Folivorous primates tend to have relatively larger guts, with either enlarged, sacculated stomachs (e.g., colobines) or larger hindguts (e.g., howler monkeys) to properly ferment plant material. The authors also found that primates that habitually feed on insects and small animals (e.g., some platyrrhines, modern humans) tend to have relatively smaller guts that are dominated by the small intestine, providing sufficient surface area for absorbing amino acids and lipids from diets higher in fat and protein. Primates classified as frugivores (e.g., *Ateles*, some guenons, chimpanzees) lack extreme size and structural specializations (Chivers and Hladik, 1980).

Ferrari and Martins (1992) and Ferrari and Lopes (1995) used the same methodology as Chivers and Hladik (1980) to expand the comparative dataset on gut size and proportions for primates. Young Owl (1994) developed a method that involved cutting the gut into segments, pinning the flattened pieces onto paper, drawing outlines of the pieces, and then tracing these outlines with a computer tablet pen that automatically calculated the surface area. When these results were compared to a modified version of the Chivers and Hladik (1980), both methods yield nearly the same results, except for estimates of colon surface area in smaller animals, for which the newer method generally generated slightly larger surface areas. Young Owl (1994) attributed the discrepancy in

colon measurements to Chivers and Hladik's use of geometric formulae that did not account for the area in the semi-lunar folds. Though this study refers to problems with the methods used by Chivers and Hladik (1980) and others, it confirmed their general accuracy.

The inclusion of juveniles and captive individuals in the Chivers and Hladik (1980) dataset introduces additional sources of intraspecific variability. Gut size and function changes with age, so averaging values from juveniles and adults could obscure any species-specific morphological signal from datasets based on adult individuals (Meier et al., 2007, Saffrey, 2014). Combining data from captive and wild individuals has a similar effect, as differences between "natural" and "captive" diets are known to affect gut dimensions and function (Liukkonen-Anttila et al., 2000; O'Regan and Kitchener, 2005). Despite the issues with the gut surface area data provided by Chivers and Hladik (1980) and others, I have used a modified version of this dataset that minimizes the number of juvenile, captive, and fixed specimens to test the relationships between diet and torso form. Furthermore, the primary proxy for diet is not gut size, but the percentage of feeding time based on observations of wild primate populations (see Chapter 2 for more information).

Relationship between diet, gut size, and the torso skeleton in extant primates

Chivers and Hladik (1980) had a significant impact on the paleoanthropological literature, as Aiello and Wheeler (1995) and subsequent research cite the slight differences in gut sizes among extant primates with different diets as evidence for the expectation that differences in hominin torso dimensions reflect diet-induced differences

in gut size. However, there is currently little research testing whether differences in diet and gut size can be determined from the torso skeleton in extant primates. Differences in the torso skeleton of extant primates are instead typically explained as a product of differences in phylogenetic history, body size, posture and/or locomotion. I review these arguments in the subsequent section.

In a very broad sense, differences in diet *can* be inferred from differences in primate torso form due to the connections between diet and body size. Larger-bodied species more often rely on leaves and other green plants (Clutton Brock and Harvey, 1977; Gaulin, 1979; Sailer et al., 1985), while smaller-bodied species often consume higher proportions of invertebrate and vertebrate prey (Gaulin, 1979; Sailer et al., 1985). Therefore, as torso form differs across primate body sizes (e.g., Lewton, 2015; Ward et al., 2018) broad generalizations about an individual's dietary preferences *could* be made from the size and shape of torso skeleton. However, frugivorous primates overlap in body size with folivores and insectivores (Gaulin, 1979), and there are also exceptions to this diet/size spectrum. For example, relatively large-bodied hylobatids have been observed to feed on prey nearly as much, or sometimes more often, as they feed on green plants (Palombit, 1997). Given these confounding factors, quantitative research on whether differences in diet among primates can be reliably inferred from differences in the torso skeleton across a wide range of body sizes is required.

Only recently has there been a focus on quantitatively testing whether the extant primate torso is related to diet and gut size. Uy and Hawks (2018) analyzed abdominal CT scans of modern humans and found that intestinal volume is related to pelvic dimensions in males but not in females, which may be due to the confounding influence

of pregnancy on the soft and hard tissues of the torso. Investigating dietary differences among the individuals was not a focus of this research.

Preliminary results from a study we conducted last year suggests that there is a relationship between iliac flare and gut size in hominoids, but not in monkeys (Boyle and Almécija, 2018). However, the sample size for hominoids is low (n = 5), and we found that the relationship between gut size and iliac flare in hominoids is strongly tied to the effect of body size on these two variables. The question remains whether a relationship between torso form and other dietary proxies (such as feeding time on different food items) remains after considering the effects of body size.

Torso form in extant primates

Monkey, ape, and modern human torsos demonstrate notable differences in form that have traditionally been attributed to differences in phylogenetic history, locomotion, posture, and body mass (Schultz, 1930; Schultz, 1950; Hunt, 1991; Ward, 1993; Schmid, 1991; Chan, 2014; Lewton, 2015; Latimer et al., 2016; Bastir et al., 2017; Middleton et al., 2017; Ward et al., 2018). Most monkeys exhibit dorsoventrally deep but mediolaterally narrow "barrel-shaped" ribcages with long, flexible vertebral columns, wide sacra, and narrow ilia that facilitate pronograde quadrupedalism (Figure 1; e.g., Schultz, 1961; Hunt, 1991; Ward, 1993; Chan, 2014; Middleton et al., 2017; Ward et al., 2018).

In the great apes, it has been suggested that the dorsoventrally narrow, "funnel-shaped" thoraces (Schultz, 1961; Schultz, 1969), shorter lumbar vertebral columns, narrow sacra, and laterally expanded, flared ilia provide stability in the lumbar spine to facilitate below-branch arboreal locomotion (Figure 1; Hunt, 1991; Ward, 1993; Chan,

2014; Middleton et al., 2017; Ward et al., 2018). Some larger, more suspensory taxa, such as atelids, are similar to apes in many aspects of torso form (e.g., Ward, 1993; Larson, 1998; Ward et al., 2018).

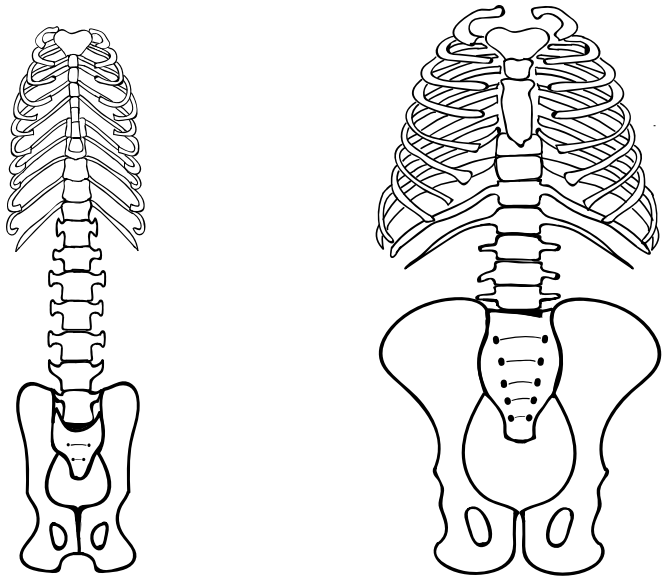

Figure 1. Monkeys generally have narrow ribcages, long lumbar vertebral columns, and narrow ilia while great apes have "funnel-shaped" ribcages, reduced lumbar vertebral columns and wide, flared ilia. These images were redrawn after Schultz (1950).

This is just one example of body mass contributing to differences in torso form among primates. For example, ilium breadth scales with positive allometry (Lewton, 2015; Ward et al., 2018), distances between the lumbosacral, sacroiliac, and hip joints decrease as body size increases (Ward et al., 2018), and body size seems to particularly affect torso form variation within hylobatids (Larson, 1998). Specifically, *Hylobates* exhibit a human-like "barrel-shaped" thorax and are similar to monkeys in iliac width (Schultz, 1933; Hunt, 2016; Lewton, 2015; Middleton et al., 2017; Ward et al., 2018), while the larger *Symphalangus* shares a more "funnel-shaped" thorax, broad ilia, and a shortened lumbar spine with the great apes (Schultz, 1933; Hunt, 2016; Ward et al.,

2018). These differences have led researchers to describe hylobatid torso form as intermediate between that of monkeys and apes (Mivart, 1865; Erickson, 1963).

In modern humans and hominins, the dorsoventrally narrow thorax, and "barrel-shaped" ribcage (Schultz, 1961; Jellema et al., 1993; Latimer et al., 2016), lordotic lumbar spine and flared, laterally-rotated ilia, have been interpreted as adaptations to bipedalism (e.g., Schmid, 1991; Latimer et al., 2016).

Torso form in fossil primates and hominins

Torso form in extant primates is used as a comparative reference for reconstructing fossil primate torso form. For the non-hominin primate fossil record, these reconstructions largely focus on finding anatomical determinants of locomotor and postural adaptations that either suggest similarities to extant monkeys or apes. For example, the monkey-like torso remains of the *c.*18 Ma remains of *Ekembo nyanzae* suggest that this basal hominoid was an above-branch quadruped (Ward, 1993; Ward et al., 1993). A later shift to more extant ape-like torso form and accompanying evolution of orthograde and/or suspensory behaviors has been documented in the clavicle, ribs, lumbar vertebrae, and pelvis of *Pierolapithecus* (Moyà-Solà et al., 2004; Hammond et al., 2013a), lumbar vertebrae of *Morotopithecus* (Nakatsukasa, 2008) and *Hispanopithecus* (Moyà-Solà and Köhler, 1996; Susanna et al., 2014), and the pelvis of *Rudapithecus* (Ward et al., 2008) and *Oreopithecus* (Wunderlich et al., 1999; Russo and Shapiro, 2013).

Reconstructions of torso morphology, and their use to infer function, within the hominin lineage have been much more contentious. Partial torso skeletons are known for several hominin species and descriptions of these and more fragmented specimens have

led to ongoing debates over when, why, and how torso anatomy has changed during hominin evolution (e.g., Tague and Lovejoy, 1986; Schmid, 1991; Ruff, 1994; Aiello and Wheeler, 1995; Wrangham et al., 1999; Franciscus and Churchill, 2002; Bramble and Lieberman, 2004; Gómez-Olivencia et al., 2009; Lovejoy et al., 2009; Kibii et al., 2011; Schmid et al., 2013; White et al., 2015; Latimer et al., 2016). For the earliest hominins, most reconstructions of torso anatomy are focused on determining the extent of arboreal and bipedal capabilities. Although little is known about the lower ribcage and lumbar spine morphology for *Ardipithecus ramidus*, a wide, more sagittally oriented ilium alongside other similarities in pelvic anatomy to *Australopithecus afarensis*, suggest that bipedal adaptations in the lower torso may have been present by *c.*4.4 Ma (Lovejoy et al., 2009; White et al., 2015).

In *A. afarensis*, however, conflicting interpretations of the A.L. 288-1 and KSD-VP-1/1 partial skeletons have resulted in debate about the torso form and locomotor adaptations of this species (e.g., Schmid 1983; Schmid 1991; Latimer et al., 2016). Reconstruction of the *c.*3.2 Ma A.L. 288-1 ("Lucy") thorax by Schmid (1983) suggested that this individual had a "funnel-shaped" thorax, which along with a flaring ilium with a broad attachment for the origin of latissimus dorsi, may signify orthograde climbing. Similar morphology in the *c.*2.5 Ma *A. africanus* Sts 14 pelvis led Schmid (1991) to conclude that australopiths were likely not efficient at bipedal walking and running. By contrast, Robinson (1972) suggested that *A. africanus* pelvic morphology is functionally equivalent to that of modern humans, and most researchers subscribe to the consensus that the lower torso of *A. afarensis* and *A. africanus* is consistent with these species being

biomechanically efficient bipeds, albeit employing a variety of locomotor behaviors (Kimbel and Delezene, 2009; Claxton et al., 2016).

The hypothesis that australopiths had a "funnel-shaped" thorax prevailed until the discovery of the KSD-VP-1/1 skeleton (Haile-Selassie et al., 2010). Based on the curvature of the second rib, and the torsion and orientation of lower ribs, Latimer et al. (2016) suggest that the thorax of KSD-VP-1/1 was not "funnel-shaped" but "bell-shaped," having a slightly broader upper thorax and slightly narrower lower thorax, relative to apes. Furthermore, although the KSD- VP-1/1 pelvis is generally similar to A.L. 288-1, the former is more modern human-like in size and lacks the extreme platypelloidy (elliptical-shaped birth canal) and iliac flaring of the latter (Lovejoy et al., 2016). Although Latimer et al. (2016) suggest that australopiths did not have a "funnel-shaped" thorax, reconstructions of the thorax and pelvis suggest that *A. afarensis* had a relatively wider lower torso than modern humans.

The 1.977 Ma torso remains of *Australopithecus sediba* seem to depart from the condition observed in *A. afarensis* and *A. africanus*. Reconstruction of the *A. sediba* partial skeletons suggest that the torso displays a unique mosaic of a narrow, ape-like upper thorax, combined with a modern human-like lower thorax, a long, lordotic lumbar spine, and pelvis narrower than other australopiths (Kibii et al., 2011; Schmid et al., 2013; Williams et al., 2013). Schmid et al. (2013) propose that this combination would have reduced arm-swinging and breathing capabilities during endurance walking and running, possibly indicating that *A. sediba* retained arboreal capabilities (but see Haile-Selassie et al., 2016 for criticisms of this interpretation).

Whereas explanations for observed torso form in australopiths are primarily linked to locomotion and posture, changes in hominin torso form that occur subsequent to the emergence of at least facultative, if not obligate, bipedalism have led researchers to suggest that other factors may influence torso proportions (Tague and Lovejoy, 1986; Ruff, 1994; Aiello and Wheeler, 1995; Wrangham et al., 1999; Bramble and Lieberman, 2004; Gruss and Schmitt, 2015; Bastir et al., 2016; Ben-Dor et al., 2016; García-Martínez et al., 2016; 2018). Some researchers have attributed torso differences to changes in thermoregulatory demands, based on the demonstrated ecogeographic influences on modern human body shape (Ruff, 1994; Franciscus and Churchill, 2002; Bramble and Lieberman, 2004). Relative to other Pleistocene *Homo* species, anatomically modern humans have narrower torsos, with "barrel-shaped" thoraces and less-flaring pelves, and latitudinal and altitudinal variation in torso dimensions have been linked to thermoregulation and respiration (Ruff 1994; Weinstein, 2008; Gruss and Schmitt, 2015). The "barrel-shaped" thorax and reduced bi-iliac breadth, which create a narrow body form in the *c.*1.5 Ma KNM-WT 15000 *H. erectus* partial skeleton, have been interpreted as conferring a thermoregulatory advantage over australopiths, especially when walking and running in open, dry, and hot environments (Wheeler, 1993; Ruff, 1994; Bramble and Lieberman, 2004). Similarly, the relatively broad, "hyper-barrel-shaped" thoraces and wider pelves in Neanderthals, and the broad *Homo* pelvis from Jinniushan, China, have been interpreted as advantageous in the closed, colder environments of Europe (Ruff, 1994; Franciscus and Churchill, 2002; Rosenberg et al., 2006).

Other researchers have suggested that torso form is linked to respiratory capability (Weinstein, 2008; Bastir et al., 2013; Chan, 2014; Bastir et al., 2016; García-

Martínez et al., 2018). For example, based on modern human respiratory kinematics, Bastir et al. (2016) suggest that relatively larger lower thoracic ribs in Neanderthals and australopiths may signify differences in breathing kinematics relative to modern humans. Additionally, García-Martínez et al. (2018) estimate that total lung capacity was about 20% larger in Neanderthals than in modern humans based on ribcage dimensions. Neanderthal thorax form may also reflect respiratory adaptations to high activity levels (Weinstein et al., 2008; Gómez-Olivencia et al., 2009).

The extent of the effect of sexual dimorphism on torso form is difficult to determine for early hominins, but differences in the shapes of the birth canal have been linked to obstetric constraints (Tague and Lovejoy, 1986; Rosenberg, 1992; Weaver and Hublin, 2009; Gruss and Schmitt, 2015). Sex not only affects pelvic shape and size in modern humans, but it also has a complex interaction with the other factors that influence the torso (Kurki, 2011; Gruss and Schmidt, 2015; Moffett, 2017; Torres-Tamayo et al., 2018). Kurki (2011) suggests that pelvic sexual dimorphism across a global sample of modern humans is not correlated with body size dimorphism. Similarly, Moffett (2017) argues that modern humans have high pelvic dimorphism, particularly in the size shape of the midplane and outlet, despite low body size dimorphism. By examining virtual models of articulated torsos compiled from CT scans of living humans, Torres-Tamayo et al. (2018) found that females tend to have wide pelves and narrow thoraces, while males have narrow pelves and wide thoraces.

Variation in torso form that is independent of locomotion is not unique to hominins. The likely body size effect on torso form in hylobatids was addressed earlier in this chapter, yet despite differences in torso form between *Hylobates* and *Symphalangus*,

both species engage in brachiation. Additionally, Chan (2014) suggests that differences in dimensions of the upper thorax between hominoids and monkeys could reflect differences in respiratory adaptations. Lastly, several researchers have noted that sexual dimorphism in the pelvis of non-human primates is linked to obstetric constraints due to neonate size, as well as body size differences between males and females (e.g., Steudel, 1981; Kurki, 2011; Moffett, 2017). However, Moffett (2017) also finds that there is birth canal dimorphism among anthropoids regardless of neonate size, but the magnitude of dimorphism is higher in species that give birth to larger neonates. This author suggests that females may achieve bigger birth canals by having overall larger pelves, highlighting the importance of quantifying dimorphism in pelvic features beyond the birth canal (Moffett, 2017).

It is therefore possible, if not probable, that across all primates torso form is influenced by factors other than locomotion and posture. Recent analyses of extinct hominin and modern human thoraces have suggested that upper and lower torso evolution may be decoupled (Bastir et al., 2013; Schmid et al., 2013; García-Martínez et al., 2016), with the upper thorax reflecting upper limb function (Schmid et al., 2013) or respiratory system development (Bastir et al., 2013; García-Martínez et al., 2016), while the lower thorax is potentially more responsive to differences in spinal musculature (Middleton et al., 2017; Ward et al., 2018) and/or in the digestive system (Bastir et al., 2013). This modularity hypothesis contrasts with the conventional wisdom that in primates the thorax, vertebral column, and pelvis all respond in an integrated way to locomotion (Ward, 2002). If locomotion is not the primary (or sole) target of selection in the torso,

and if the torso can respond in different ways to a range of selection pressures, then it is reasonable to consider that differences in diet may also influence torso morphology.

History of inferring diet and gut size from torso morphology

Linking torso form to diet assumes that the hard tissues of the trunk carry a dietary signal, but for this to be the case in primates there needs to be a link between torso form and the size, shape, and functional morphology of the soft tissues it surrounds. But the abdominal organs are not entirely encased by the ribs and pelvis, nor do they leave any obvious marks (e.g., grooves, fossae) on bone that are helpful for reconstructing soft tissue size and shape (Witmer, 1995). It is also unclear if the gut influences torso form during development (Bastir et al., 2013).

Despite the poorly understood anatomical and developmental relationships between the gut and the torso, several features of the thorax and pelvis have been linked to differences in gut size and diet among non-primate mammals. The first researcher to draw the link between torso form and diet was Elftman (1929), who conducted research on marsupials and suggested that lower thorax breadth and pelvis breadth are wider in the herbivorous kangaroo than in the omnivorous bandicoot. In bovids, differences in lumbar transverse process morphology and iliac flare between small-bodied and large-bodied species have been linked to allometric differences in gut size (Halpert et al., 1987; Cartmill and Brown, 2017). Similarly, recent analyses of a large sample of articulated torsos indicate that relative body cavity volume in herbivores is about 1.5 times larger than that in carnivores (Clauss et al., 2017).

Although similar relationships have not yet been tested in extant primates, features of the torso have been used to make inferences about fossil primate torso form,

gut size, and diet. For example, Shapiro et al. (2005) cite Halpert et al.'s (1987) claims about the relationship between gut size and torso form in bovids when suggesting that lumbar transverse process morphology in *Palaeopropithecus* may be related to folivory. However, other studies have found reliable evidence in extant primates that lumbar transverse process orientation and position are more closely correlated with the size of erector spinae musculature (Ward, 1993; Russo and Williams, 2015). As a result, these specific variables are not a focus of this project.

The first researcher to link bony torso anatomy to gut size in hominins was Robinson (1972). In his descriptions of the Sts 14 pelvis attributed to *A. africanus*, Robinson (1972, p. 60) argues that the laterally extended, flared iliac blades in this specimen signify a "well-developed and protuberant abdomen." Robinson (1972) goes on to say that *A. africanus* was therefore "pot-bellied" in a manner similar to pongids. Robinson's (1972) conclusions about the SK 50 os coxa attributed to *P. robustus* are similar. He claims that this species also had a "chunky trunk with a protuberant abdomen," and suggests that this "thickset trunk" was even more exaggerated in *P. robustu*s than in *A. africanus* (Robinson, 1972, p. 95). Schmid (1991, p. 229) applied this idea to all australopiths following his reconstruction of the A.L. 288 partial skeleton (Schmid, 1983), arguing that thoracic and pelvic form across *Australopithecus* individuals reflect "short, stout torsos with protuberant abdomens." However, neither Robinson (1972) or Schmid (1991) explicitly link a wide pelvis, flared ilium, or a protuberant abdomen to dietary preferences in australopiths or *Paranthropus*. However, Robinson (1972) did suggest that a long, powerful ischium in *Paranthropus* would have facilitated the tree climbing necessary for gathering food to sustain an herbivorous diet.

These publications were integral to Aiello and Wheeler's (1995) argument that shifts in torso form between *Australopithecus* and *Homo* reflect a dietary shift (Figure 2). Specifically, Aiello and Wheeler (1995) state that the wide lower thorax, broad pelvis, and flared ilia in *A. afarensis* and *A. africanus* indicate that australopiths had larger guts and a lower-quality diet relative to *H. erectus* (KNM-WT 15000). The reconstructed KNM-WT 15000 skeleton has a narrower lower ribcage, reduced bi-iliac breadth, and reduced iliac flare, which Aiello and Wheeler (1995) suggest reflects a reduced hindgut (caecum and colon) following a shift to a higher-quality diet. The obvious consequence of this argument is stated by the authors in their concluding paragraph (p. 211):

> "…diet can be inferred from aspects of anatomy other than teeth and jaws. For example, an indication of the relative size of the gastro-intestinal tract and consequently the digestibility of the food stuffs being consumed is provided by the morphology of the rib cage and pelvis."

The hypothesis that *H. erectus* exhibits a diet-induced reduction in gut size has not been revised to accommodate recent reconstructions of KNM-WT 15000 (e.g., Fornai and Haeusler, 2017), or evidence from other specimens, such as the BSN49/P27 pelvis, which suggest that relatively wide bi-iliac breadths, pronounced iliac flaring, and broad trunks were retained in *H. erectus* and other middle to late Pleistocene *Homo* individuals (Simpson et al., 2008). This may signify that narrow torso form, and potentially a reduced gut, is unique to anatomically modern humans (Wrangham, 2017).

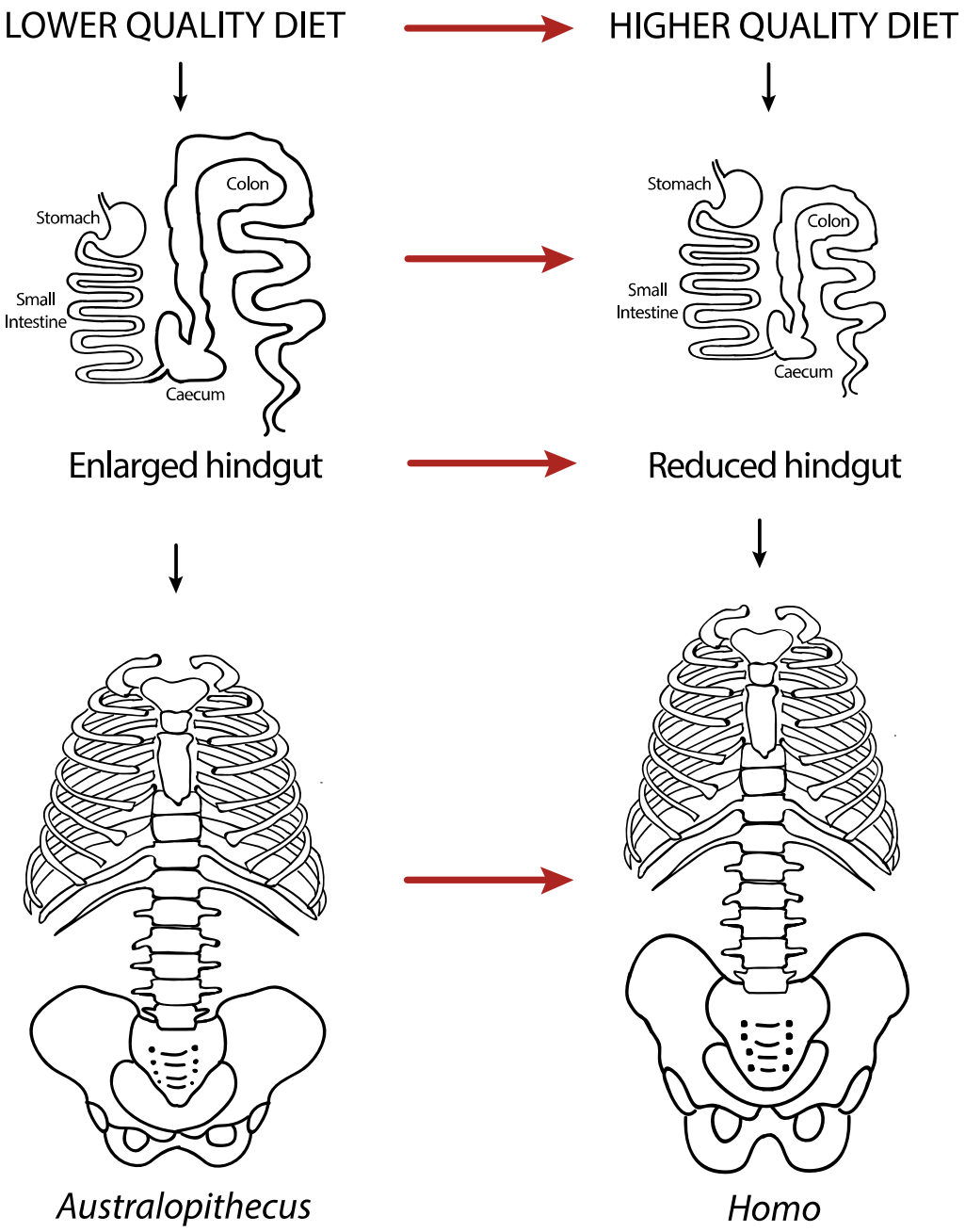

Figure 2. Hypothesized diet-induced shift in torso form between *Australopithecus* and *Homo*. *Australopithecus* redrawn from Aiello and Wheeler (1995).

In Neanderthals, Ben-Dor et al. (2016) speculate that the broad lower thorax and wide pelvis indicate an enlarged liver and urinary organ sizes resulting from a high protein diet. This argument goes against the assumption that primate faunivores would have more narrow torsos than herbivores. Altneratively, Wrangham (2017) suggests that

it is possible that the broad torso in Neanderthals and other pre-modern *Homo* species reflect large guts needed for digesting raw, low-quality foods (Wrangham, 2017).

Despite the recovery of partial skeletons with torso remains, no inferences have been made about gut size in *Ar. ramidus*, *A. sediba*, and *Homo naledi*. However, descriptions of torso form in these species reference claims about gut size and diet in other hominins and extant primates (Lovejoy et al., 2009; Schmid et al., 2013; Williams et al., 2017). For example, in their descriptions of the *Ar. ramidus* pelvis and femur, Lovejoy et al. (2009) mention that a relatively long lumbar region with six vertebrae in *A. afarensis* would have accommodated a voluminous gut. These authors also mention that ilium breadth in large anthropoids could reflect a larger gut and folivory or frugivory (Lovejoy et al., 2009). Additionally, Williams et al. (2017) suggest lower thorax breadth reflects a large gut size and herbivorous diet in great apes.

These hypotheses are compelling, but some are based on inferences about hominin morphology that we now know are not likely. For example, *Au. afarensis* most likely had only five lumbar vertebrae, not six (Ward et al., 2017). It also might be more intuitive to infer that accommodating a larger gut would require fewer lumbar vertebrae in order to stabilize the lower torso, not a longer lumbar region. Moreover, as mentioned above, the parts of the torso that researchers relate to gut size, abdominal volume, and/or diet in primates are almost certainly also linked to body size, locomotion and posture (e.g., Hunt, 1991; Ward, 1993; Schmid, 1991; Lewton, 2015; Latimer et al., 2016; Middleton et al., 2017; Ward et al., 2018) and are also influenced by phylogenetic history. Lastly, the assumptions about how diet-induced differences have not been tested in a large comparative sample of primates. We cannot confidently claim that torso

differences amongst fossil hominin species reflect shifts in diet until we have comparative evidence that the torsos of closely-related extant primates carry a dietary signal, after considering the effects of body size and locomotion.

Dissertation objectives

In order to establish a comparative context for attempts to infer diet from torso form in extinct hominins, this study looked for evidence of a link between torso form (e.g., lower thorax breadth, lumbar spine length, bi-iliac breadth, ilium width, iliac flare, and abdominal cavity volume), gut size and diet by comparing these variables among primate species that feed on substantial amounts of vertebrates and invertebrates (smaller guts), or on fruit (intermediate gut sizes), or other plant tissues (larger guts).

Chapter 2 presents the results of three analyses that if, and how, diet is related to the form of the torso in a sample of primates that differ in their diet, locomotion, and body size. In Analysis A, which translates hypotheses from the literature about how each torso feature relates to diet and/or gut size into phylogenetic least squares (PGLS) regressions, I found there was no relationship between diet and the torso that was independent of body size. In Analysis B, I tested how several torso variables features together, as an approximation of lower torso shape, relate to diet and locomotion, and found that the best fitting models for both males and females were where acetabular diameter was the only covariate (the null model). Models that include diet variables are not significantly different from the null model in both sexes, but the locomotion-only models are significantly different from the null. In Analysis C, I perform six discriminant function analyses to test how the torso variables distinguish among dietary and locomotor

groups. I found that there is substantial overlap among dietary categories, and the torso variables are better at discriminating amongst locomotor groups.

In Chapter 3, I perform comparisons between similarly-sized pairs of species within platyrrhines, cercopithecoids, and hominoids that have different diets. These pairwise comparisons simulate how paleoanthropologists have inferred shifts in diet from the fossil record (i.e., stating that differences in torso between two similarly-sized hominin taxa, *Australopithecus* and *Homo*, reflect different diets). Therefore, these comparisons are particularly useful for establishing a framework to apply to the hominin fossil record. I found that out of 11 comparisons of species pairs, only four provide partial support for the hypothesis that more folivorous species are broader in torso dimensions that frugivores or more faunivorous species. The seven other comparisons yield various results that do not support this hypothesis. There are two instances where more faunivorous species are broader in torso dimensions, an example where species with different diets do not show differences, and four comparisons where species with similar diets demonstrate significant differences in torso dimensions.

In Chapter 4, I test how volume of the lower torso (below the level of the 6^{th} rib) correlates with diet, gut size, body size, and maximum habitat altitude. Lower torso volumes were measured from the convex hulls of 3D models of articulated torsos of 44 individuals representing 20 anthropoid taxa. Variation in lower torso volume across the sample is related to body size, and phylogenetic signal in this trait is strong. Of the diet variables tested, only percent of roots and tubers in diet demonstrates a significant relationship with relative torso form. However, this result should be accepted with

caution as only four species in the sample have a value for roots and tubers above 0%. Variation in lower torso volume is also not related to gut size or altitude.

I summarize the implications of the results of this dissertation in the Conclusions chapter (Chapter 5). None of the analyses presented in Chapters 2, 3, and 4 suggest that there is a link between the bones of the extant primate torso and diet. Variation in torso form across the sample appears to be patterned by differences in body size, locomotion, and phylogenetic relatedness.

Chapter 2: Are torso variables related to diet after accounting for phylogeny, body mass, and locomotion?

Introduction

Paleoanthropologists have used torso differences among hominin species to infer shifts in diet across evolutionary time. Most notably, Aiello and Wheeler (1995) argue that flared ilia, wide pelvis, ape-like "funnel-shaped" ribcage in *c.*3-2 Ma *Australopithecus* indicate a large gut and thus a lower-quality diet dominated by leaves and fruits. This contrasts with the less flared ilia, narrower pelvis, and less broad, "barrel-shaped" ribcage in *c.*1.5 Ma *Homo*, which are linked to a smaller gut and higher-quality diet comprised of "animal products, nuts, or underground tubers" (Aiello and Wheeler, 1995, p. 211). A similar argument was made by Lovejoy et al. (2009), who suggested that a broader ilium reflects larger gut size in folivorous and frugivorous anthropoids, and that a long lumbar vertebral column in *Australopithecus* is indicative of a large gut. These hypotheses about how torso morphology relates to diet are based on the reconstructed morphology of just a few, fragmentary specimens. Furthermore, these hypotheses have not been tested in extant primates, which is important for establishing a comparative framework that can be applied to the hominin fossil record.

Iliac flare, ilium width, pelvis breadth, ribcage breadth, and lumbar vertebral column length vary across anthropoid primates in a way that has been linked to differences in locomotion and posture. For example, apes are characterized by wide pelves with broad, laterally-flared ilia and transversely broad but dorsoventrally-narrow lower thoraces, which provide broad attachment areas for *m. quadratus laborum* and *m. latissimus dorsi* to stabilize the reduced lumbar spine in orthograde postures and suspensory locomotion (Chan, 2014; Lewton, 2015; Middleton et al., 2017; Ward et al.,

2018). The narrower torso in monkeys allows for a more ventral orientation of the glenoid fossa of the scapula so that it is weight-bearing in pronograde postures, and the relatively long lumbar vertebral column in monkeys facilitates flexion and extension of the back during quadrupedal locomotion (Schultz, 1961; Chan, 2014; Middleton et al., 2017; Ward, 1993; Ward et al., 2018). Additionally, despite having narrower ilia and narrower pelves overall relative to apes, in monkeys the expanded dorsal space between the ilia (Middleton et al., 2017) accommodates a larger erector spinae muscle mass.

Differences in torso form among primates cannot be compared without acknowledging the substantial influence of body size on the torso variables of interest here. In general, larger primates have mediolaterally broader torsos and wider ilia, and differences across anthropoids are driven by strong positive allometry (Lewton, 2015; Middleton et al., 2017; Ward et al., 2018). Larger primates also have shorter lumbar vertebral columns relative to smaller anthropoids (Schultz, 1933; Schultz, 1961; Benton, 1967; Ward, 1991; Ward et al., 1993; Hunt, 2016; Middleton et al., 2017; Ward et al., 2018). Moreover, body size dimorphism between males and females in some species may contribute to differences in pelvic form (e.g., Steudel, 1981; Leutenegger and Larson, 1985; Tague, 2005; Kurki 2011; Moffett, 2017). Therefore, in order to identify if there are differences in anthropoid torso form that can be attributed to diet, relationships between diet and torso variables must be tested while considering body size and locomotion.

In this chapter, I report the results of three analyses to identify whether or not diet is related to the skeletal form of the torso. Table 1 summarizes the goals of each analysis, as well as the sample sizes and variables included in each. In the first analysis (Analysis

A) I conducted phylogenetic generalized least squares (PGLS) regressions across a sample of 44 anthropoids to test specific hypotheses from the literature about how diet is related to torso form. Specifically, I test whether ilium width, iliac flare, bi-iliac breadth, lumbar vertebral column length, and ribcage breadth (in a smaller sample) show any relationship with gut size or the percentages of various food items in a species' diet (Elftman, 1929; Schmid, 1991; Aiello and Wheeler, 1995; Lovejoy et al., 2009).

Recent research (e.g., Middleton et al., 2017; Ward et al., 2018) indicates that studying multiple elements of the torso together may offer other insights than those from analyses that consider these elements in isolation. Therefore, in Analysis B, I selected five torso features and used multivariate, multiple PGLS regressions to test the relationship between these measures and acetabular diameter, diet, and locomotion in 31 species. This analysis tests whether variation in lower torso shape can be best explained by variation in acetabular diameter (body size proxy), or by models that also consider variation in diet or locomotion. In Analysis C, I performed a series of discriminant function analyses (DFA) using torso, diet, and locomotor data for 31 species. This analysis tests whether or not torso variables better distinguish among dietary or locomotor categories. Analysis C is therefore similar to Analysis B but provides a way to visualize the relationships between the torso, diet, and locomotion variables.

QUESTION:	ANALYSIS A		No. Species:		Diet data:	Measurements size-adjusted?	Body size control in models?	Locomotion data in models?	Analyses performed:
	Measurements:		F	M					
Does testing specific hypotheses about how diet relates to the torso reveal a signficant relationship between the two?	Ribcage breadth	✓	21	21	% Feeding time & Gut size	Yes, by acetabular diameter	Yes, logged acetabular diameter	No	Multiple PGLS regressions
	Lumbar spine length	✓	44	44					
	Upper ilium width	✓	45	45					
	Lower ilium width	X	-	-					
	Bi-iliac breadth	✓	45	45					
	Iliac flare	✓	45	45					
	False pelvis length	X	-	-					
QUESTION:	**ANALYSIS B**		**No. Species:**		**Diet data:**	**Measurements size-adjusted?**	**Body size control in models?**	**Locomotion data in models?**	**Analyses performed:**
	Measurements:		F	M					
Is there a relationship between multiple torso variables and diet after considering body size and locomotion?	Ribcage breadth	X	-	-	% Feeding time	Yes, by the geometric mean	Yes, acetabular diameter	Yes, for all species	Multivariate multiple PGLS regressions
	Lumbar spine length	✓	31	31					
	Upper ilium width	✓	31	31					
	Lower ilium width	✓	31	31					
	Bi-iliac breadth	✓	31	31					
	Iliac flare	X	-	-					
	False pelvis length	✓	31	31					
QUESTION:	**ANALYSIS C**		**No. Species:**		**Diet data:**	**Measurements size-adjusted?**	**Body size control in models?**	**Locomotion data in models?**	**Analyses performed:**
	Measurements:		F	M					
Do torso variables discriminate among dietary and locomotor groups?	Ribcage breadth	X	-	-	Diet categories	Yes, by acetabular diameter	N/A	Yes, locomotor categories for 31 species	Discriminant function analyses
	Lumbar spine length	✓	31	31					
	Upper ilium width	✓	31	31					
	Lower ilium width	X	-	-					
	Bi-iliac breadth	✓	31	31					
	Iliac flare	✓	-	-					
	False pelvis length	X	31	31					

Table 1. Summary of Analyses A through C.

Materials and Methods

Sample size differences

Linear measurements were taken on the skeletons of 429 adult wild shot individuals representing 48 species of primates in collections at the American Museum of Natural History (AMNH), Cleveland Museum of Natural History (CMNH), National Museum of Natural History (NMNH), Museum of Comparative Zoology at Harvard (MCZ), and the University of Zurich (UZIA). This is the total skeletal sample size collected for most measurements, but sample sizes for the statistical analyses in this chapter are smaller due to 1) the limited availability of lumbar vertebral column lengths and ribcage breadths for some species, and 2) the limited availability of diet, locomotion, and gut size data for some species. The samples of species included in each of the three statistical analyses are described in the sections below, and either listed in the phylogenetic trees for that analysis (Analysis A, Figure 4; Analysis B, Figure 5), or tables when subsample sizes are lower for some parts of the analyses.

Torso morphology

Nine linear measurements were taken on the torso skeletons. Sex-specific species averages for each measurement are provided in Table 2. These measurements are defined in Table 3 and illustrated in Figure 3. Raw data for each individual is provided in a GitHub repository (search for "torso-diet" on github). All measurements other than bi-iliac breadths and some ilium widths on the larger specimens (>154 mm) were taken with Mitutoyo digital calipers. The longer measurements on the largest specimens were taken with a 450 mm-long ruler. Measurements were taken following definitions in Middleton et al. (2017) and Lewton (2015) (Table 2). Upper ilium width, iliac fossa width, false

pelvis length, and acetabular diameter were all measured on the left os coxa (Table 3). To measure bi-iliac breadth and bi-acetabular breadth, ilia were articulated with putty at the sacroiliac joints and the pubis. The thickness of the putty did not exceed 3 mm (Li, 2002; Middleton et al., 2017). Ribcage breadths at rib levels 7 through 11 were taken on articulated ribcages of 65 individuals representing 31 species. The breadths at the level of the 7th rib were used in statistical analyses because the sample size for these values is larger than ribcage breadths at other rib levels. Iliac flare is defined as the ratio between false pelvis length and iliac fossa width (Hammond et al. 2013a). I calculated the ratio as the inverse of the ratio provided in Hammond et al. (2013a) so species that are more flared (e.g. gorillas) have larger values, as opposed to a value closer to 0.

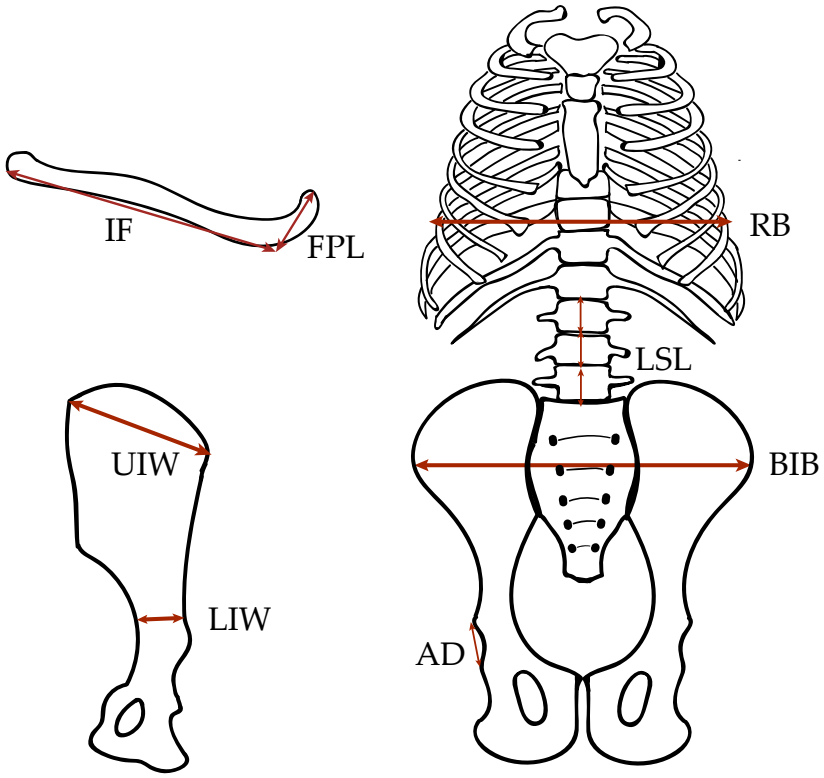

Figure 3. Linear measurements collected from primate torsos. Top left, right ilium in superior view, illustrating iliac flare (IF) and false pelvis length (FPL). Bottom left, right ilium in dorsal view, illustrating upper ilium width (UIW) and lower ilium width (LIW). Right, articulated torso illustrating acetabular diameter (AD), bi-iliac breadth (BIB), lumbar spine, or lumbar vertebral column, length (LSL), and ribcage breadth (RB). Measurement abbreviations correspond to measurements defined in Table 1.

Table 2. Sex-specific averages for torso measurements.

Group	Taxon	Sex	Acet	Sacr	UIW	Fossa	FPL	Flare	BIB	NP	Lumb	NL	Rib7	Rib8	Rib9	Rib10	Rib11	NT
Plat	*Alouatta palliata**†	F	16.81	40.08	30.03	20.18	14.41	1.4	80.7	4	91.82	4	81	86.02	NA	99.83	95.46	1
Plat	*Alouatta palliata**†	M	18.27	41.7	30.8	19.17	16.05	1.19	80.14	6	87.14	6	96.13	99.82	105.84	113.34	110.59	2
Plat	*Alouatta seniculus**†	F	17.26	39.08	27.43	16.81	15.39	1.09	70.61	6	84.17	6	NA	NA	NA	NA	NA	0
Plat	*Alouatta seniculus**†	M	19.54	43.31	28.96	18.86	17.59	1.07	78.19	7	93.29	7	97.36	NA	NA	NA	NA	1
Plat	*Aotus trivirgatus*†	F	9.48	25.68	12.16	3.01	10.07	0.3	30.9	5	90.35	5	46.55	49.55	50.5	NA	NA	1
Plat	*Aotus trivirgatus*	M	9.06	24.09	9.69	2.49	8.54	0.29	27.26	5	84.73	5	NA	NA	NA	NA	NA	0
Plat	*Ateles belzebuth**†	F	21.52	48.97	37.06	24.06	18.2	1.32	100.08	2	51.98	2	NA	NA	NA	NA	NA	0
Plat	*Ateles belzebuth**†	M	24.96	50.48	42.98	25.82	25.23	1.02	100.7	1	81.43	1	105.89	107.5	112.85	114.86	NA	1
Plat	*Ateles geoffroyi**	F	22.3	52.71	42.12	28.77	20.16	1.43	109.89	3	54.59	3	NA	NA	NA	NA	NA	0
Plat	*Ateles geoffroyi**	M	21.23	47.81	39.53	26.9	17.98	1.50	101.99	3	51.49	3	NA	NA	NA	NA	NA	0
Plat	*Cacajao calvus**†	F	14.72	31.6	16.63	5.51	13.17	0.42	45.44	1	NA	NA	61.59	63.36	65.59	66.33	NA	1
Plat	*Cacajao calvus**†	M	15.13	34.51	22.19	5.81	16.5	0.35	47.89	1	87.88	1	NA	NA	NA	NA	NA	0
Plat	*Callicebus moloch**†	F	9.1	26.92	13.28	2.34	10.75	0.22	32.15	3	102.41	3	NA	NA	NA	NA	NA	0
Plat	*Callicebus moloch**†	M	8.96	25.74	13.21	2.5	10.81	0.23	31.45	4	91.76	4	46.56	48.65	49.72	49.86	42.92	2
Plat	*Cebus apella**	F	12.41	37.05	19.04	6.8	13.76	0.49	50.18	6	66.1	6	NA	NA	NA	NA	NA	0
Plat	*Cebus apella**	M	13.42	38.76	21.84	6.83	17.88	0.38	53.51	6	69.56	6	NA	NA	NA	NA	NA	0
Plat	*Cebus capucinus**†	M	14.7	42.91	24.53	7.15	20.1	0.36	56.05	4	74.8	4	NA	NA	NA	NA	NA	0
Plat	*Lagothrix lagotricha**†	F	17.86	39.86	27.92	17.84	14.62	1.22	75.5	5	56.67	4	NA	NA	NA	NA	NA	0
Plat	*Lagothrix lagotricha**†	M	18.79	40.82	31.03	17.3	17.39	0.99	77.5	4	65.21	4	NA	NA	NA	NA	NA	0
Plat	*Pithecia pithecia**	F	11.51	27.50	15.44	2.91	12.33	0.24	38.64	2	78.13	2	62.12	63.73	NA	NA	NA	1
Plat	*Pithecia pithecia**	M	11.99	30.3	15.87	2.58	12.67	0.2	40.25	2	90.11	2	68.89	69.53	72.28	82.74	NA	1
Plat	*Pithecia irrorata*†	M	12.92	36.47	23.08	3.04	18.58	0.16	46.33	1	85.83	1	67.24	71.55	NA	NA	NA	1
Plat	*Saguinus fuscicollis**†	F	6.06	18.77	9.27	2.11	7.93	0.27	23.33	4	52.04	4	31.92	32.19	32.52	28.5	NA	1
Plat	*Saguinus fuscicollis**†	M	6.03	18.77	9.23	1.77	8.24	0.21	22.56	4	55.4	4	NA	NA	NA	NA	NA	0
Plat	*Saimiri boliviensis**	F	7.48	26.47	12.44	2.62	9.81	0.27	29.58	5	70.2	5	31.59	33.28	30.23	27.42	NA	2
Plat	*Saimiri boliviensis**	M	8	27.08	13.19	2.54	10.34	0.25	31.89	6	76.77	6	40.71	43.58	41.39	38.65	36.8	1
Plat	*Saimiri sciureus**†	F	7.59	24.71	11.46	2.03	8.83	0.23	27.29	7	73.27	7	34.82	35.42	34.68	35.29	36.57	2
Plat	*Saimiri sciureus**†	M	7.83	24.21	12.22	2.22	9.23	0.24	27.50	7	75.43	7	37.47	37.98	39.36	39.34	38.75	5

Cerco	*Cercopithecus cephus*†	F	12.40	33.61	24.30	8.49	17.27	0.49	56.82	4	114.24	2	NA	NA	NA	NA	NA	0
Cerco	*Cercopithecus cephus*†	M	15.44	41.2	29.38	9.2	21.57	0.43	65.61	4	131.07	3	NA	NA	NA	NA	NA	0
Cerco	*Cercopithecus neglectus*†	F	14.18	40.01	25.27	10.1	18.09	0.56	64.16	3	112.25	3	NA	NA	NA	NA	NA	0
Cerco	*Cercopithecus neglectus*	M	17.59	47.19	32.25	10.07	22.39	0.45	74.65	1	126.92	1	NA	NA	NA	NA	NA	0
Cerco	*Cercopithecus nictitans**†	F	13.33	42.28	27.77	10.77	19.16	0.56	73.05	1	111.29	1	NA	NA	NA	NA	NA	0
Cerco	*Cercopithecus nictitans**†	M	16.25	46.3	33.2	11.96	21.38	0.56	73.71	1	142.82	1	NA	NA	NA	NA	NA	0
Cerco	*Chlorocebus aethiops**	F	16.08	41.21	30.8	14.98	17.71	0.85	75.24	5	113.78	5	NA	NA	NA	NA	NA	0
Cerco	*Chlorocebus aethiops**	M	16.13	42.64	29.49	10.03	21.29	0.47	69.85	4	120.38	4	NA	NA	NA	NA	NA	0
Cerco	*Lophocebus ugandae**†	F	16.45	42.9	29.96	14.23	18.34	0.78	66.84	2	123.02	2	NA	NA	NA	NA	NA	0
Cerco	*Lophocebus ugandae**	M	20.01	47.58	36.97	15.75	24.92	0.63	84.67	3	144.11	3	101	106	113	119	125	1
Cerco	*Macaca assamensis*	F	17.22	37.07	32.49	20.1	16.47	1.22	78.93	1	111.29	1	NA	NA	NA	NA	NA	0
Cerco	*Macaca assamensis*	M	17.21	44.32	31.06	15.12	18.3	0.83	76.31	1	111.75	1	NA	NA	NA	NA	NA	0
Cerco	*Macaca fascicularis**†	F	13.82	36.52	23.73	13.15	14.28	0.92	65.93	10	97.97	10	NA	NA	NA	NA	NA	0
Cerco	*Macaca fascicularis**†	M	16.2	39.38	28.70	13.59	18.26	0.74	72.22	10	99.98	10	NA	NA	NA	NA	NA	0
Cerco	*Macaca mulatta**†	F	18.23	45.39	34.57	18.59	21.20	0.88	88.15	5	113.72	5	95.42	100.27	104.8	100.04	103.25	2
Cerco	*Macaca mulatta**†	M	21.05	51.2	43.65	20.05	26.93	0.74	98.21	5	134.64	5	95	97.25	100.56	99.55	90.15	2
Cerco	*Macaca sylvanus*†	F	20.34	47.53	40.8	17.67	25.73	0.69	90.69	3	130.14	3	NA	NA	NA	NA	NA	0
Cerco	*Macaca sylvanus*	M	21.99	52.32	44.62	21.92	29.23	0.75	102.3	3	133.1	3	NA	NA	NA	NA	NA	0
Cerco	*Mandrillus sphinx**†	F	26.87	53.4	54.5	25.6	30.15	0.85	113.74	1	153.8	1	NA	NA	NA	NA	NA	0
Cerco	*Mandrillus sphinx**†	M	27.67	63.71	63.49	29.17	41.36	0.71	128.01	4	152.77	3	NA	NA	NA	NA	NA	0
Cerco	*Miopithecus talapoin*†	F	8.4	27.95	17.12	6.89	11.38	0.61	44.72	6	71.36	6	49.22	54.31	57.81	62.45	62.72	2
Cerco	*Miopithecus talapoin*†	M	9.46	25.63	18.17	6.74	11.65	0.58	43.6	6	72.46	6	52.33	53.77	54.34	55.27	56.29	1
Cerco	*Papio anubis**	F	25.3	62.03	54.56	26.83	31.68	0.85	126.69	3	121.52	3	NA	NA	NA	NA	NA	0
Cerco	*Papio anubis**	M	31.16	76.13	77.1	43.38	35.54	1.22	159.14	1	149.17	1	NA	NA	NA	NA	NA	0
Cerco	*Papio cynocephalus*	F	23.42	53.27	48.82	25.06	26.65	0.94	112.3	4	127.24	4	NA	NA	NA	NA	NA	0

Cerco	*Papio cynocephalus*	M	27.58	65.43	61.67	34.13	32.21	1.06	149.48	2	141.97	2	NA	NA	NA	NA	NA	0
Cerco	*Papio hamadryas*	F	22.13	53.37	44.62	23.83	24.56	0.97	108.37	5	104.18	5	127	139	156	165	177	1
Cerco	*Papio hamadryas*	M	25.95	64.7	58.89	33.49	31.46	1.06	132.61	5	121.83	5	145.5	152	154	163	155	1
Cerco	*Theropithecus gelada*	F	22.8	57.14	52.92	29.9	27.94	1.07	125.93	4	132.04	4	154.16	173	174	175	NA	1
Cerco	*Theropithecus gelada*	M	26.61	65.62	59.14	34.5	29.49	1.17	133.67	4	123.4	4	156	167	181	183	182	1
Colo	*Colobus guereza**	F	20.08	47.97	37.27	16.18	23.18	0.7	87.43	3	138.96	3	NA	NA	NA	NA	NA	0
Colo	*Colobus guereza**	M	21.77	50.54	37.23	16.39	24.59	0.67	91.76	4	157.1	4	134.31	137.32	139.08	130.83	128.17	2
Colo	*Colobus polykomos**†	F	21.3	47.94	40.93	18.24	26.28	0.69	98.23	1	150.84	1	NA	NA	NA	NA	NA	0
Colo	*Colobus polykomos**	M	22.56	52	42.84	16.26	28.85	0.56	92.74	1	142.83	1	NA	NA	NA	NA	NA	0
Colo	*Nasalis larvatus**	F	22.04	46.23	40.25	23.14	20.83	1.11	102.6	10	131.2	10	114.5	110.55	114.88	113.27	99.99	1
Colo	*Nasalis larvatus**†	M	27.69	57.19	53.32	31.68	27.75	1.14	132.63	10	152.6	10	NA	NA	NA	NA	NA	1
Colo	*Piliocolobus badius**	F	17.46	42.99	35.99	19.62	18.57	1.06	90.98	1	138.32	1	110	122	129	124	110	1
Colo	*Piliocolobus badius**	M	19.32	51.25	44.6	19.2	28.00	0.69	100.41	1	125.58	1	NA	NA	NA	NA	NA	0
Colo	*Presbytis rubicunda*	F	17.61	43.95	36.32	16.69	20.5	0.81	86.02	7	136.23	7	89.07	NA	NA	NA	NA	1
Colo	*Presbytis rubicunda*	M	24.47	40.5	35.87	15	19.9	0.75	81.9	6	132.59	6	NA	NA	NA	NA	NA	0
Colo	*Semnopithecus entellus*	F	22.99	58.29	49.27	26.65	26.07	1.02	116.38	1	132.34	1	101.03	105.98	113.59	118.07	127.51	1
Colo	*Semnopithecus entellus*†	M	26.08	64.04	52.01	25.16	30.93	0.81	123.27	3	169.97	3	NA	NA	NA	NA	NA	0
Colo	*Trachypithecus cristatus*†	F	17.25	45.9	32.59	17.32	19.13	0.91	84.01	10	133.74	10	92.16	102.54	114.33	NA	NA	1
Colo	*Trachypithecus cristatus*	M	18.43	44.48	34.78	15.99	20.27	0.79	85.27	10	132.35	10	110.13	105.45	117.42	103.1	NA	1
Colo	*Trachypithecus obscurus**†	F	17.79	38.5	31.52	16	18.99	0.84	82.06	1	108.45	1	NA	NA	NA	NA	NA	0
Colo	*Trachypithecus obscurus**†	M	17.75	45.3	34.37	15.93	22.67	0.7	83.76	3	137.36	3	104.96	112.64	116.5	122.5	NA	1
Hylo	*Hylobates agilis**	F	20.48	39.35	44.8	31.64	16.5	1.92	105.41	1	NA	0	NA	NA	NA	NA	NA	0
Hylo	*Hylobates agilis**	M	19.96	37.11	47.72	35.18	19.58	1.8	105.28	1	60.65	1	124.6	133.56	148.86	146.75	151.47	1
Hylo	*Hylobates lar**†	F	20.74	40.14	41	30.4	15.21	2	100.34	14	70.59	14	119.78	120.67	124.07	118.91	112.99	5
Hylo	*Hylobates lar**	M	20.35	36.83	39.36	29.14	15.3	1.9	96.38	12	64.27	12	124.1	126	127	127.5	124.5	2
Hylo	*Hylobates moloch**	F	21.5	42.24	50.34	36.56	13.94	2.62	114.58	2	68.27	2	NA	NA	NA	NA	NA	0

Hylo	*Hylobates moloch**	M	20.87	39.04	44.3	32.88	17.47	1.88	105.42	2	71.61	2	128	136.2	137	130.9	119.13	1
Hylo	*Hylobates muelleri*	F	19.97	39.42	43.54	31.44	14.44	2.18	102.69	8	61.13	8	119.04	128	133.12	134.4	140	1
Hylo	*Hylobates muelleri*	M	20.2	35.83	40.8	30.76	13.69	2.25	97.4	8	61.43	7	122.88	127.69	129	129.15	134.1	2
Hylo	*Symphalangus syndactylus**	F	25.41	49.09	64.18	46.66	17.45	2.67	139.84	7	72.82	6	170	190	193	194.5	191	1
Hylo	*Symphalangus syndactylus*†*	M	25.87	46.24	65.97	48.11	17.1	2.81	140.95	5	73.74	4	NA	NA	NA	NA	NA	0
Hom	*Gorilla beringei**	F	46.58	91.62	184.88	162.04	25.11	6.45	370.56	2	102.27	2	NA	NA	NA	NA	NA	0
Hom	*Gorilla beringei**	M	58.34	102.93	227.4	203.69	32.82	6.21	460.61	6	114.94	6	NA	NA	NA	NA	NA	0
Hom	*Gorilla gorilla**	F	46.71	83.26	173.05	141.85	23.77	5.97	342.16	8	91.16	8	279.09	310.15	346.68	342.75	338.24	2
Hom	*Gorilla gorilla*†*	M	58.87	90.7	212.99	180.74	29.53	6.12	411.21	9	96.57	9	NA	NA	NA	NA	NA	0
Hom	*Pan troglodytes**	F	39.01	581.1	115.52	96.31	24.97	3.86	249.98	14	75.07	14	179	190	216	237	251	1
Hom	*Pan troglodytes*†*	M	40.55	66.62	119.25	98.24	23.86	4.12	252.85	12	76.76	12	206.67	219.67	236.33	247.37	256.83	3
Hom	*Pongo abelii**	F	36.88	70.36	103.98	83.57	23.17	3.61	230.48	8	83.12	7	211	234.5	259	241	230.5	1
Hom	*Pongo abelii**	M	46.98	80.52	128.84	103.23	30.92	3.34	281.87	4	99.41	4	NA	NA	NA	NA	NA	0
Hom	*Pongo pygmaeus*†*	F	36.75	70.5	109.83	92.35	23.95	3.86	244.06	7	80.22	7	NA	NA	NA	NA	NA	0
Hom	*Pongo pygmaeus**	M	46.4	82.54	132.83	107.45	33.08	3.25	288.57	8	91.09	7	NA	NA	NA	NA	NA	0

* = Locomotion data available for both males and females of this species
† = Gut size data available for this sex of this species
Plat = Platyrrhine monkey
Cerco = Cercopithecine monkey
Colo = Colobine monkey
Hylo = Hylobatid
Hom = Hominid
Acet = Acetabular diameter
Sacr = Sacrum breadth
UIW = Upper ilium width
Fossa = Iliac fossa breadth
FPL = False pelvis length
Flare = Fossa:FPL
BIB = Bi-iliac breadth
NP = Sample size for pelvis measurements
Lumb = Lumbar spine length
NL = Sample size for lumbar spine length
Rib7 = Ribcage breadth at the level of the 7^{th} rib
Rib8= Ribcage breadth at the level of the 8^{th} rib
Rib9 = Ribcage breadth at the level of the 9^{th} rib
Rib10 = Ribcage breadth at the level of the 10^{th} rib
Rib11 = Ribcage breadth at the level of the 11^{th} rib
NT = Sample size for the thorax measurements

Table 3. Linear measurements collected from adult, wild-shot individuals. Measurement abbreviations correspond to measurements illustrated in Figure 3.

Measurement	Description
Ribcage breadth (RB)*	Widest mediolateral breadth of the ribcage at rib levels 7 through 11, where preserved.
Lumbar spine length (LSL)*	Length of the lumbar vertebral column, estimated from the combined superior-inferior heights of lumbar vertebrae
Ventral bi-iliac breadth (BIB)*	Maximum distance between left and right ventral cranial iliac spines.
Upper ilium width (UIW)*	Distance from dorsal cranial iliac spine to ventral cranial iliac spine.
Lower ilium width (LIW)	Narrowest width of the ilium just above the ventral caudal iliac spine.
Iliac fossa width (IF)	Distance between the arcuate line and the ventral cranial iliac spine
False pelvis length (FPL)	Distance between the arcuate line and the medial border of the ilium
Acetabular diameter (AD)	Distance between the most cranial and most caudal borders of the acetabulum
Iliac flare*	Ratio between false pelvis length and iliac fossa width

Many measurements were taken to capture torso shape or size. Measurements hypothesized to relate to diet are noted with an asterisk.

Diet

Information about diet, which is taken from the literature, is based on percent time spent feeding (or percent of feeding observations) on different categories of food (Table 4). These data are available for males for 48 species and for 46 species for females. Food items consumed in the wild were allocated into eight categories: seeds, fungi, flowers and gums, roots and tubers, green plants, fruit, and prey, according to the classifications used by Pineda-Munoz and Alroy (2014). The ‘seeds’ category includes both nuts and seeds. The ‘flowers and gums’ category includes values for flowers, gums, resins, and nectars. The ‘green plants’ category includes leaves, stalks, stems, grasses, barks, and similar plant parts. ‘Fruit’ includes both ripe and unripe fruit. ‘Prey’ includes values for both invertebrate and vertebrate prey. Percentages are averaged across sites/populations. Fungi

percentages were not included in statistical analyses as only seven species in this sample consume foods from this category. A dietary quality index was calculated according to the formula provided by Sailer et al. (1985):

$$\text{Dietary Quality} = (\text{Roots.Tubers+Green.Plants}) + (2*(\text{Seeds} + \text{Flowers.Gum} + \text{Fruit})) + (3.5*(\text{Prey}))$$

This index weighs plant structural parts, plant reproductive parts, and animal prey according to their relative abundance and quality, and also provides a way of simultaneously accounting for all major food categories consumed by primates in this sample.

In Analyses A and B, and in the other chapters of this dissertation, I utilize the food item feeding time percentages as continuous data, since they are used as continuous predictor variables in the regressions for these analyses. In Analysis C, I use the percentages to categorize the sample into five dietary categories: folivore (leaf-eater), frugivore (fruit-eater), faunivore (prey-eater), granivore (seed-eater), and generalist, since they are used as categorical response variables for the discriminant function analyses. I categorized the species according to the protocol used by Pineda-Munoz and Alroy (2014), in which a species that relies on less than ~50% a food item is categorized as a generalist.

Table 4. Percent of overall feeding time spent consuming different food items/% feeding records in wild populations, with species averages.

Gr	Taxon	S	Fn	FG	RT	GP	Fr	Pr	DQ	Obs	Hrs	Site	Ref	Notes
Plat	*Alouatta palliata*	0	0	22.5	0	49	28.5	0	151	NA	394	Santa Rosa National Park, Costa Rica	1	% = % feeding time. Although the text says 394 hrs of observation, the table 1 caption says 393.
Plat	*Alouatta palliata*	0	0	10	0	48	42	0	152	NA	-	Barro Colorado Island, Panama Canal Zone	2	% = % feeding time. In this text, says data was collected over 15 months. In Milton 1981, says it was over 9 months.
Plat	*Alouatta palliata*	0	0	5.6	0	55.5	38.8	0	144.3	NA	43.1	Barro Colorado Island, Panama Canal Zone	3	% = % feeding time. I computed the average between wet and dry seasons. FG % also includes buds. The author notes leaf-heavy diet differs from fruit-heavy diet determined by Hladik & Hladik (1969).
Plat	*A. palliata* average	0	0	12.7	0	50.83	36.43	0	149.1	-	-	-	-	-

Plat	*Alouatta seniculus*	0	0	12.6	0	57.4	25.5	1.5	138.85	9256	NA	Nouragues Station, French Guiana	4	% = % feeding units (feeding obs?) for each item. 3% of unknown excluded from this row. GP includes 0.4% of "bark and moss."
Plat	*Alouatta seniculus*	0	0	5.4	0	52.1	42.3	0	147.5	NA	340	Finca Merenberg, Colombia	5	% = % feeding time. GP includes mature leaves (7.5%) and young leaves (44.5%) and petiole (0.1%). Fruit includes ripe fruit (28.4) and unripe fruit (13.9). 340 hrs are total focal hours.
Plat	*Alouatta seniculus*	0	0	2.4	0	28.6	69	0	171.4	42	NA	Ralieghvallen-Voltzberg Nature Reserve, Surinam	6	% = % feeding observations.

Plat	*Alouatta seniculus*	0	0	0.7	0	56.9	42	0.5	144.05	1209	NA	Les Noragues, French Guiana	7	Near or same site as Julliot & Sabatier (1993), but this study is a few years later. Potentially same individuals? GP includes young leaves (55.7%) and mature leaves (1.2%). Fruit includes ripe fruits (41.5%) and unripe fruits (0.5%).
Plat	*A. seniculus* average	0	0	5.28	0	48.75	44.7	0.5	150.4	-	-	-	-	-
Plat	*Aotus trivirgatus*	0	0	0	0	10	75	15	212.5	NA	NA	Peru	8	

Plat	*Ateles belzebuth*	0	0	0	0	17	83	0	183	2156	NA	Colombian National Park, Colombia	9	Percentages calculated by multiplying number of *A. belzebuth* observed eating a particular substance by the amount of time they were observed eating (animal feeding minutes) separately for each month during the last 11 months of the study, and for intervals of 2 weeks.
Plat	*Ateles belzebuth*	0	0	5	0	12	74	0	170	NA	672	Tinigua, Colombia	10	Excludes 9% other.
Plat	*Ateles belzebuth*	0	0	1	0	9	87	0	185	1759	NA	Yasuní, Ecuador	10	Excludes 0.7% other and 3% unidentified.
Plat	*Ateles belzebuth*	0	0	1.3	0	7.7	7.8	0	167.9	NA	NA	Yasuní, Ecuador	10	Excludes 12.2% other.
Plat	*Ateles belzebuth*	0	0	5	0	2	83	0	178	NA	NA	Maraca Ecological Station, Roraima,Brazil	11	

Plat	*Ateles belzebuth*	0	0	0	0	8.3	88.5	0	185.3	NA	NA	Maraca Ecological Station, Roraima,Brazil	11	Excludes 3.2% unripe fruits, flowers, aerial roots, bark and fungi. 1356 total observation hours, not feeding specific.
Plat	*A. belzebuth* average	0	0	2.05	0	9.33	82.38	0	178.2	-	-	-	-	-
Plat	*Ateles geoffroyi*	0	0	7.1	0	21	67	0	169.2	NA	NA	Multiple (Mexico, Guatemala, El Salvador, Costa Rica, Panama)	12	Average of the 17 studies listed in this paper. 0.5% of diet is unaccounted for. 'Other plant parts and insects average' = 2.6 +/- 4.3 (range = 0-14). Other plant parts include petioles, bark, decaying wood. Some data provided are unpublished, so did not to hunt down and find insect %.
Plat	*Cacajao calvus*	55.4	0	3.4	0	0	38.9	1.5	200.65	2583	945	Lago Preto Conservation Concession, Loreto, Peru	13	% = % of feeding records. Excludes 0.7% other plant parts including leaves, bark, and gums.

Plat	*Cacajao calvus*	66.9	0	6.2	0	0	18.4	5.2	201.2	2345	NA	Lake Teiú, Brazil	14	% = proportions of food items selected. FG includes 6.2% nectar. Excludes 3.3% non-identified items.
Plat	*C. calvus* average	61.15	0	4.8	0	0	28.65	3.35	200.93	-	-	-	-	-
Plat	*Callicebus moloch*	0	0	0	0	26	70	0	166	NA	57	Cocha Cashu Biological Station, Manu National Park, Peru	15	% = % of time-sample obtained for each food item. Excludes 4 % unknown.
Plat	*Cebus apella*	11.4	0	5.7	0	1.1	81.8	0	198.9	88	NA	Ralieghvallen-Voltzberg Nature Reserve, Surinam	6	% = % feeding observations.
Plat	*Cebus apella*	0	0	0	0	72.3	2.9	24.9	165.25	229	NA	El Rey National Park, Argentina	16	% = % feeding observations.
Plat	*Cebus apella*	0	0	3.9	0	18.6	37.2	40.3	241.85	440	NA	Iguazú National Park, Argentina	16	% = % feeding observations.
Plat	*Cebus apella*	16	0	11.1	1.5	20.2	53.9	0	183.7	367	NA	Santa Genebra Reserve, Brazil	17	% = % feeding observations.
Plat	*C. apella* average	6.85	0	5.18	0.38	28.05	43.95	16.3	197.43	-	-	-	-	-
Plat	*Cebus capucinus*	0	0	0.2	0	1.3	81.2	16.9	223.25	NA	171	Santa Rosa National Park, Costa Rica	1	% = % feeding time.
Plat	*Lagothrix lagotricha*	0	0	5	0	10	73	6	187	1758	NA	Yasuní, Ecuador	18	Excludes 12% unidentified. Subspecies = *L. l. poeppigii*.

Plat	*Lagothrix lagotricha*	0	0	1.7	0	15.3	60	23	219.2	1244	NA	Tinigua, Colombia	19	Leaves, stems, roots, and flowers were lumped together as 17%, but was able to calculate that 1.7% of the diet is flowers because the text said 10% of the plant diet was flowers.
Plat	*Lagothrix lagotricha*	0.54	0.15	3.51	0	9.85	76.7	9.3	203.9	4074	NA	Yasuní, Ecuador	20	GP includes 7.44% leaves and 2.41% other plant vegetative parts. Subspecies = *L. l. poeppigii*.
Plat	*Lagothrix lagotricha*	4.3	0	0.1	0	11.8	78.9	4.9	195.55	1719	NA	Estacion Biologica Caparu, Colombia	21	GP = 11.4% leaves, 0.1% tendrils, and 0.3% bark. 2243 is number of total foraging observations, but food only identified in 1719 of them.
Plat	*Lagothrix lagotricha*	7	0	9.3	0	16.2	67.5	0	183.8	3298	NA	Tefe, Brazil	22	
Plat	*L. lagotricha* average	2.37	0.03	3.92	0	12.63	71.22	8.64	197.89	-	-	-	-	-

Plat	*Pithecia irrorata*	75.6	0	3	0	1	20	0	198.2	8800	3100	Los Amigos Conservation Concession, Madre de Dios region, Peru	23	% = % feeding observations. 0.4% is unaccounted for.
Plat	*Pithecia pithecia*	33.3	0	6.7	0	0	60	0	200	15	NA	Ralieghvallen-Voltzberg Nature Reserve, Surinam	6	% = % feeding observations.
Plat	*Saguinus fuscicollis*	0	0	19	0	0	49	26	227	934	NA	San Sebastian, Bolivia	24	% = % food items in annual average diet. Excludes 6% unknown. FG = 12% exudates and 7% nectar.
Plat	*Saguinus fuscicollis*	0	0	7.6	0	0	39.2	53.1	279.45	396	NA	Rio Blanco Research Station, Tahuayo River Basin, Peru	25	% = % feeding and foraging time. 0.1% is unaccounted for.
Plat	*Saguinus fuscicollis*	0	0	20.3	0	0	73.5	5.7	207.55	3707	NA	Manaus, Amazon, Brazil	26	% = % feeding time. FG = 14.4% exudates and 5.9% floral nectar. 0.5% is unaccounted for.
Plat	*S. fuscicollis* average	0	0	15.63	0	0	53.9	28.27	238	-	-	-	-	-
Plat	*Saimiri boliviensis*	0	0	28.07	0	0	18.18	52.67	277.65	374	NA	Pacaya-Samiria National Reserve, Peru	27	% = % feeding observations.
Plat	*Saimiri sciureus*	0	0	7.4	0	0	92.6	0	200	27	NA	Ralieghvallen-Voltzberg	6	% = % feeding observations.

												Nature Reserve, Surinam		
Cerco	*Cercopithecus cephus*	6.9	0	6.9	0	17.2	62.1	6.9	193.15	NA	NA	Lopé Reserve, Gabon	28	% = % of species eaten, or the % of the number of food species recorded in each food category. 58 species were eaten total.
Cerco	*Cercopithecus cephus*	6.8	0	5.7	0	11.4	67	9.1	202.25	88	NA	Lopé Reserve, Gabon	28	% = % feeding observations.
Cerco	*C. cephus* average	6.85	0	6.3	0	14.3	64.55	8	197.7	-	-	-	-	-
Cerco	*Cercopithecus mitis*	2.5	0	5.6	0	20	54.6	16.8	204.2	10167	NA	Kakamega Forest, Kenya	29	% = % feeding observations. GP = 16.6% young leaves, 2.3% mature leaves, 1.1% stems and shoots. FG = 3.7% flowers, 1.9% gums. Excludes 0.5% other.
Cerco	*Cercopithecus neglectus*	1.2	1.8	6.6	0	34.3	44.7	10.2	175	1786	NA	Kisere Forest, Kenya	30	% = relative frequencies with which different plant parts were eaten. Excludes 0.9% other, and 0.3% is unaccounted for.

Cerco	*Cercopithecus nictitans*	49.9	0	4.1	0	10.3	35.5	0	189.3	2919	NA	Makandé Forest, Gabon	31	% = % feeding observations. 0.2% is unaccounted for.
Cerco	*Chlorocebus aethiops*	13	1	16	0	7	50	13	210.5	NA	NA	Mt. Assirik, Senegal	32	% = % feeding time. Subspecies = *C. a. sabaeus*.
Cerco	*Lophocebus ugandae*	0	0	3.4	0	12.2	60.3	24.1	223.95	NA	NA	Kibale forest, Uganda	33	Data includes values for adults and juveniles.
Cerco	*Macaca assamensis*	0	0	10	0	21.2	42.4	20.2	196.7	3978	NA	Phu Khieo Wildlife Sanctuary, NE Thailand	34	Based on graph, attributed 10% to flowers and 6.2% to other. Feeding data averaged across age-sex classes.
Cerco	*Macaca fascicularis*	0	1	2.5	0	8	87	1	190.5	NA	280	Kutai Nature Reserve, Indonesia	35	% = % feeding observations. 280 hours of total observation (hours of follow) are estimated from the text ("animals followed from 0600 to 1300 hours for 40 days distributed over 14 months"). Excludes 0.5% clay.

Cerco	*Macaca fascicularis*	0	0	4.7	0	25.8	64.9	4.6	181.1	487	NA	Krau Game Reserve, Pahang, West Malaysia	36	% = % feeding observations. Different values for this study in MacKinnon & MacKinnon (1980).
Cerco	*M. fascicularis* average	0	0.5	3.6	0	16.9	75.95	2.8	185.8	-	-	-	-	-
Cerco	*Macaca mulatta*	0	0	4.8	2.2	84.4	8.5	0	113.2	2942	NA	Muree Hills, Pakistan	37	% = % feeding observations. FG = 1.1% sap/resin and 3.7% flowers. 0.1% is unaccounted for.
Cerco	*Macaca sylvanus*	26.7	3.4	2.6	7.7	48.1	4.3	5.6	142.6	3282	NA	Djurdjura, Greater Kabylie, Algeria (Tigounatine troop)	38	% = % feeding time. 0.2% is unaccounted for. Excludes 0.6% water and 0.8% indeterminate.
Cerco	*Macaca sylvanus*	32.2	18.3	3.5	6.9	27.3	0.8	10.5	143.95	3309	NA	Akfadou, Grande Kabylie, Algeria	39	% = % feeding time. Excludes 0.2% water and 0.3% indeterminate.
Cerco	*M. sylvanus* average	29.45	10.85	3.05	7.3	37.7	2.55	8.05	143.28	-	-	-	-	-
Cerco	*Mandrillus sphinx*	26	0	2.7	0	15	50.7	4.1	188.15	NA	NA	Lopé Reserve, Gabon	28	% = % species eaten. A total of 73 species were eaten. Excludes 1.4% other, which includes bark, roots,

														wood, soil, and fungi.
Cerco	*Mandrillus sphinx*	34.4	0	0.8	0	11.4	46.7	4.9	192.35	122	NA	Lopé Reserve, Gabon	28	% = % feeding observations.
Cerco	*M. sphinx* average	30.2	0	1.75	0	13.2	48.7	4.5	190.25	-	-	-	-	-
Cerco	*Miopithecus talapoin*	13	0	0	0	8	78	0	190	NA	NA	CNRS Field Station, Makokou, Gabon	30	% = frequency of the vegetable parts consumed. 1% unaccounted for.
Cerco	*Papio anubis*	22.52	0.06	6.28	0	29.37	31.87	0.2	151.41	2116	NA	Comoé, National Park, Ivory Coast	41	Individuals = GP group. % = % feeding records. Excludes 1.85% soil and 8.3% unidentified items. FG includes flowers + exudates. GP includes grass + bark + leaves.
Cerco	*Papio anubis*	13.54	0	8.58	0	38.69	26.56	1.43	141.06	1355	NA	Comoé, National Park, Ivory Coast	41	Individuals = IS group. % = % feeding records. Excludes 2.31% soil and 9.84% unidentified items. FG includes flowers + exudates. GP includes grass + bark + leaves.

Cerco	*Papio anubis*	4	1	0	7	40	46	1	150.5	190	NA	Kibale National Park, Kenya	42	GP = 33% stems and 7% leaves. Excludes 1% bark, gums, and soil, so total = 99%.
Cerco	*Papio anubis*	8.9	0	7.4	1.6	33.6	46	2.7	169.25	447	NA	Bole Valley Ethiopia	43	% = % feeding records. Values derived from tables V and VI. Very different values for this study in Dunbar (1988). GP includes 0.7% bark, among other plant parts.
Cerco	*P. anubis* average	12.24	0.27	5.57	2.15	35.42	37.61	1.33	153.05	-	-	-	-	-
Cerco	*Papio cynocephalus*	16.93	0	2.1	48.34	2.55	25.56	4.48	155.75	NA	172	Ruaha National Park, Tanzania	44	Excludes 0.59% dung. FG = 1.81% gum and 0.29% buds. RT = 4.37% tubers and 43.97% corms. Due to table 3, *C. paniculatum* fruit assumed to be seeds, so that value was combined with grass seeds and *C. ugogensis* seeds.

Cerco	*Papio cynocephalus*	0	0	1	52	19	16	9	136.5	NA	NA	Ruaha National Park, Tanzania	45	Review chapter so no data on times/hours. Actual data from Rasmussen dissertation (1978). Seems like fruit and seeds combined. Adds up to 97%.
Cerco	*Papio cynocephalus*	17	0	16	31	19	10	0	136	NA	NA	Amboseli, Kenya	46	% estimated from bar graph because Hill and Dunbar (2002) provide very different values for Post dissertation (1978). FG = ~15% and 1% flower. GP = 4% buds, 3% leaves, 12% grass. <1% mixed prey value excluded.
Cerco	*P. cynocephalus* average	11.31	0	6.37	43.78	13.52	17.19	4.49	142.75	-	-	-	-	-

Cerco	*Papio hamadryas*	15.39	0	11.88	4.64	18.06	49	0.25	176.14	NA	79.4	Filoha, Awash National Park, Ethiopia	47	4764 minutes of feeding. Ref only lists total feeding time % for parts eaten of specific plants, so I divided the total time by the number of parts eaten when there were multiple parts eaten of the same plant. 0.731 of diet unaccounted for%. 0.038% unknown excluded.
Cerco	*Theropithecus gelada*	5	0	0.8	0.5	91.8	1.9	0	107.7	764	82	Bole Valley, Ethiopia	43	% = % feeding records. Values derived from tables V and VI.
Colo	*Colobus guereza*	0	0	0	0	78.3	13.1	0	104.5	2366	NA	Kanyawara, Kibale National Park, Uganda	48	% = % feeding records. 8.6% of diet unaccounted for. Other items listed as 24.1% but 14% are leaf parts, and 4.8% from non-tree species.

Colo	*Colobus guereza*	0.23	0	2.51	0	88.75	7.33	0	108.89	4167	NA	Kanyawara, Kibale National Park, Uganda	49	% = % feeding observations. Data averaged across 8 groups of *C. guereza*. FG = 2.21% flowers and 0.3% gums. Excludes 0.22% soil, 0.44% concrete, and 0.01% lichens. GP = 0.01% stems/twigs, 1.55% bark, 0.19% petioles, and 87.5% leaves.
Colo	*C. guereza* average	0.12	0	1.26	0	83.53	10.22	0	106.7	-	-	-	-	-
Colo	*Colobus polykomos*	33	0	3	0	61	3	0	139	NA	NA	Tiwai Island, Sierra Leone	50	% = % contributions of different plant parts to diet. 4% "other" category is likely woody tissues: "Another interesting difference is the relatively large amount of woody tissues (3.6% including stems, pith and bark of twigs)," so it was added

														to green plants. Data results from 72 full day follows.
Colo	*Nasalis larvatus*	0	0	2.97	0	51.94	40.33	0	138.54	3739	NA	Natai Lengkuas Station, Tanjung Putting National Park, Kalimantan Tengah, Indonesia	51	% = % feeding records. Insects and bark were <1% of diet. Excludes 4.68% unknown.
Colo	*Piliocolobus badius*	30.8	0	1.4	0	60.7	7.1	0	139.3	2317	NA	Salong National Park, DRC	52	% = % feeding records. GP = 54.3% young leaves and 6.4% mature leaves. Seeds includes 19% legume seeds, 6.3% unripe fruit seeds, and 5.5% arillate seeds.
Colo	*Presbytis rubicunda*	30.1	0	11.1	0	37.6	19.2	0	158.4	4941	NA	Sepilok Virgin Jungle Reserve, N. Borneo	53	% = % feeding records. 13 months total of observation. GP = 36.5% young leaves and 1.1% mature leaves. Excludes 2% other. Supplemented

														with information from Koyabu and Endo (2010).
Colo	*Presbytis melalophos*	32.4	0	11.5	0	35.2	17.1	0	157.2	1486	NA	Kuala Lompat, Krau Game Reserve, Malaysia	53	% = % feeding records. GP = 27.7% young leaves and 8% mature leaves. Excludes 3.3% other. 14.2% "fruits and/or seeds" was split, so 7.1% was added to both 10% fruit and 25.3% seeds.
Colo	*Semnopithecus entellus*	0	0	5	0	54	37	0	138	NA	NA	Singur, West Bengal, India	54	% = % feeding time. 4952 total observation hours.
Colo	*Semnopithecus entellus*	0	0	23.94	0	52.63	23.03	0	146.57	4632	NA	Kaludiyapokuna forest reserve, Sri Lanka	55	% = % feeding time. Excludes 0.39% sap and 0.02% soil.
Colo	*Semnopithecus entellus*	0	0	13.42	0	57.44	29.14	0	142.56	4725	NA	Kaludiyapokuna forest reserve, Sri Lanka	55	% = % feeding time.
Colo	*Semnopithecus entellus*	0	0	7	0	48	45	0	152	NA	118.75	Polonnaruwa, Sri Lanka	56	% = % total fresh weight of food ingested.
Colo	*S. entellus* average	0	0	12.34	0	53.02	33.54	0	144.78	-	-	-	-	-
Colo	*Trachypithecus cristatus*	0	0	10	0	80	10	0	120	NA	612	Pagandaran Nature Reserve, West Java Indonesia	57	% = % foods in diet.

Colo	*Trachypithecus obscurus*	0	0	6.2	0	37.9	55.9	0	162.1	437	NA	Krau Game Reserve, Pahang, West Malaysia	36	% = % feeding observations. Different values for this study in MacKinnon and MacKinnon (1980).
Colo	*Trachypithecus phayrei*	23.2	0	20.6	0	49.4	6.4	0	149.8	4954	NA	Gumti Wildlife Sanctuary, Tripura, India	58	% = % feeding records.
Hylo	*Hylobates agilis*	0	0	3	0	39	58	1	164.5	1684	NA	Sungai Dal, Malaysia	59	% = % feeding observations after averaging foraging + feeding bouts. Data add up to 101%.
Hylo	*Hylobates lar*	0	0	1	0	22	66	9	187.5	NA	NA	Mo Singto, Khao Yai, Thailand	60	
Hylo	*Hylobates lar*	0	0	0	0	33	67	0	167	NA	NA	Tanjon Tiang, Malaysia	60	
Hylo	*Hylobates lar*	0	0	6	0	22	58	0	150	NA	NA	Phu Khieo, Thailand	60	
Hylo	*Hylobates lar*	0	0	2	0	4	72	22	229	912	NA	Ketambe Research Station, Gunung Leuser National Park, Sumatra	61	% = % feeding time. Individuals from Group A.
Hylo	*Hylobates lar*	0	0	1	0	4	70	25	233.5	520	NA	Ketambe Research Station, Gunung Leuser National Park, Sumatra	61	% = % feeding time. Individuals from Group G.

Hylo	*Hylobates lar*	0	0	7	0	29	50	13	188.5	6852	NA	Krau Game Reserve, Pahang, West Malaysia	62	% = % feeding observations.
Hylo	*Hylobates lar*	0	0	0.4	0	31.4	63.7	4.5	175.35	531	NA	Krau Game Reserve, Pahang, West Malaysia	63	% = % feeding observations.
Hylo	*Hylobates lar*	0	0	8	0	12	77	2	189	58	NA	Sungai Tekam Forestry Concession, Pahang, West Malaysia	64	Primary forest. % = % feeding observations. Fruit value includes seeds. 1% unaccounted for.
Hylo	*Hylobates lar*	0	0	0	0	36	60	4	170	29	NA	Sungai Tekam Forestry Concession, Pahang, West Malaysia	64	Logged forest. % = % feeding observations. Fruit value includes seeds.
Hylo	*H. lar average*	0	0	2.82	0	21.49	64.86	8.83	187.76	-	-	-	-	-
Hylo	*Hylobates moloch*	0	0	0	0	38	61	0	160	NA	NA	Turalak, Ujung Kulon, W. Java, Indonesia	60	
Hylo	*Hylobates moloch*	0	0	11.8	0	24.6	62.5	1.2	177.4	NA	NA	Gunung Halimun-Salak National Park, Indonesia	65	Adds up to 100.1%. GP = 23.7% young leaves and 0.9% mature leaves.
Hylo	*H. moloch* average	0	0	5.9	0	31.3	61.75	0.6	168.7	-	-	-	-	-
Hylo	*Hylobates muelleri*	0	0	4	0	32	62	8	192	NA	NA	Kutai Nature Reserve, Indonesia	60	Adds up to 106%.

Hylo	*Symphalangus syndactylus*	0	0	6	0	43	36	15	179.5	13142	NA	Krau Game Reserve, Pahang, West Malaysia	62	% = % feeding observations.
Hylo	*Symphalangus syndactylus*	0	0	5	0	48	41	6	161	NA	NA	Ulu Sempam, Malaysia	60	
Hylo	*Symphalangus syndactylus*	0	0	3.6	0	43.7	44.6	8.1	168.45	686	NA	Krau Game Reserve, Pahang, West Malaysia	63	% = % feeding observations.
Hylo	*Symphalangus syndactylus*	0	0	1	0	19	65	15	203.5	622	NA	Ketambe Research Station, Gunung Leuser National Park, Sumatra	61	% = % feeding time. Individuals from Group C.
Hylo	*Symphalangus syndactylus*	0	0	1	0	15	56	28	227	699	NA	Ketambe Research Station, Gunung Leuser National Park, Sumatra	61	% = % feeding time. Individuals from Group P.
Hylo	*Symphalangus syndactylus*	0	0	12	0	32	56	0	168	NA	NA	Way Canguk, Sumatra	60	
Hylo	*Symphalangus syndactylus*	0	0	12	0	25	63	0.1	175.35	NA	NA	Way Canguk, Sumatra	60	
Hylo	*S. syndactylus* average	0	0	5.8	0	32.24	51.66	10.31	183.26	-	-	-	-	-
Hom	*Gorilla gorilla*	0	0	0	0	48	51	0	150	826	NA	Bai Hokou, Dzanga-Ndoki National Park, Dzangha-Sangha Reserve, Central African Republic	66	% = % feeding observations.

Hom	*Gorilla gorilla*	9.9	0	1.1	1.1	24.7	63.2	0	174.2	93	54.95	Nouabalé-Ndoki National Park, Republic of Congo	67	% = proportion of plant parts. Total 182 items eaten. Hour estimate from 3297 min of observation.
Hom	*Gorilla gorilla*	0	0	0	0	55.25	39.75	0	134.75	NA	NA	Río Muni, Equatorial Guinea	68	% = % of foods consumed. Excludes 5% other. 54.5 total observation hours.
Hom	*G. gorilla average*	3.3	0	0.37	0.37	42.65	51.32	0	152.98	-	-	-	-	-
Hom	*Gorilla beringei*	0	0	2.3	3.3	92.7	1.7	0	104	NA	NA	Virunga volcanoes region, Rwanda	69	
Hom	*Pan troglodytes*	6.3	0	1.7	0.9	27.1	60.7	1.8	171.7	NA	NA	Bossou, Guinea	70	% = % feeding time. FG = 1.1% flower and 0.6% resin. GP = 10.8% leaves, 10.1% woody pith, 5.3% herb pith, and 0.9% bark. Excludes 1.5% other.
Hom	*Pan troglodytes*	0	0	0	0	28	68	4	178	NA	451	CNRS Field Station, Ipassa, Gabon	71	

Hom	*Pan troglodytes*	7.66	0	0	0	31.75	44.83	3.83	150.14	NA	119	Okorobikó Mountains, Río Muni, Equatorial Guinea	72	119 hours described as "sustained contact with the animals" out of 640 h. % likely % of foods consumed. Paper notes that chimpanzees fed on plantation crops (cassava, bananas, sugar cane) which totaled to 21% of the diet. In this row, it is unclear where the missing ~12 percent should be allocated.
Hom	*P. troglodytes* average	4.65	0	0.57	0.3	28.95	57.84	3.21	166.61	-	-	-	-	-
Hom	*Pongo abelii*	0	0	0	0	16.6	66	13.4	195.5	NA	NA	Suaq Balimbing, Sumatra	73	% = % feeding time. 17084 total observation hours. Excludes 3.8 % other. GP = 15.5% leaves and 1.1% bark.
Hom	*Pongo abelii*	0	0	3.5	0	19.3	67.5	8.8	192.1	NA	NA	Ketambe, Sumatra	73	% = % feeding time. 17109 total observation hours. Excludes 1.3 % other. GP = 16.4% leaves and 2.7% bark.

Hom	*P. abelii* average	0	0	1.75	0	17.95	66.75	11.1	193.8	-	-	-	-	-
Hom	*Pongo pygmaeus*	0	0	1	0	34	62	3	170.5	NA	NA	Ulu Segama Reserve, Sabah, Borneo	74	% = % food was chosen during feeding occasions. 1200 total hours of observation.
Hom	*Pongo pygmaeus*	0	0	2.2	0	43.2	53.8	0.8	158	NA	4000-6000	Kutai Nature Reserve, Indonesia	75	% = % feeding time
Hom	*P. pygmaeus* average	0	0	1.6	0	38.6	57.9	1.9	164.25	-	-	-	-	-

Note: Data categorized following Pineda-Munoz and Alroy (2014)
Gr = Group: Plat = Platyrrhine monkey; Cerco = Cercopithecine monkey; Colo = Colobine monkey; Hylo = Hylobatid; Hom = Hominid
S = % of seeds and nuts in diet; Fn = % of fungi in diet; FG = combined % of flowers, nectars, and gums in diet; RT = combined % of roots and tubers in diet; GP = combined % of leaves, stalks, grass, and other green plants in diet; Fr = % of fruits in diet; Pr = combined % of invertebrate and vertebrate prey in diet
DQ = Dietary Quality: Index of dietary quality from Sailer et al. 1985 = (Roots.Tubers+Green.Plants) + (2*(Seeds + Flowers.Gum + Fruit)) + (3.5*(Prey))
Obs = Number of feeding observations or feeding bouts; Hrs = Hours spent feeding
Ref = References: 1. Chapman (1988); 2. Milton (1978); 3. Smith (1977); 4. Julliot and Sabatier (1993); 5. Gaulin and Gaulin (1982); 6. Mittermeier and van Roosmalen (1981); 7. Simmen and Sabatier (1996); 8. Rosenberger (1992); 9. Klein and Klein (1977); 10. Russo et al. (2005); 11. Nunes (1998); 12. González-Zamora et al. (2009); 13. Bowler and Bodmer (2011); 14. Ayres (1989); 15. Kinzey (1978); 16. Brown and Zunino (1990); 17. Galetti and Pedroni (1994); 18. Dew (2005); 19. Stevenson et al. (1994); 20. Di Fiore (2004); 21. Defler and Defler (1996); 22. Peres (1994); 23. Palminteri et al. (2012); 24. Porter (2001); 25. Garber (1988); 26. Peres (1993); 27. May (2013); 28. Tutin et al. (1997); 29. Cords (1986); 30. Wahome et al. (1993); 31. Brugiere et al. (2002); 32. Harrison (1984); 33. Waser (1997); 34. Schulke et al. (2011); 35. Wheatley (1978); 36. MacKinnon and MacKinnon (1978); 37. Goldstein and Richard (1989); 38. Menard and Vallet (1986); 39. Menard (1985); 40. Gautier-Hion (1971); 41. Kunz and Linsenmair (2008); 42. Johnson et al. (2012); 43. Dunbar and Dunbar (1974a); 44. Pochron (2000); 45. Hill and Dunbar (2002); 46. Post (1982); 47. Swedell et al. (2008); 48. Oates et al. (1977); 49. Harris and Chapman (2007); 50. Davies et al. (1999); 51. Yeager (1989); 52. Maisels et al. (1994); 53. Bennett and Waterman (1988); 54. Oppenheimer (1978); 55. Vandercone et al (2012); 56. Hladik (1977); 57. Brotoisworo and Dirgayusa (1991); 58. Gupta and Kumar (1994); 59. Gittins (1982); 60. Elder (2009); 61. Palombit (1997); 62. Raemaekers (1979); 63. MacKinnon and MacKinnon (1980); 64. Johns (1986); 65. Kim et al. (2011); 66. Remis (1997); 67. Nishihara (1995); 68. Sabater Pí (1977); 69. Fossey and Harcourt (1977); 70. Yamakoshi (1998); 71. Gautier-Hion et al. (1980); 72. Sabater Pí (1979); 73. Morrogh-Bernard et al. (2008); 74. Mackinnon (1977); 75. Rodman (1977)

Gut size

Gut size, which is defined as the summed surface areas of the stomach, caecum, small intestine, and colon, in cm^2, was available for the 31 species listed in Table 5. I used surface area instead of weight or volume for two reasons. First, digestive organ surface area reflects digestive and absorptive function, while digestive organ weight is associated with mechanical activity (e.g., smooth muscle mass) and more closely correlates with body mass (Chivers and Hladik, 1980). Second, gut volumes are not available for all of the taxa for which Ferrari and Martins (1992) and Ferrari and Lopes (1995) provide gut surface areas.

Most of the measurements come from wild-shot, adult individuals according to the protocol described in Chivers and Hladik (1980). The different parts of the gut were weighed and then opened and flattened under water in dissecting trays. Once the intestines were flattened, the lengths and widths of the components were recorded and used to calculate surface area and volume with geometric formulae. The irregularity of the stomach led the authors to fit pieces of aluminum foil to the nontubular pieces, and then weigh the pieces to calculate surface area from the weight to area ratio (Chivers and Hladik, 1980). Data from captive animals, juveniles, or from specimens that were fixed in formol saline are indicated in Table 5. Gut size data for each species were matched to the torso measurements for the same sex, except for *Cebus capucinus*, for which there is a gut size measurement from a female individual, but data on torso morphology from males only. When no sex was provided for the measurement, which is the case for three species, the gut size estimate was allocated to both males and females. See the introductory chapter for more information and potential issues with these data.

Table 5. Gut sizes for 31 species, with sex-specific species averages.

Gr	Taxon	S	Stom	SI	Caec	Colon	Total Gut	Ref	Notes
Plat	*Alouatta palliata*	F	296	815	156	778	2045	1	
Plat	*Alouatta palliata*	M	230	719	148	630	1727	1	
Plat	*Alouatta palliata*	M	430	1052	289	1059	2830	1	
Plat	*A. palliata* male average	M	330	885.5	218.5	844.5	2278.5	-	
Plat	*Alouatta seniculus*	F	236	663	199	732	1830	2	
Plat	*Alouatta seniculus*	M	165	487	95	590	1337	2	
Plat	*Aotus trivirgatus*	F	84	288	47	120	539	1	
Plat	*Ateles belzebuth*	F	281	1632	136	289	2338	1	Sex not listed, used for both
Plat	*Ateles belzebuth*	M	281	1632	136	289	2338	1	Sex not listed, used for both
Plat	*Cacajao calvus*	F	113	1166	159	382	1820	2	
Plat	*Cacajao calvus*	F	102	987	194	322	1605	2	
Plat	*Cacajao calvus*	F	219	1304	179	318	2020	2	
Plat	*C. calvus* female average	F	144.7	1152.3	177.3	340.67	1815	-	
Plat	*Cacajao calvus*	M	125	1164	180	337	1806	2	
Plat	*Callicebus moloch*	F	42.7	286.1	54.5	180.6	563.9	3	
Plat	*Callicebus moloch*	M	74.5	329.7	54.8	165.7	624.7	3	
Plat	*Cebus apella*	M	122	846	12	104	1084	2	
Plat	*Cebus apella*	M	150	811	15	111	1087	2	
Plat	*Cebus apella*	M	112	670	13	107	902	2	
Plat	*C. apella* male average	M	128	775.67	13.33	107.33	1024.3	-	
Plat	*Cebus capucinus*	M	111	852	2	20	985	1	Data from a female individual
Plat	*Lagothrix lagotricha*	F	264	2115	181	660	3220	1	Data from captive animal
Plat	*Lagothrix lagotricha*	M	488	1796	293	699	3276	1	Data from captive animal
Plat	*Pithecia irrorata*	M	84	335.1	74	217.9	711	3	
Plat	*Saguinus fuscicollis*	F	9.9	68.3	10.2	47.4	135.7	4	Only species average available; data from eight individuals

Plat	*Saguinus fuscicollis*	M	9.9	68.3	10.2	47.4	135.7	4	Only species average available; data from eight individuals
Plat	*Saimiri sciureus*	F	57	256	10	35	358	2	
Plat	*Saimiri sciureus*	M	51	236	10	35	332	2	
Plat	*Saimiri sciureus*	M	37	235	17	32	321	2	
Plat	*Saimiri sciureus*	M	32	224	16	33	305	2	
Plat	*Saimiri sciureus*	M	76	351	15	38	480	2	
Plat	*S. sciureus* male average	M	49	261.5	14.5	34.5	359.5	-	
Cerco	*Cercopithecus cephus*	F	144	582	60	458	1244	1	
Cerco	*Cercopithecus cephus*	F	187	784	76	371	1418	1	
Cerco	*C. cephus* female average	F	165.5	683	68	414.5	1331	-	
Cerco	*Cercopithecus cephus*	M	70	446	45	325	886	1	
Cerco	*Cercopithecus cephus*	M	155	1008	56	877	2096	1	
Cerco	*C. cephus* male average	M	112.5	727	50.5	601	1491	-	
Cerco	*Cercopithecus neglectus*	F	206	710	83	827	1826	1	
Cerco	*Cercopithecus neglectus*	F	144	556	69	728	1497	1	
Cerco	*C. neglectus* female average	F	175	633	76	777.5	1661.5	-	
Cerco	*Cercopithecus nictitans*	F	73	763	65	563	1464	1	
Cerco	*Cercopithecus nictitans*	M	99	760	87	654	1600	1	
Cerco	*Cercopithecus nictitans*	M	177	798	95	753	1823	1	
Cerco	*Cercopithecus nictitans*	M	120	927	80	816	1943	1	
Cerco	*C. nictitans* male average	M	132	828.33	87.33	741	1788.67	-	
Cerco	*Lophocebus ugandae*	F	124	559	69	977	1729	1	
Cerco	*Lophocebus ugandae*	F	91	657	67	580	1395	1	
Cerco	*L. ugandae* female average	F	107.5	608	68	778.5	1562	-	
Cerco	*Macaca fascicularis*	F	178	1144	67	866	2255	1	
Cerco	*Macaca fascicularis*	M	143	1011	28	693	1875	1	
Cerco	*Macaca fascicularis*	M	306	918	29	659	1912	1	

Cerco	*Macaca fascicularis*	M	232	1411	90	1803	3536	2	
Cerco	*M. fascicularis* male average	M	227	1113.33	49	1051.67	2441	-	
Cerco	*Macaca mulatta*	F	77	618	81	377	1153	1	Sex not listed, used for both; data from a juvenile specimen
Cerco	*Macaca mulatta*	M	77	618	81	377	1153	1	Sex not listed, used for both; data from a juvenile specimen
Cerco	*Macaca sylvanus*	F	270	1187	72	1323	2852	1	
Cerco	*Mandrillus sphinx*	F	250	1143	50	1228	2671	1	
Cerco	*Mandrillus sphinx*	F	322	2435	70	2240	5067	1	
Cerco	*M. sphinx female average*	F	286	1789	60	1734	3869	-	
Cerco	*Mandrillus sphinx*	M	402	2854	64	1894	5214	1	
Cerco	*Miopithecus talapoin*	F	59	157	26	214	456	1	
Cerco	*Miopithecus talapoin*	F	44	149	25	87	305	1	
Cerco	*M. talapoin* female average	F	51.5	153	25.5	150.5	380.5	-	
Cerco	*Miopithecus talapoin*	M	49	231	12	122	414	1	
Colo	*Colobus polykomos*	F	1021	556	26	549	2152	1	
Colo	*Colobus polykomos*	F	1056	925	15	630	2626	1	
Colo	*C. polykomos* female average	F	1038.5	740.5	20.5	589.5	2389	-	
Colo	*Nasalis larvatus*	M	1978	3120	100	1234	6432	1	Data from captive animal
Colo	*Semnopithecus entellus*	M	1585	1673	105	978	4341	1	
Colo	*Semnopithecus entellus*	M	1439	1167	140	760	3506	1	
Colo	*S. entellus* male average	M	1512	1420	122.5	869	3923.5	-	
Colo	*Trachypithecus cristatus*	F	1694	1929	90	966	4679	1	
Colo	*Trachypithecus obscurus*	F	1524	1259	64	1394	4241	2	
Colo	*Trachypithecus obscurus*	M	1363	1953	64	670	4050	1	
Colo	*Trachypithecus obscurus*	M	1351	1969	88	902	4310	1	
Colo	*T. obscurus* male average	M	1357	1961	76	786	4180	-	

Hylo	*Hylobates lar*	F	104	268	6	403	781	1	Fixed specimen
Hylo	*Symphalangus syndactylus*	M	140	1708	81	954	2883	1	Data from captive animal
Hylo	*Symphalangus syndactylus*	M	256	1263	70	978	2567	1	Data from captive animal
Hylo	*S. syndactylus* male average	M	198	1485.5	75.5	966	2725	-	
Hom	*Gorilla gorilla*	M	1087	4018	590	4813	10508	1	
Hom	*Gorilla gorilla*	M	1126	7771	1186	7657	17740	2	
Hom	*G. gorilla* male average	M	1106.5	5894.5	888	6235	14124	-	
Hom	*Pan troglodytes*	M	690	3761	386	2925	7662	1	
Hom	*Pongo pygmaeus*	F	585	4312	81	4198	9176	2	

Gr. = Group: Plat = Platyrrhine monkey; Cerco = Cercopithecine monkey; Colo = Colobine monkey; Hylo = Hylobatid; Hom = Hominid. S = Sex: F = Female; M = Male. Stom = surface area of the stomach (cm^2); SI = surface area of the small intestine (cm^2); Caec = surface area of the caecum (cm^2); Colon = surface area of the colon (cm^2); References: 1) Chivers and Hladik (1980); 2) Chivers personal communication (2016); 3) Ferrari and Lopes (1995); 4) Ferrari and Martins (1992)

Locomotion

Locomotion data in the form of the percent frequency of locomotor modes in the wild (Table 6) are available for male individuals for 34 of the species and for female individuals for 33 of the species for which linear measurements were collected. The six locomotor modes were quadrupedalism, bipedalism, climbing, bridging, leaping, and suspension as defined by Jarrell (2011) and they include both arboreal and terrestrial locomotion, where applicable. Percentages are averaged across sites/populations, and include data from observations of traveling, feeding, foraging, and gap crossing. In Analysis B, I utilize these percentages as continuous data, since they are used as continuous predictor variables in the regressions for this analysis. In Analysis C, the percentages are utilized as categorical response variables for the discriminant function analyses. I thus used these data and locomotor classifications according to Jarrell (2011) and Schmidt (2010) to categorize locomotion for each species into four categories: suspensory, leaping, arboreal quadrupeds (AQ) and terrestrial quadrupeds (TQ).

Table 6. Percent frequency of locomotor modes observed in wild primate populations, with species averages**.**

Gr	Taxon	Q	Bi	Cl	Br	L	S	Pop	Act	N	Site	Ref	Notes
Plat	*Alouatta palliata*	47	0	37	10	4	2	A	All	4977	La Pacifica, Costa Rica	1	Suspension = quadrupedal suspension = movement in which the body is progressing below a support using three or four limbs (with or without tail support).
Plat	*Alouatta seniculus*	80	0	16	0	4	0	A	T	NA	Raleighvallen-Voltzberg Nature Reserve, Surinam	2	Pronograde = leap
Plat	*Alouatta seniculus*	59	0	41	0	0	0	A	F	NA	Raleighvallen-Voltzberg Nature Reserve, Surinam	2	
Plat	*Alouatta seniculus*	79.6	0	5.2	12.3	1.9	1	A	T	1191	Station des Nouragues, French Guiana	3	Leaping = Air (gap crossing modes involving an airborne phase such as leaping and dropping), Wet season.
Plat	*Alouatta seniculus*	72.7	0	6.1	15.6	4.1	1.5	A	T	707	Station des Nouragues, French Guiana	3	Leaping = Air (gap crossing modes involving an airborne phase such as leaping and dropping), Dry season.
Plat	*Alouatta seniculus*	84.4	0	6.2	7.3	1.6	0.5	A	F	372	Station des Nouragues, French Guiana	3	Leaping = Air (gap crossing modes involving an airborne phase such as leaping and dropping), Wet season.

Plat	*Alouatta seniculus*	86.5	0	3.2	5.6	2.5	2.2	A	F	283	Station des Nouragues, French Guiana	3	Leaping = Air (gap crossing modes involving an airborne phase such as leaping and dropping), Dry season.
Plat	*A. seniculus* average	77.03	0	12.95	6.8	2.35	0.87	-	-	-	-	-	-
Plat	*Ateles belzebuth*	49	0.6	12.5	10.7	2.3	23.1	A	All	3760	Yasuní National Park, Ecuador	4	Excludes 1.8% sway. Quad = 28.2% clamber and 20.8% quad. Leap = drop and leap because they are combined.
Plat	*Ateles geoffroyi*	51.07	2.23	9.22	1.65	10.88	22.6	A	All	1927	Barro Colorado Island	5	Excludes 2.32% drop. 0.04 missing from total percentages.
Plat	*Cacajao calvus*	78	0	0	0	8	9	A, J	F	117	Lake Teiú, Brazil	6	Excludes 5% drop. Susp = hindlimb suspension. Bout total = 288. Estimated locomotor bouts = 117. Original percentages included sitting and other positions.
Plat	*Cacajao calvus*	61	0	3	1	23	2	A, J	T	222	Lake Teiú , Brazil	6	Excludes 10% drop. Susp - hindlimb suspension. Bout total = 239. Estimated locomotor bouts = 222. Original percentages included sitting and other positions.
Plat	*C. calvus* average	69.5	0	1.5	0.5	15.5	5.5	-	-	-	-	-	-
Plat	*Callicebus moloch*	71.6	0	9.2	1.2	17.7	0.3	A	All	325	Yasuní National Park, Ecuador	7	

Plat	*Cebus apella*	84	0	5	0	10	0	A	T	NA	Raleighvallen-Voltzberg Nature Reserve, Surinam	2	Pronograde = leap
Plat	*Cebus apella*	88	0	8	0	4	0	A	F	NA	Raleighvallen-Voltzberg Nature Reserve, Surinam	2	Subspecies: *C. a. apella.*
Plat	*Cebus apella*	41.9	2.1	19.1	13.3	19.7	0	A	T	1218	Station des Nouragues, French Guiana	8	Excludes 3.9% drop. Subspecies: *C. a. apella.* Quad walk = 31. 8%. Quad scramble/ pronograde clamber = 10.1%. Climb vertical climb = 11.4%. Climb vertical descent = 7.7%.
Plat	*Cebus apella*	40.9	3	39.4	3.1	11.3	0	A	F	319	Station des Nouragues, French Guiana	8	Excludes 3.9% drop. Subspecies: *C. a. apella.* Quad walk = 24.2%. Quad scramble/ pronograde clamber = 16.7%. Climb vertical climb = 17.4%. Climb vertical descent = 22%.
Plat	*Cebus apella*	56	0	9	9	22	0	A, J	All	895	Iwokrama Rainforest Reserve, Guyana	9	Excludes 4% drop. Quad walk = 46%. Quad bound = 7%. Quad scramble/ pronograde clamber = 3%.
Plat	*Cebus apella*	54	0	6	7	27	0	A, J	T	NA	Iwokrama Rainforest Reserve, Guyana	9	Excludes 4% drop. Quad walk = 46%. Quad bound = 6%. Quad scramble/ pronograde clamber = 2%.

Plat	*Cebus apella*	56	0	11	11	17	0	A, J	F	NA	Iwokrama Rainforest Reserve, Guyana	9	Excludes 4% drop. Quad walk = 45%. Quad bound = 8%. Quad scramble/ pronograde clamber = 3%.
Plat	*C. apella* average	60.11	0.73	13.93	6.2	15.86	0	-	-	-	-	-	-
Plat	*Cebus capucinus*	54	1	26	3	15	0	A	All	1000	Santa Rosa National Park, Costa Rica	1	All = traveling and feeding. Excludes 1% bimanualism and <1% quad susp.
Plat	*Cebus capucinus*	65	0	4	0	28	0	A	T	78	Agua Clara Bay, Panama	10	
Plat	*Cebus capucinus*	67	0	33	0	0	0	A	F	45	Agua Clara Bay, Panama	10	
Plat	*C. capucinus* average	62	0.33	21	1	14.33	0	-	-	-	-	-	-
Plat	*Lagothrix lagotricha*	58.8	0.2	14.4	10.2	3.9	11.1	A	All	3926	Yasuní National Park, Ecuador	4	Excludes 1.4% sway. Quad = 30.1% clamber and 28.7% quad. Leap = drop and leap because they are combined.
Plat	*Pithecia pithecia*	25	0	5	0	70	0	A	T	NA	Raleighvallen -Voltzberg Nature Reserve, Surinam	11	
Plat	*Saguinus fuscicollis*	54	1	6	0	39	0	A, J	T	686	Fazenda Experimental Catuaba, Brazil	12	Estimated from numbers in text and from chart. Quad includes scan/ scansorial locomotion (vertical ascent). Hop - in bipedal.
Plat	*Saimiri boliviensis*	73.58	0.5	4.26	1.03	19.83	0.3	A	All	4933	Barro Colorado Island	5	Excludes 0.8% drop. Percentages equal over 100 = 100.3.

Plat	*Saimiri sciureus*	60.4	0	8.9	4.4	25.4	0.9	A	All	569	Yasuní National Park, Ecuador	7	
Plat	*Saimiri sciureus*	87	0	11	0	2	0	A	F	NA	Raleighvallen-Voltzberg Nature Reserve, Surinam	2	
Plat	*Saimiri sciureus*	55	0	42	0	3	0	A	T	NA	Raleighvallen-Voltzberg Nature Reserve, Surinam	2	
Plat	*S. sciureus* average	67.47	0	20.63	1.47	10.13	0.3	-	-	-	-	-	-
Cerco	*Cercopithecus nictitans*	74.3	0	15.2	0	10.4	0	A	All	604	Tai National Park, Ivory Coast	13	
Cerco	*Chlorocebus aethiops*	68.93	0	29.17	0	1.9	0	A (F)	All	NA	Laikipia, Kenya	14	
Cerco	*Lophocebus ugandae*	46	0	31	0	21	0	A	T	2328	Kibale, Uganda	15	Excludes 1% bi-manualism.
Cerco	*Lophocebus ugandae*	48	0	40	0	11	0	A	F	1583	Kibale, Uganda	15	Excludes 1% bi-manualism.
Cerco	*L. ugandae* average	47	0	35.5	0	16	0	-	-	-	-	-	-
Cerco	*Macaca fascicularis*	81.9	0	5.4	0	10.8	1.2	A (M)	T	NA	Ketambe Research Station, Gunung Leuser National Park, Aceh Tenggara, northern Sumatra, Indonesia	16	Excludes 0.7% drop. Quad walk = 65.2%, Quad scramble/ pronograde clamber = 16.7%. Vertical climb = 4.9%, Vertical Descent = 0.5%. Susp - orthograde clamber/ cautious climb. All locomotion bouts - 1369.

Cerco	*Macaca fascicularis*	87.5	0	8.8	0	3.6	0.2	A (M)	F	NA	Ketambe Research Station, Gunung Leuser National Park, Aceh Tenggara, northern Sumatra, Indonesia	16	Quad walk = 74.0%, Quad scramble/ pronograde clamber = 13.5%. Vertical climb = 7.7%, Vertical Descent = 1.1%. Susp - orthograde clamber/ cautious climb. All locomotion bouts - 1369.
Cerco	*Macaca fascicularis*	74.8	0	18	0.9	6.4	0	A	T	94	Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan, Indonesia	17	Quad walk = 59.8%, Quad scramble/ pronograde clamber = 15.0%. Vertical climb = 12.0%, Vertical bound = 6.0%. Pronograde = leap.
Cerco	*Macaca fascicularis*	11.8	0	3.9	48.7	35.5	0	A	GC	68	Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan, Indonesia	17	Quad walk = 10.5%, Quad scramble/ pronograde clamber = 1.3%. Vertical climb - 2.6%, Vertical bound - 1.3%. Pronograde = leap.
Cerco	*M. fascicularis* average	64	0	9.03	12.4	14.08	0.35	-	-	-	-	-	-
Cerco	*Macaca mulatta*	75	2	12	0	11	0	A	All	NA	Cayo Santiago, Puerto Rico	18	Vertical climb = 12%.
Cerco	*Macaca mulatta*	48	1	31	0	17	0	J	All	NA	Cayo Santiago, Puerto Rico	18	Excludes 3% drop. Vetical climb = 28%. Bound = 3%.
Cerco	*M. mulatta* average	61.5	1.5	21.5	0	14	0	-	-	-	-	-	-
Cerco	*Mandrillus sphinx*	90	0	4.5	1	4.5	0	NA	All	NA	Rio Muni, Equatorial Guinea	19	Quad = walk. All numbers are estimates and have ~ in front.

Cerco	*Papio anubis*	98.6	0	0.7	0	0.5	0	A	All	497	Gombe, Tanzania	20	Quad = walking and running. Pronograde = leap.
Cerco	*Papio anubis*	68.3	0	21.3	0	10.4	0	A	All	26	Gombe, Tanzania	20	Quad = walking and running. Pronograde = leap. Observations made in arboreal context.
Cerco	*Papio anubis*	96.8	0	3.2	0	0	0	A, J	All	NA	Gilgil, Kenya	21	Quad = walking. 183 instances of leaping noted.
Cerco	*P. anubis* average	87.9	0	8.4	0	3.63	0	-	-	-	-	-	-
Colo	*Colobus guereza*	29.9	0	36.5	0	19.6	0	NA	All	NA	Rift Valley	14	Vertical climb = 20.9%. Vertical descent = 15.6%.
Colo	*Colobus guereza*	39	0	16	0	44	0	A	T	2056	Kibale, Uganda	15	Susp = "<1" %. Vertical climb = 11%. Vertical bound = 5%.
Colo	*Colobus guereza*	43	0	22	0	33	1	A	F	2087	Kibale, Uganda	15	Biped = "<1". Vertical climb = 18%. Vertical bound = 4%.
Colo	*C. guereza* average	37.3	0	24.83	0	32.2	0.33	-	-	-	-	-	-
Colo	*Colobus polykomos*	74.4	0	8	0	17.6	0	A	T	538	Tai National Park, Ivory Coast	22	Quad = walk and run. Quadrupedal run includes bounding.
Colo	*Colobus polykomos*	62.5	0	24.2	0	13.3	0	A	Fo	380	Tai National Park, Ivory Coast	22	Quad = walk and run. Quadrupedal run includes bounding.
Colo	*C. polykomos* average	68.45	0	16.1	0	15.45	0	-	-	-	-	-	-
Colo	*Nasalis larvatus*	59.92	0	11.34	0	23.89	4.85	A	T	247	Indonesia	23	Leap = jump. Susp = brachiate.
Colo	*Piliocolobus badius*	64.1	0	12.2	0	20.8	0	A	T	797	Tai National Park, Ivory Coast	22	Quad = walk and run. Quadrupedal run includes bounding.

Colo	*Piliocolobus badius*	58.4	0	21.6	0	15	0	A	Fo	669	Tai National Park, Ivory Coast	22	Quad = walk and run. Quadrupedal run includes bounding.
Colo	*P. badius* average	61.25	0	16.9	0	17.9	0	-	-	-	-	-	-
Colo	*Trachypithecus obscurus*	50.6	0	9.2	0	40.2	0	A	T	348	Selangor, West Malaysia	24	
Colo	*Trachypithecus obscurus*	68.6	0	16.4	0	15	0	A	F	235	Selangor, West Malaysia	24	
Colo	*T. obscurus* average	59.6	0	12.8	0	27.6	0	-	-	-	-	-	-
Hylo	*Hylobates agilis*	4	26.7	5.3	0	16	48	A	T	75	Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan, Indonesia	17	Bipedalism = walking & stepping. Susp = brachiation.
Hylo	*Hylobates agilis*	0	4.8	0	4.8	33	57	A	GC	21	Cabang Panti Research Station, Gunung Palung National Park, West Kalimantan, Indonesia	17	Bipedalism= walking & stepping. Susp = brachiation.
Hylo	*H. agilis* average	2	15.75	2.65	2.4	24.5	52.5	-	-	-	-	-	-
Hylo	*Hylobates lar*	0	8	21	0	15	56	A	T	118	Krau Game Reserve, Pahang, Malaysia	25	
Hylo	*Hylobates lar*	0	2	51	0	2	45	A	F	93	Krau Game Reserve, Pahang, Malaysia	25	
Hylo	*H. lar* average	0	5	36	0	8.5	50.5	-	-	-	-	-	-
Hylo	*Hylobates moloch*	0	7.62	14.58	0	27	50.8	All	All	NA	Mount Malabar Protected Forest, West Java, Indonesia	26	Gibbons were previously in protected care.
Hylo	*Symphalangus syndactylus*	0	6	37	0	6	51	A	T	643	Krau Game Reserve, Pahang, Malaysia	25	
Hylo	*Symphalangus syndactylus*	0	3	74	0	0	23	A	F	563	Krau Game Reserve, Pahang, Malaysia	25	
Hylo	*S. syndactylus* average	0	4.5	55.5	0	0	57.5	-	-	-	-	-	-

Hom	*Gorilla beringei*	68.2	4.2	21.9	0	0	5.6	A (M)	All	35	Karisoke, Rwanda	27	
Hom	*Gorilla beringei*	47.9	1.4	45	0	0	5.2	A (F)	All	118	Karisoke, Rwanda	27	Excludes 0.5% acrobat.
Hom	*G. beringei* average	58.05	2.8	33.45	0	0	5.4	-	-	-	-	-	-
Hom	*Gorilla gorilla*	39	0	54	0	0	0	A (M)	All	41	Bai Hokou, CAR	27	Excludes 7% acrobat. Lone males. Quad walk = 22%. Quad scramble/ pronograde clamber = 17%.
Hom	*Gorilla gorilla*	45.2	2.6	42.1	0	0	7.9	A (M)	All	38	Bai Hokou, CAR	27	Excludes 7.9% acrobat. Group males. Quad walk = 21.5%. Quad scramble/ pronograde clamber = 23.7%.
Hom	*Gorilla gorilla*	47.2	4.2	40	0	0	4.2	A (F)	All	95	Bai Hokou, CAR	27	Excludes 4.2% acrobat. Quad walk = 23.2%. Quad scramble/ pronograde clamber = 24%.
Hom	*Gorilla gorilla*	93.7	0.4	4.9	0.3	0.1	0.5	A	All	2239	Gombe/ Mahale, Tanzania	20	Quad walk/run = 93.4%. Quad scramble = 0.3%. Biped walk/run = 0.4%. Pronograde leap = 0.1%.
Hom	*G. gorilla* average	43.8	2.27	45.37	0	0	4.03	-	-	-	-	-	-
Hom	*Pan troglodytes*	39	6.7	48.9	2.4	0.4	5.9	A	All	223	Gombe/ Mahale, Tanzania	20	Quad walk/run = 36.7%. Quad scramble = 2.3%. Biped walk/run = 6.7%. Pronograde leap = 0.4%.
Hom	*Pan troglodytes*	89.3	0.2	9.6	0	0.2	0.8	A (M)	T	605	Tai National Park, Ivory Coast	28	
Hom	*Pan troglodytes*	85.7	0	12.6	0	0.2	1.5	A (F)	T	533	Tai National Park, Ivory Coast	28	

Hom	*Pan troglodytes*	81.1	5.4	9	0	0	4.5	A (M)	F	111	Tai National Park, Ivory Coast	28	
Hom	*Pan troglodytes*	85.5	4.6	5.3	0	0.7	3.9	A (F)	F	152	Tai National Park, Ivory Coast	28	
Hom	*P. troglodytes* average	79.05	2.88	15.05	0.45	0.27	2.85	-	-	-	-	-	-
Hom	*Pongo abelii*	15	7	22	4	0	39	A, J	T	NA	Ketambe Research Station, Gunung Leuser National Park, Aceh Tenggara, northern Sumatra, Indonesia	29	Excludes 2% drop, 7% sway, 1% ride, 3% pronograde suspension. Vertical climb = 14%. Vertical descent = 8%. Brachiate= 16%. Orthograde clamber/ cautious climb = 23%. Ref also includes tree sway (7%) and suspension (3%). 2811 total observations.
Hom	*Pongo abelii*	24	8	33	0	0	26	A, J	F	NA	Ketambe Research Station, Gunung Leuser National Park, Aceh Tenggara, northern Sumatra, Indonesia	29	Excludes 2% drop, 1% sway, 1% forelimb hindswing, 5% pronograde suspension. Vertical climb - 21%. Vertical descent - 12%. Brachiate - 12%. Orthograde clamber/ cautious climb - 14%. Ref also includes tree sway (1%) and pronograde suspension (5%). 2811 total observations.
Hom	*P. abelii* average	19.5	7.5	27.5	2	0	32.5	-	-	-	-	-	-

Hom	*Pongo pygmaeus*	12	0	18	0	0	62	A (F)	T	NA	Kutai National Park, East Kalimantan, Indonesia	30	Excludes 7% sway and 1% pronograde suspension.
Hom	*Pongo pygmaeus*	12	0	33	0	0	53	A (F)	F	NA	Kutai National Park, East Kalimantan, Indonesia	30	Excludes 2% pronograde suspension.
Hom	*P. pygmaeus* average	12	0	25.5	0	0	57.5	-	-	-	-	-	-

Note: Data categorized following Jarrell (2011).
Plat = Platyrrhine monkey
Cerco = Cercopithecine monkey
Colo = Colobine monkey
Hylo = Hylobatid
Hom = Hominid
Q = % quadrupedalism. Includes arboreal and terrestrial quadrupedalism.
Bi = % bipedalism. Includes arboreal and terrestrial bipedalism.
Cl = % climbing.
Br = % bridging.
L = % leaping.
S = % suspension. Includes quadrupedal suspension.
Pop = Population: A = adults, A (F) = adult females, A (M) = adult males, J = juveniles
Act = Activity: All = all activity, T = traveling, F = feeding, Fo = foraging, GC = gap crossing.
Ref = References: 1. Gebo (1992); 2. Fleagle and Mittermeier (1980); 3. Youlatos (1998a); 4. Cant et al. (2001); 5. Fontaine (1990); 6. Walker and Ayres (1996); 7. Youlatos (1999); 8. Youlatos (1998b); 9. Wright (2007); 10. Bergeson (1989); 11. Fleagle and Meldrum (1988); 12. Garber and Leigh (2001); 13. Bitty and McGraw (2007); 14. Rose (1979); 15. Gebo and Chapman (1995); 16. Cant (1988); 17. Cannon and Leighton (1994); 18. Wells and Turnquist (2001); 19. Sabater Pí (1972); 20. Hunt (1991); 21. Rose (1977); 22. McGraw (1998); 23. Bismark (1994); 24. Fleagle (1980); 25. Fleagle (1976); 26. Ario et al. (2018); 27. Remis (1998); 28. Doran (1993); 29. Thorpe and Crompton (2006); 30. Cant (1987).

Statistical analyses

Analyses for this dissertation are separated by sex to minimize the effects of body size dimorphism on torso morphology within a species.

Analysis A

In this analysis, I tested the hypotheses proposed in the paleoanthropology literature about how torso dimensions relate to diet, which are described at length in the introductory chapter for this dissertation and listed in Table 7. I conducted PGLS regressions on natural log-transformed, size-adjusted torso variables, where each torso variable (response variables) was a function of the diet variables (predictor variables) it is hypothesized to be related to.

The torso variables featured here include bi-iliac breadth, upper ilium width, iliac flare, lumbar vertebral column length, and ribcage breadth at rib level 7. PGLS analyses were conducted using the caper package version 1.0.1 (Orme et al. 2011) in R version 3.3.1 (R Core Development Team 2015). Locomotion variables were not included in Analysis A, given the small subset of the sample for which all diet, gut size, locomotion, and torso variables exist.

Table 7. Hypotheses about how diet is related to the torso. These hypotheses are translated into functions for the PGLS regressions in Analysis A.

Morphology	Link to diet	Ref	Functions for Analysis A
Bi-iliac breadth	Related to gut volume and diet type. Wider bi-iliac breadths are associated with a folivorous, green plant-based diet (larger guts) while narrow bi-iliac breadths are associated with a higher-quality diet via cooking, eating more animal foods, prey, nuts and seeds, and underground storage organs (smaller guts).	1,2,3	log(adj.Bi-iliac breadth) ~ log(Acetab) log(adj.Bi-iliac breadth) ~ log(Acetab) + Green Plants log(adj.Bi-iliac breadth) ~ log(Acetab) + Prey log(adj.Bi-iliac breadth) ~ log(Acetab) + Seeds log(adj.Bi-iliac breadth) ~ log(Acetab) + Roots/Tubers **Reduced sample size:** log(adj.Bi-iliac breadth) ~ log(Acetab) log(adj.Bi-iliac breadth) ~ log(Acetab) + log(adj.Gut)

Iliac flare	Related to gut volume and diet type. Higher flare is associated with a folivorous, green plant-based diet while less flare are associated with a higher-quality diet via cooking, eating more animal foods, prey, nuts and seeds, and underground storage organs (smaller guts).	2,4	log(adj.Flare) ~ log(Acetab) log(adj.Flare) ~ log(Acetab)+ Green.Plants log(adj.Flare) ~ log(Acetab) + Prey log(adj.Flare) ~ log(Acetab) + Seeds log(adj.Flare) ~ log(Acetab) + Roots/Tubers **Reduced sample size:** log(adj.Flare) ~ log(Acetab) log(adj.Flare) ~ log(Acetab) + log(adj.Gut)
Ilium width	Related to gut volume and diet type. Wider ilia are associated with larger guts in frugivorous and folivorous anthropoids.	5	log(adj.Ilium width) ~ log(Acetab) log(adj.Ilium width) ~ log(Acetab) + Green.Plants log(adj.Ilium width) ~ log(Acetab) + Fruits **Reduced sample size:** log(adj.Ilium width) ~ log(Acetab) log(adj.Ilium width) ~ log(Acetab) + log(adj.Gut)
Ribcage breadth	Related to gut volume and diet type. Wider bi-iliac breadths are associated with a folivorous, green plant-based diet (larger guts) while narrow bi-iliac breadths are associated with a higher-quality diet via cooking, eating more animal foods, prey, nuts and seeds, and underground storage organs (smaller guts).	2,3	log(adj.Ribcage breadth) ~ log(Acetab) log(adj.Ribcage breadth) ~ log(Acetab) + Green.Plants log(adj.Ribcage breadth) ~ log(Acetab) + Prey log(adj.Ribcage breadth) ~ log(Acetab) + Seeds **Reduced sample size:** log(adj.Ribcage breadth) ~ log(Acetab) log(adj.Ribcage breadth) ~ log(Acetab) + log(adj.Gut)
Lumbar vertebral column length	Related to gut volume and diet type. Longer lumbar spines are associated with larger guts in frugivorous and folivorous anthropoids.	5	log(adj.Lumbar) ~ log(Acetab) log(adj.Lumbar) ~ log(Acetab) + Green.Plants log(adj.Lumbar) ~ log(Acetab) + Fruits **Reduced sample size:** log(adj.Lumbar) ~ log(Acetab) log(adj.Lumbar) ~ log(Acetab) + log(adj.Gut)

Ref = References 1. Elftman (1929); 2. Aiello and Wheeler (1995); 3. Wrangham and Carmody (2010); 4. Schmid, 1991; 5. Lovejoy et al. (2009).

The samples used for this analysis comprised the 45 (out of 48) species for which the pelvic measurements and diet data are available for both sexes (excluding *Hylobates agilis*, *Pithecia irrorata*, and *Cebus capucinus*), and the 44 species for which diet data and lumbar vertebral column length is available in both sexes (excluding *Hylobates agilis*, *Pithecia irrorata*, *Cebus capucinus*, and *Cacajao calvus*) Phylogenetic topologies for the primate species and accompanying branch lengths were obtained from 10ktrees, version 3 (Arnold et al., 2010). Figure 4 provides the phylogenetic tree for the whole sample (45 species).

Each linear measurement except for iliac flare was divided by acetabular diameter. Since the iliac flare measurement is a ratio, it was not re-calculated by dividing size-adjusted iliac fossa width by size-adjusted false pelvis length, since the ratio of two numbers divided by the same number is equivalent to the original ratio (and thus it is inherently already a relative measure).

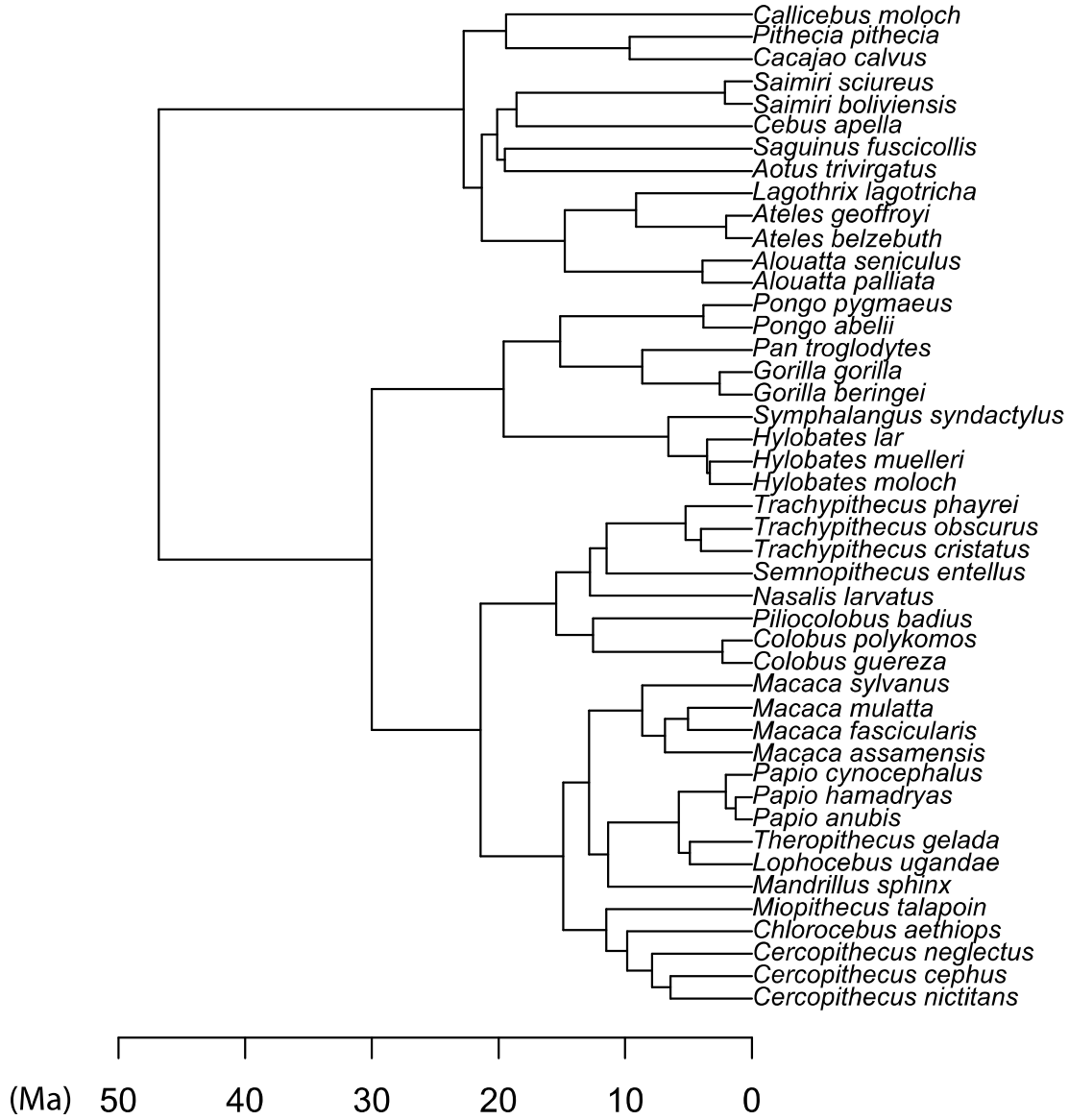

Figure 4. Time-calibrated phylogenetic tree showing the relationships among the whole sample (45 species) included in Analysis A.

Acetabular diameter is a good proxy for body mass in primates, as the hip joint is highly correlated with body mass (Jungers, 1988; Jungers, 1991; Hammond et al., 2013b). However, using acetabular diameter as a body size proxy has some flaws, due to slight differences in how the acetabulum scales with body mass in some species (Ward, 1991). Nevertheless, 1) it has been demonstrated that the acetabulum scales with isometry across a large sample of anthropoids (Lewton, 2015), and 2) a regression of logged acetabular diameter against logged species-mean body weights from Smith and Jungers (1997) for the 45 species in this sample was significant ($p < 0.001$) and the coefficient of determination was high ($R^2 = 0.96$). This result supports the use of acetabular diameter as a proxy for body size.

Logged acetabular diameter was also included as a covariate in the models. Including logged acetabular diameter as a covariate facilitates testing whether or not torso shape differences (response variables) show a relationship with diet beyond the relationship that these variables have with body size. This approach is not intended to "control" for body size completely, as there are meaningful differences in torso form across anthropoids related to body size. See "Limitations" sections for more information about the intentions and flaws of this approach.

The remainder of the regressions tested the hypotheses that there was a relationship between diet and ribcage breadth (in the 21 species of females and the 21 species of males for which these data are available; Table 8), between gut size and the pelvis (in the 23 species of females and the 23 species of males for which these data are available; Table 9), between gut size and lumbar vertebral column length (in the 22 species of females and the 23 species of males for which these data are available; Table

10), and between diet and gut size with lower ribcage breadths (in the 9 species of females and the 9 species of males for which these data are available; Table 11). Gut size was size-adjusted by dividing the square root of gut size by acetabular diameter, see Table 5 for sample size information. Ribcage breadth sample sizes are listed in Table 3.

Table 8. 21 species of females and 21 species of males that were included in tests of how diet is related to ribcage breadth.

Females	**Males**
Alouatta palliata	*Alouatta palliata*
Aotus trivirgatus	*Alouatta seniculus*
Cacajao calvus	*Ateles belzebuth*
Gorilla gorilla	*Callicebus moloch*
Hylobates lar	*Colobus guereza*
Hylobates muelleri	*Hylobates agilis*
Macaca mulatta	*Hylobates lar*
Miopithecus talapoin	*Hylobates moloch*
Nasalis larvatus	*Hylobates muelleri*
Pan troglodytes	*Lophocebus ugandae*
Papio hamadryas	*Macaca mulatta*
Piliocolobus badius	*Miopithecus talapoin*
Pithecia pithecia	*Pan troglodytes*
Pongo abelii	*Papio hamadryas*
Saguinus fuscicollis	*Pithecia irrorata*
Saimiri boliviensis	*Pithecia pithecia*
Saimiri sciureus	*Saimiri boliviensis*
Semnopithecus entellus	*Saimiri sciureus*
Symphalangus syndactylus	*Theropithecus gelada*
Theropithecus gelada	*Trachypithecus cristatus*
Trachypithecus cristatus	*Trachypithecus obscurus*

Table 9. 23 species of females and 23 species of males that were included in tests of how gut size is related to the pelvis.

Females	**Males**
Alouatta palliata	*Alouatta palliata*
Alouatta seniculus	*Alouatta seniculus*
Aotus trivirgatus	*Ateles belzebuth*
Ateles belzebuth	*Cacajao calvus*
Cacajao calvus	*Callicebus moloch*
Callicebus moloch	*Cebus apella*
Cercopithecus cephus	*Cebus capucinus*
Cercopithecus neglectus	*Cercopithecus cephus*
Cercopithecus nictitans	*Cercopithecus nictitans*
Colobus polykomos	*Gorilla gorilla*
Hylobates lar	*Lagothrix lagotricha*
Lagothrix lagotricha	*Macaca fascicularis*
Lophocebus ugandae	*Macaca mulatta*
Macaca fascicularis	*Mandrillus sphinx*
Macaca mulatta	*Miopithecus talapoin*

Macaca sylvanus	*Nasalis larvatus*
Mandrillus sphinx	*Pan troglodytes*
Miopithecus talapoin	*Pithecia irrorata*
Pongo pygmaeus	*Saguinus fuscicollis*
Saguinus fuscicollis	*Saimiri sciureus*
Saimiri sciureus	*Semnopithecus entellus*
Trachypithecus cristatus	*Symphalangus syndactylus*
Trachypithecus obscurus	*Trachypithecus obscurus*

Table 10. 22 species of females and 23 species of males that were included in tests of how gut size is related to lumbar vertebral column length.

Females	**Males**
Alouatta palliata	*Alouatta palliata*
Alouatta seniculus	*Alouatta seniculus*
Aotus trivirgatus	*Ateles belzebuth*
Ateles belzebuth	*Cacajao calvus*
Callicebus moloch	*Callicebus moloch*
Cercopithecus cephus	*Cebus apella*
Cercopithecus neglectus	*Cebus capucinus*
Cercopithecus nictitans	*Cercopithecus cephus*
Colobus polykomos	*Cercopithecus nictitans*
Hylobates lar	*Gorilla gorilla*
Lagothrix lagotricha	*Lagothrix lagotricha*
Lophocebus ugandae	*Macaca fascicularis*
Macaca fascicularis	*Macaca mulatta*
Macaca mulatta	*Mandrillus sphinx*
Macaca sylvanus	*Miopithecus talapoin*
Mandrillus sphinx	*Nasalis larvatus*
Miopithecus talapoin	*Pan troglodytes*
Pongo pygmaeus	*Pithecia irrorata*
Saguinus fuscicollis	*Saguinus fuscicollis*
Saimiri sciureus	*Saimiri sciureus*
Trachypithecus cristatus	*Semnopithecus entellus*
Trachypithecus obscurus	*Symphalangus syndactylus*
-	*Trachypithecus obscurus*

Table 11. 9 species of females and 9 species of males that were included in tests of how gut size is related to ribcage breadth.

Females	**Males**
Alouatta palliata	*Alouatta palliata*
Aotus trivirgatus	*Ateles belzebuth*
Cacajao calvus	*Callicebus moloch*
Hylobates lar	*Macaca mulatta*
Macaca mulatta	*Miopithecus talapoin*
Miopithecus talapoin	*Pan troglodytes*
Saguinus fuscicollis	*Pithecia irrorata*
Saimiri sciureus	*Saimiri sciureus*
Trachypithecus cristatus	*Trachypithecus obscurus*

Model fit was compared using the Akaike Information Criterion (AIC). AIC is a model selection tool that quantifies goodness of fit, and a lower AIC value means the model is better fitting, as a lower value indicates the model explains more of the variance after controlling for the number of terms in the model. After determining which model is best-fitting, whether the predictors are having an effect on the response variables was determined from the predictor p-values. A significant p-value ($p < 0.05$) suggests that changes in the predictors, either diet variables or acetabular diameter, contribute to changes in the response. Insignificant predictors ($p > 0.05$) suggest that the predictors add net explanatory power to the models, though these variables themselves are not significant predictors of the response variables. Best-fitting models that have significant diet predictors from this first step were then included in PGLS regressions within each taxonomic sub-group, to examine if patterns hold between variables in each group (platyrrhines, cercopithecoids, and hominoids).

See Appendix A for an initial, exploratory analysis that was conducted to test how natural-log adjusted torso variables relate to diet, locomotion, and sex-specific species averages of body mass. See Appendix B for an analysis similar to Analysis A, which uses the same targeted, hypothesis testing approach that is used here but includes logged torso variables that were not divided by acetabular diameter as the response variables in the PGLS regressions.

Analysis B

While Analysis A analysis considers how torso variables relate individually to diet, Analysis B tests how a matrix of features—selected to capture lower torso shape—relate to diet, acetabular diameter, and locomotion in the 31 species for which these data

exist for both males and females. As there are no lumbar vertebral column lengths available for *Hylobates agilis* females and *Cacajao calvus* females, these species were excluded from this analysis although locomotor data is available from the literature.

I used the 'lm.rrpp' function in the RRPP package version 0.3.0 (Collyer and Adams, 2018) in R version 3.3.1 (R Core Development Team, 2015) to run sex-specific multivariate multiple PGLS regressions, with the matrix of linear measurements as the response variables. Phylogenetic topologies for the 31 primate species and accompanying branch lengths were obtained from 10ktrees, version 3 (Figure 5, Arnold et al., 2010). The measurements included in the matrix of torso variables include upper ilium width, lower ilium width, false pelvis length, bi-iliac breadth, and lumbar vertebral column length. These measurements were size-adjusted using the geometric mean of these five measurements. Four models were run and then compared for each sex:

1. Null model = torso ~ Acetabular diameter
2. Diet-only model = torso ~ Acetabular diameter + Green Plants + Roots/Tubers + Fruit + Seeds + Prey + Flowers/Gum
3. Locomotion-only model = torso ~ Acetabular diameter + Quadrupedalism + Bipedalism + Climbing + Bridging + Leaping + Suspension
4. Full model = torso ~ Acetabular diameter + Green Plants + Roots/Tubers + Fruit + Seeds + Prey + Flowers/Gum + Quadrupedalism + Bipedalism + Climbing + Bridging + Leaping + Suspension

Whether the more complex models were significantly different from the null model were evaluated using the anova.lm.rrpp function, which yields p-values, and comparisons of model fit using AIC were generated with the model.comparison function.

While lm.rrpp does not provide a measure of phylogenetic signal for each regression, the function 'physignal' in the geomorph package version 3.0.6 (Adams, 2014; Adams et al., 2018) estimates the degree of phylogenetic signal in a multivariate dataset using the multivariate version of the K-statistic (K_{mult}). I therefore used 'physignal' to estimate the degree of phylogenetic signal in the matrix of torso variables for both males and females.

It should be noted that among anthropoids, locomotor behaviors appear to show phylogenetic clustering (e.g., Fleagle, 1984; Almécija et al., 2015). Therefore, it may be difficult to tease apart the effects of phylogeny from the effects of locomotion. By 1) relying on locomotor data as percentages, which introduces more nuance than categorical groupings, and 2) dividing torso variables by the geometric mean, to reduce some of the size effects that contribute to the patterning of locomotion among anthropoids (Fleagle, 1984), I hope to minimize the conflation of these two variables.

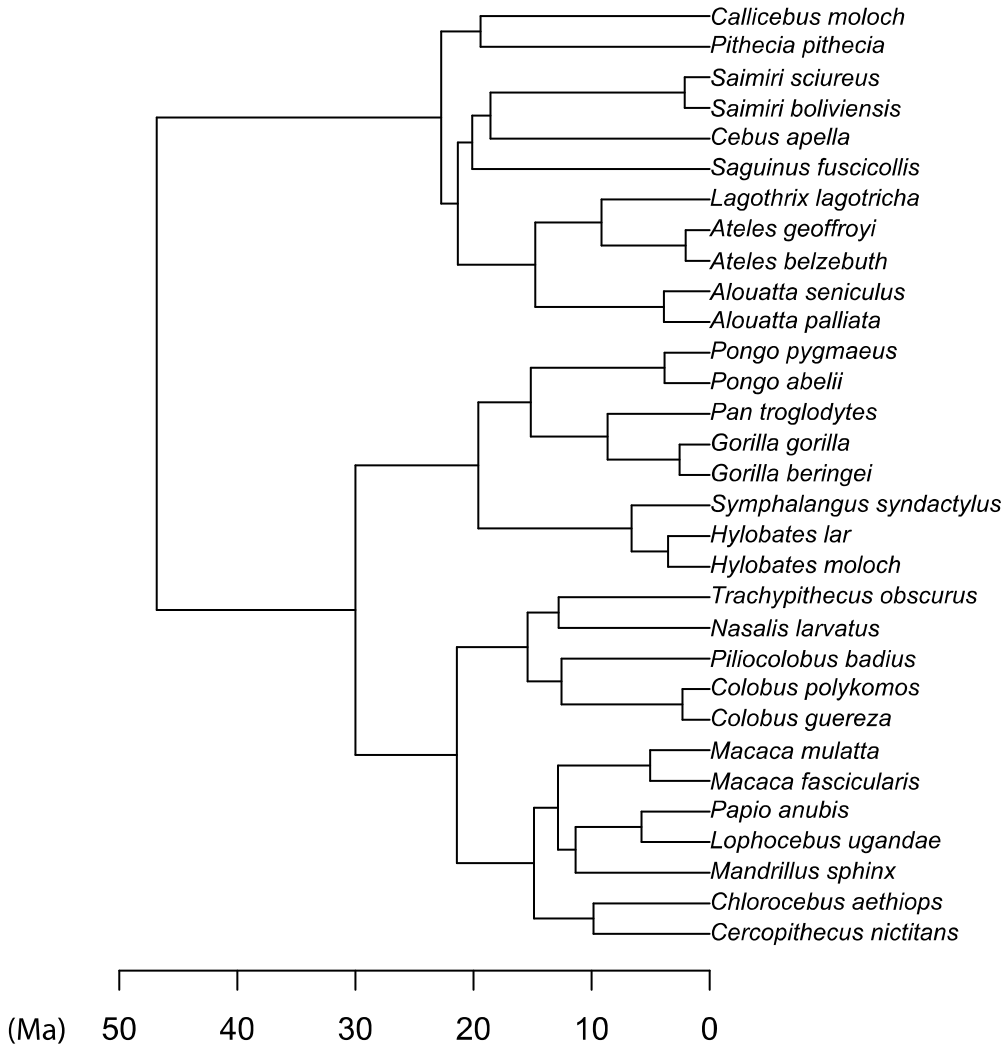

Figure 5. Time-calibrated phylogenetic tree showing the relationships among the 31 species included in Analysis B.

Analysis C

Analysis C was conducted in R version 3.6.0 (R Core Team 2019). Analysis C is divided features discriminant function analyses (DFA) to test whether torso variables can differentiate among diet groups. The torso variables included are the species averages for upper ilium width, bi-iliac breadth, iliac flare, and lumbar vertebral column length. All measurements except for flare (which is already a 'relative' measurement, see methods description for Analysis A) were size-adjusted by acetabular diameter and natural log-

transformed. The analyses were separated by sex. The DFA were conducted using the MASS package version 7.3-50 (Venables and Ripley, 2002) and visualized using ggord version 1.0.0 (Beck, 2017).

For this analysis, I used the sample size of 31 species featured in Analysis B. I first tested whether the torso variables can distinguish among five diet groups (folivore, frugivore, faunivore, generalist, and granivore), and then tested if these variables could distinguish among four locomotor groups (suspensory, leaping, arboreal quadrupeds, and terrestrial quadrupeds). Determination of diet categories is described above in the "Diet" section. Determination of locomotor categories is described above in the "Locomotion" section.

Wilk's lambda was computed to test the statistical significance of each DFA. A significant ($p < 0.05$) value for Wilk's lambda indicates that the discriminant function separates the groups better than by chance. Each DFA was also evaluated with leave-one-out cross-validation, which excludes each observation, calculates a DFA using the remaining observations, and then uses the new DFA to classify the excluded observation. This process yields a percentage success of predictive accuracy for the DFA.

Analysis C also suffers from the issue of closely related primates exhibiting similar locomotor behaviors (e.g., Fleagle, 1984; Almécija et al., 2015). As this analysis does not include methods to account for phylogenetic relatedness among the taxa, the results should best be interpreted as whether or not torso variables can better distinguish among closely-related feeders or closely-related locomotors.

See Appendix C for a test of how these variables can distinguish between the five diet groups in the 44 species for which the four torso variables are available for both

sexes. This analysis uses the same sample size featured in Analysis A. See Appendix D for the results of four discriminant function analyses that test how well five variables—raw torso variables and acetabular diameter—discriminate among diet and locomotor groups in 31 species.

Results

Analysis A

The relationships between the diet variables and logged size-adjusted pelvic measurements and lumbar vertebral column length were tested in 45 and 44 species, respectively. All models are significant ($p < 0.05$), likely due to the inclusion of logged acetabular diameter (the body size proxy) as a covariate. Best-fitting models for each torso variable are listed in Table 12.

For females, all best-fitting models include diet variables, however the diet variable does not have a significant effect in the model where log(adj.Flare) is the response variable. Log(adj.UIW) and log(adj.Lumbar) appear to have a relationship with percent fruit in diet, and percent fruit in diet has a small, negative, but significant effect on these models. Log(adj.BIB) appears to have a relationship with percent green plants in diet, and percent green plants appears to have a small, positive effect on this model. However, the relationship between logged, size-adjusted bi-iliac breadth and green plants across the sample is driven by the relationship between these torso variables and acetabular diameter in hominoids (model $p < 0.001$, adjusted $r^2 = 0.92$, log(Acetab) $p < 0.001$, Green Plants $p = 0.3$). When hominoids are removed from the sample, these models are no longer significant.

Table 12. Best-fitting models for the pelvic and lumbar measurements, from Analysis A.

Torso var	N	Model	Lambda	Slopes	Rsq	Effect of diet coefficients
Females						
Flare	45	log(adj.Flare) ~ log(Acetab) + Seeds	0.99	log(Acetab) = 0.99; Seeds = -0.004	0.44	Seeds (p = 0.14)
UIW	45	log(adj.UIW) ~ log(Acetab) + Fruits	1	log(Acetab) = 0.18; Fruits = -0.001	0.27	Fruits (p = 0.02)
BIB	45	log(adj.BIB) ~ log(Acetab) + Green Plants	0.99	log(Acetab) = 0.1; Green Plants = 0.001	0.18	Green Plants (p = 0.02)
Lumbar	44	log(adj.Lumbar) ~ log(Acetab) + Fruits	1	log(Acetab) = -0.79; Fruits = -0.002	0.57	Fruits (p = 0.02)
Males						
Flare	45	log(adj.Flare) ~ log(Acetab)	0.97	log(Acetab) = 0.99	0.47	NA
UIW	45	log(adj.UIW) ~ log(Acetab) + Fruits	0.99	log(Acetab) = 0.25, Fruits = -0.001	0.35	Fruits (p = 0.06)
BIB	45	log(adj.BIB) ~ log(Acetab) + Roots/Tubers	0.84	log(Acetab) = 0.19; Roots/Tubers = 0.002	0.29	Roots/Tubers (p = 0.15)
Lumbar	44	log(adj.Lumbar) ~ log(Acetab)	0.91	log(Acetab) = -0.67	0.52	NA

Torso var = Torso variables: Lumbar = lumbar vertebral column length, Flare = ratio between false pelvis length and iliac fossa width, UIW = upper ilium width, BIB = bi-iliac breadth
N = Total number of species included in the PGLS regression
Model = Function included in the PGLS regression
Lambda = Pagel's lambda estimate of phylogenetic signal in the residuals (Pagel, 1999); Slopes = slopes of the model predictors, indicating the direction of the interaction of the relationship between the predictor variables and the response variables; Rsq = adjusted R^2 value; Effect of diet coefficients = Indicates p-values of diet covariates. $p < 0.05$ indicates the diet variables have a significant effect on the model after accounting for body size and phylogenetic relatedness

The relationships between log(adj.Lumbar) and log(adj.UIW) with fruit in the female subsample only holds in cercopithecoids. The relationships between logged, size-adjusted lumbar vertebral column length and upper ilium width with fruit in hominoids are driven by the inclusion of acetabular diameter as a covariate (Table 13). The relationship between logged, size-adjusted lumbar vertebral column length and fruit is driven by the inclusion of acetabular diameter in platyrrhines, but there is no significant relationship between logged, size-adjusted upper ilium width with acetabular diameter

and fruit in this subgroup. For the 23 species of cercopithecoids, percent fruit in diet does have an effect on the model for lumbar vertebral column length (Fruit p = 0.03) and for logged, size-adjusted upper ilium width (Fruit p = 0.04). However, this relationship is driven by the relationship between percent fruit in diet and acetabular diameter in female cercopithecoids (model p = 0.01, slope = -0.006, adjusted r^2 = 0.24, Fruit p = 0.009).

For males, the best-fitting models for log(adj.Flare) and log(adj.Lumbar) are these variables as a function of acetabular diameter, only. The best-fitting models for log(adj.BIB) and log(adj.UIW) are models that include diet variables, but diet variables do not have a significant effect on the models (Table 12). In other words, the inclusion of diet variables adds net explanatory power to the models, though these variables themselves are not significant predictors.

Table 13. Relationships between lumbar vertebral column length and upper ilium width with fruit in female anthropoid groups.

Group	N	Model	Lambda	Slopes	Rsq	P model	Effect of coefficients
Platyrrhine	12	log(adj.Lumbar) ~ log(Acetab) + Fruits	1	log(Acetab) = -1; Fruits = 0.0001	0.59	0.007	log(Acetab) = 0.002 Fruits (p = 0.92)
Platyrrhine	13	log(adj.UIW) ~ log(Acetab) + Fruits	0.98	log(Acetab) = 0.03; Fruits = -0.001	-0.02	0.44	log(Acetab) = 0.83 Fruits (p = 0.22)
Cerco	23	log(adj.Lumbar) ~ log(Acetab) + Fruits	0.26	log(Acetab) = -0.63; Fruits = -0.002	0.68	< 0.001	log(Acetab) < 0.001 Fruits (p = 0.03)
Cerco	23	log(adj.UIW) ~ log(Acetab) + Fruits	0.89	log(Acetab) = 0.05; Fruits = -0.001	0.23	0.027	log(Acetab) = 0.5 Fruits (p = 0.04)
Hom	9	log(adj.Lumbar) ~ log(Acetab) + Fruits	0	log(Acetab) = -0.67; Fruits = -0.003	0.9	< 0.001	log(Acetab) < 0.001 Fruits (p = 0.12)
Hom	9	log(adj.UIW) ~ log(Acetab) + Fruits	0	log(Acetab) = 0.59; Fruits = -0.002	0.93	< 0.001	log(Acetab) < 0.001 Fruits (p = 0.2)

Cerco = cercopithecoids (cercopithecines and colobines); Hom = hominoids (hylobatids and hominids)

N = Total number of species included in the PGLS regression; Lambda = Pagel's lambda estimate of phylogenetic signal in the residuals (Pagel, 1999); Slopes = slopes of the model predictors, indicating the direction of the interaction of the relationship between the predictor variables and the response variables; Rsq = adjusted R^2 value; P model = p-value of the model; Effect of coefficients = p-values for log(Acetab) and percent fruit in diet

The relationship between diet and logged, size-adjusted ribcage breadth was tested in 21 species of males, and 21 species of females. None of these models were significant, despite the significant relationship between ribcage breadth and acetabular diameter for both females (adjusted $r^2 = 0.92$, $p < 0.001$) and males (adjusted $r^2 = 0.9$, $p < 0.001$).

The relationship between logged relative gut size and logged, size-adjusted pelvic measurements was tested in 23 species for females and 23 species for males. For females, the models in which logged, size-adjusted bi-iliac breadth and upper ilium width are included as response variables were not significant. The two models with logged, size-adjusted flare as response variables are significant, but relative gut size has no effect ($p = 0.5$). For males, all models are significant, but relative gut size has no effect on any of the models.

The relationship between logged relative gut size and logged, size-adjusted lumbar vertebral column length was tested in 22 species for females and 23 species for males. Both models are significant for both sexes, but relative gut size has no effect ($p = 0.7$ in females, $p = 0.6$ in males). The relationship between relative gut size and logged, size-adjusted ribcage breadth was tested in 9 species for males and 9 species for females. None of these models were significant ($p > 0.05$), suggesting there is no relationship between gut size and ribcage breadth at rib level 7.

Analysis B

Results are presented in Table 14. For both males and females, the best-fitting model (the model with the lowest AIC value) is the matrix of the geometric-mean-adjusted torso variables as a function of acetabular diameter. Including locomotor variables improves model fit for both sexes. For females, the locomotion-only model and full model are significantly different from the null model ($p = 0.001$ and $p = 0.03$, respectively). For males, the only model significantly different from the null model is locomotion-only ($p = 0.05$).

There are sex differences with respect to which covariates have a statistically significant effect in the models. Four locomotion variables are significant in the locomotion-only and full models in female sample, while only leaping shows a significant effect in the male sample (locomotion-only, $p = 0.01$; all-variables, $p = 0.007$). The K_{mult} estimate for both females ($K = 1.51$) and males ($K = 1.37$) are greater than 1, indicating that variance in the torso measurements tends to be among clades rather than within clades, *i.e.* close relatives are more similar to each other than expected under Brownian motion (Adams, 2014).

Table 14. Analysis B results for females and males.

	Rsq	**P-val**	**AIC**	**AICw**	**Coefficients with significant effect ($p < 0.05$)**
Females					
torso ~ Acetab (Null)	0.53	NA	-138	0	Acetab (p = 0.001)
torso ~ Acetab + Green Plants + Roots/Tubers + Fruit + Prey + Seeds + Flowers/Gum	0.58	0.4	-109	28.838	Acetab (p = 0.001)
torso ~ Acetab + Quad + Biped + Climb + Bridg + Leap + Susp	0.68	0.001	-124	13.759	Acetab (p = 0.001), Biped (p = 0.016), Climb (p = 0.011), Bridg (p = 0.008), Leap (p = 0.009)
torso ~ Acetab + Green Plants + Roots/Tubers + Fruit + Prey + Seeds + Flowers/Gum + Quad + Biped + Climb + Bridg + Leap + Susp	0.72	0.03	-110	28.091	Acetab (p = 0.001), Quad (p = 0.05), Climb (p = 0.04), Bridg (p = 0.015), Leap (p = 0.015)

Males					
torso ~ Acetab (Null)	0.36	NA	-99	0	Acetab (p = 0.001)
torso ~ Acetab + Green Plants + Roots/Tubers + Fruit + Prey + Seeds + Flowers/Gum	0.45	0.42	-71.9	27.089	Acetab (p = 0.001)
torso ~ Acetab + Quad + Biped + Climb + Bridg + Leap + Susp	0.52	0.05	-83.3	15.742	Acetab (p = 0.001), Leap (p = 0.01)
torso ~ Acetab + Green Plants + Roots/Tubers + Fruit + Prey + Seeds + Flowers/Gum + Quad + Biped + Climb + Bridg + Leap + Susp	0.6	0.24	-60.3	38.743	Acetab (p = 0.001), Leap (p = 0.007)

Rsq = R^2 value; P-val = P-value for the model
AIC = Akaike Information Criterion value for the model; AICw = AIC weight for the model

Analysis C

Four discriminant function analyses were conducted. The Wilk's lambda values for all four analyses were statistically significant ($p < 0.05$). Percent success of each DFA, resulting from the leave-one-out cross-validation tests, are summarized in Table 15. The DFA are illustrated in Figures 6 through 9. Tables 16 through 19 provide the variable loadings for these analyses.

Table 15. Success of each DFA as determined by leave-one-out cross validation.

	Sample Size	**% Success**
Females		
Diet Category ~ torso vars	31	53.3
Locomotor Category ~ torso vars	31	61.3
Males		
Diet Category ~ torso vars	31	60
Locomotor Category ~ torso vars	31	67.7

Torso vars = the four logged, size-adjusted (divided by acetabular diameter) torso variables: bi-iliac breadth, upper ilium width, iliac flare, and lumbar vertebral column length

Two DFA test whether torso variables discriminate among diet categories, and two test whether torso variables discriminate among locomotor categories. For the diet DFA for females, logged, size-adjusted bi-iliac breadth has strong negative loadings on the first two discriminant functions (Figure 6, Table 16). Together these first two discriminant functions account for ~96% of the among-group variation. As with the

larger sample, there is overlap of the diet categories (Figure 6). The two generalists plot together, but within the range of frugivores. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 53% (Table 15).

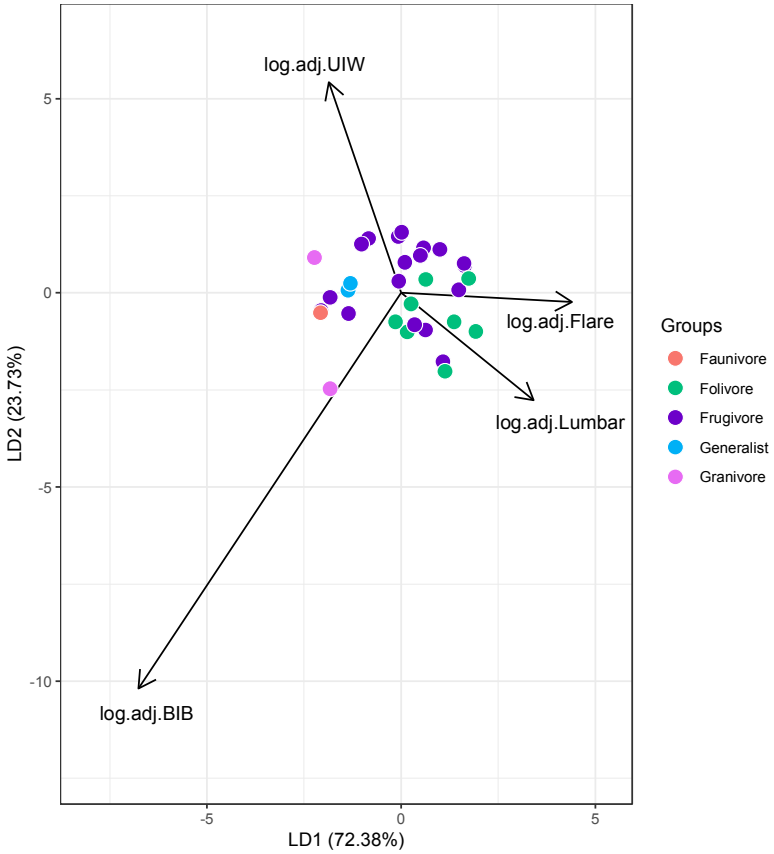

Figure 6. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among diet groups for 31 species of female anthropoids.

Table 16. Variable loadings, from the DFA testing how torso variables distinguish among diet groups for 31 species of female anthropoids.

	LD1	LD2	LD3	LD4
log.adj.BIB	-6.758776	-10.18800	14.6689491	3.761737
log.adj.Flare	4.40126	-0.235621	-0.6165362	-1.04513
log.adj.UIW	-1.856743	5.4201581	-10.906402	3.249363
log.adj.Lumbar	3.41553	-2.767561	-1.3220092	-0.166278

For the diet DFA for males, logged, size-adjusted upper ilium width has a strong negative loading on the first discriminant function, while logged size-adjusted bi-iliac

breadth has a strong positive loading on the second discriminant function (Figure 7, Table 17). Together these first two discriminant functions account for ~96% of the among-group variation. As with the larger sample, there is overlap of the diet categories (Figure 7). Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 60% (Table 15).

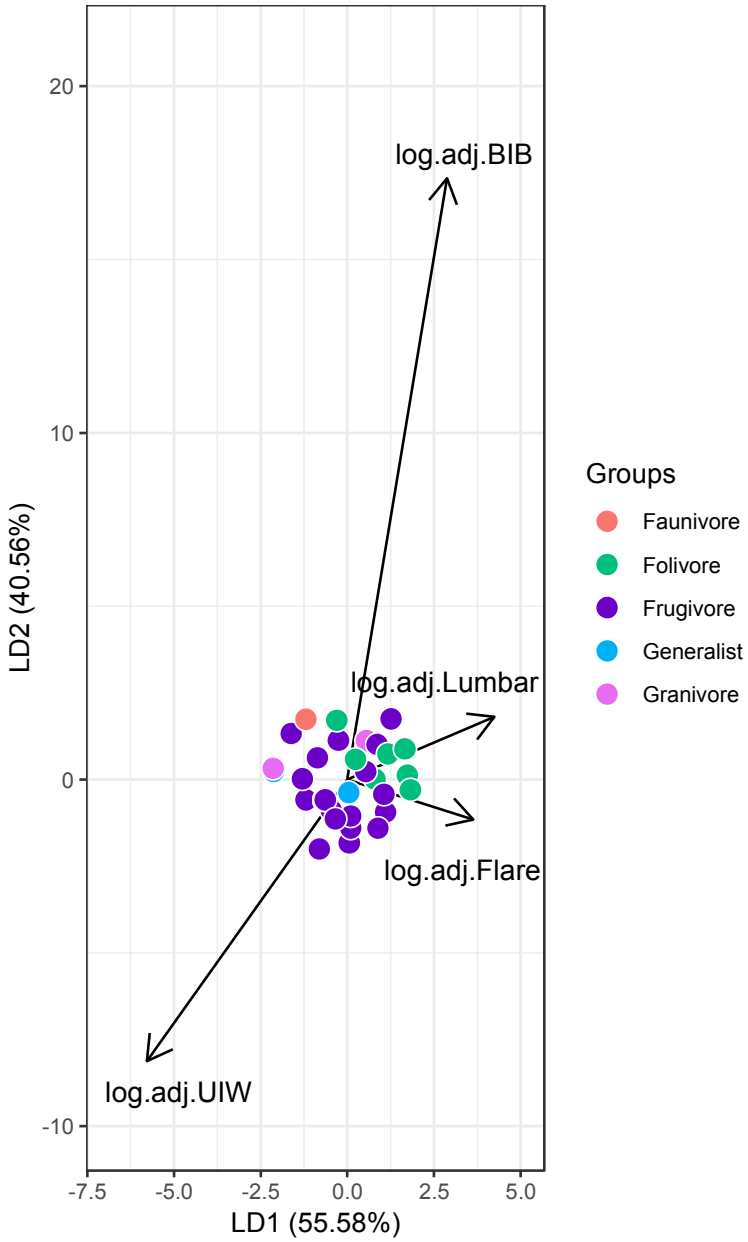

Figure 7. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among diet groups for 31 species of male anthropoids.

Table 17. Variable loadings, from the DFA testing how torso variables distinguish among diet groups for 31 species of male anthropoids.

	LD1	LD2	LD3	LD4
log.adj.BIB	2.873563	17.343878	-19.34476	10.5467409
log.adj.Flare	3.62754	-1.157258	2.499229	-0.6311839
log.adj.UIW	-5.777918	-8.127778	7.516703	-10.683256
log.adj.Lumbar	4.237704	1.802857	2.054624	-1.6853276

For the locomotion DFA for females, logged, size-adjusted bi-iliac breadth has strong negative loadings on the first two discriminant functions, while logged, size-adjusted upper ilium width has strong positive loadings on the first two discriminant functions (Figure 8, Table 18). Together these first two discriminant functions account for ~98% of the among-group variation. There is a bit of overlap of the locomotor categories, but there are more distinct groupings of the locomotor categories than there were for the diet groups (Figure 8). Leapers are subsumed within the arboreal quadruped cluster. There is some overlap between the terrestrial quadrupeds and suspensory taxa. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 61% (Table 15).

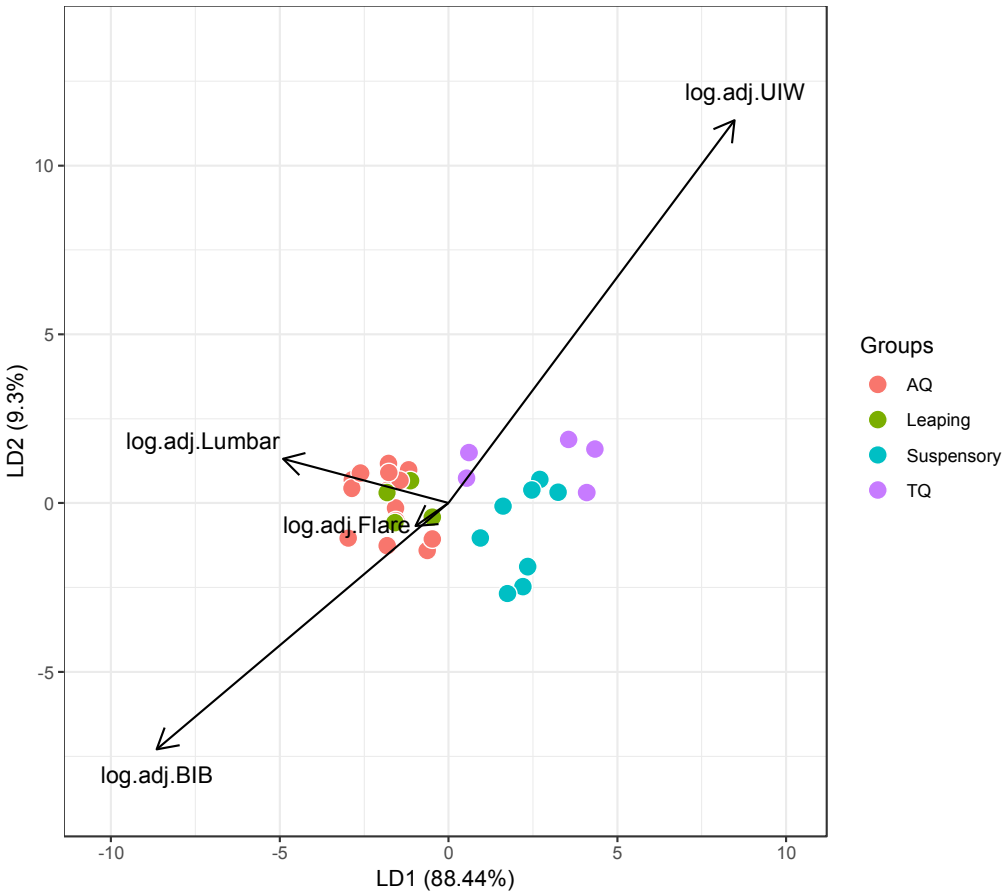

Figure 8. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among locomotor groups for 31 species of female anthropoids.

Table 18. Variable loadings from the DFA testing how torso variables distinguish among locomotor groups for 31 species of female anthropoids.

	LD1	LD2	LD3
log.adj.BIB	-8.644896	-7.2951126	-4.83901
log.adj.Flare	-0.980265	-0.6764771	-2.366991
log.adj.UIW	8.4752503	11.3452476	5.027175
log.adj.Lumbar	-4.908087	1.3100998	-2.790682

For the locomotion DFA for males, logged, size-adjusted bi-iliac breadth has a strong negative loading on the first discriminant function, while logged, size-adjusted upper ilium width has a strong positive loading on this first discriminant function (Figure 9, Table 19). The opposite is true for the second discriminant function. Together these first two discriminant functions account for ~99% of the among-group variation. Similar

to the results for females, there is a bit of overlap of the locomotor categories, but there are more distinct groupings of the locomotor categories than there were for the diet groups (Figure 9). Leapers are subsumed within arboreal quadrupeds and there is some overlap between the terrestrial quadrupeds and suspensory taxa. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 68% (Table 15).

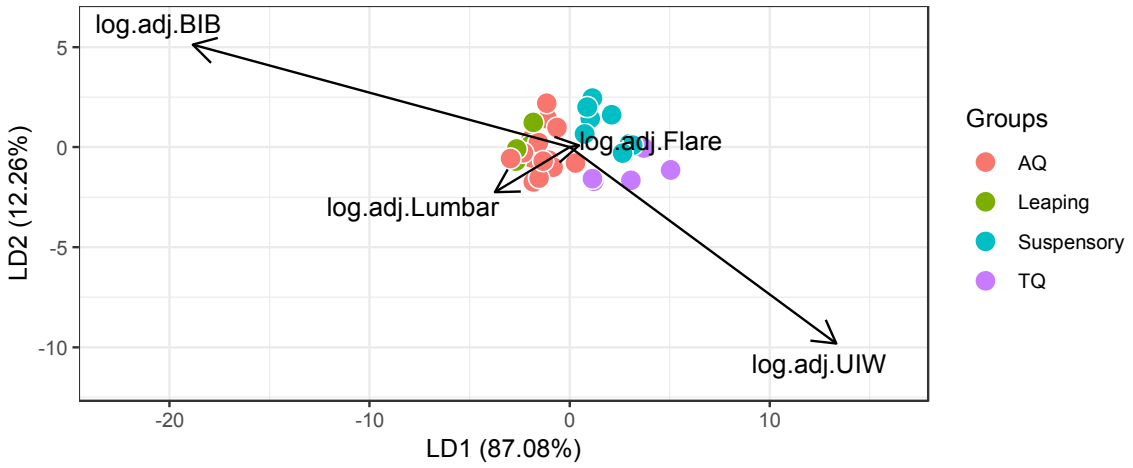

Figure 9. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among locomotor groups for 31 species of male anthropoids.

Table 19. Variable loadings from the DFA testing how torso variables distinguish among locomotor groups for 31 species of male anthropoids.

	LD1	LD2	LD3
log.adj.BIB	-18.840562	5.1368404	-18.50118
log.adj.Flare	0.4682476	0.09061761	4.208609
log.adj.UIW	13.3274081	-9.813174	6.123007
log.adj.Lumbar	-3.7321414	-2.246604	3.729759

Discussion

The analyses presented in this chapter, while indicating there is little evidence to support the practice of inferring diet from torso morphology, provide three main insights into the factors that influence anthropoid torso form. First, this research confirms previous suggestions that body size influences torso form (e.g., Larson, 1998; Lewton,

2015; Hunt, 2016, Ward et al., 2018). In Analysis A, diet variables have no relationship with torso measurements in males (Table 12), and there is no relationship between gut size and the torso after accounting for phylogeny and body mass. For the females in this sample, the relationships between green plants and bi-iliac breadth are driven by the relationships between the body size proxy (acetabular diameter) and these pelvis variables in hominoids. Even the apparent relationships between lumbar vertebral column length and fruit, and upper ilium width and fruit, in female cercopithecoids (Table 13) is driven by body size, as there is a significant relationship between percent fruit in the diet and logged acetabular diameter for this subgroup. Therefore, there appears to be no relationship between torso form and the diet variables that is independent of the relationship between the body size proxy and the torso variables. Lastly, in Analysis B, when considering how five torso variables relate to diet and locomotion in a subsample of 31 species, the model with the lowest AIC value for both sexes is the model that only includes acetabular diameter as a predictor variable (Table 14). Therefore, the models that best fit the data are those that include the body size proxy, only.

While the impact of body size on the relationships between torso, diet, and locomotion is pervasive throughout the sample of primates included in these analyses, recent research on the effect of body mass on torso form suggests that larger anthropoids (i.e., apes) show only a slight effect relative to smaller anthropoids (i.e., monkeys) (Middleton et al., 2017; Ward et al., 2018). The results presented in this chapter are likely due to the current analyses including 1) more anthropoid taxa than in previous studies, and 2) more small-bodied species (e.g., platyrrhines).

A second insight resulting from these analyses is that torso form has a relationship with percent frequency of locomotor modes. In Analysis B, the locomotion-only models for males and females are significantly different from the null model, while the diet-only models are not. In Analysis C, the discriminant function analyses (DFA) indicate that logged, size-adjusted torso variables are better at distinguishing among locomotor groups than diet groups. The two diet DFA are significant, so there are detectable differences in group means, but there is substantial overlap of the diet groups (e.g., nearly all folivores fall within the range of frugivores) and the predictive accuracy of these analyses ranges between ~50 to 60%. The predictive accuracy of the locomotion DFA are higher (~61% for females and ~68% for males), and the locomotor groups plot into distinct clusters with overlap that is expected (e.g., leapers are subsumed within arboreal quadrupeds).

Lastly, as I have mentioned throughout this discussion, there are sex differences among the relationships between the torso variables, body size, diet variables, and locomotion in all three analyses. Variation in male torso form is strongly tied to body size and locomotion, and diet variables have an effect in more models that include data from females. There are two potential reasons for the disparity in results between males and females. First, the variances in the female measurements are lower in most cases than those in males (Table 20), except for in platyrrhines, where variance in females is higher than in males. The higher variance in male torso measurements could make regressions with data from males less sensitive to the inclusion of diet and locomotor variables.

A second possibility is that this disparity provides evidence to support the hypothesis that females are the 'ecological sex' and are more responsive to environmental variables, such as diet, due to the energetic constraints of pregnancy and lactation

(Gordon et al., 2013). Although there is little evidence of a statistically significant and consistent dietary influence on the female torso that is independent of phylogeny, body mass, and locomotion, this hypothesis could explain why torso form in females seem to show a closer relationship with diet variables than males.

Table 20. Variance of the four torso measurements that are available for nearly all species in the sample.

Measurement	Group	NSp (F)	NInd (F)	Variance: Females	NSp (M)	NInd (M)	Variance: Males
Flare	Platyrrhine	13	53	0.26	15	56	0.2
	Cercopithecine	15	57	0.04	15	54	0.07
	Colobine	8	34	0.02	8	38	0.03
	Hylobatid	5	32	0.12	5	28	0.18
	Hominid	5	40	1.82	5	39	2.14
Upper Ilium Width	Platyrrhine	13	53	114.01	15	56	111.46
	Cercopithecine	15	57	152.79	15	54	287.56
	Colobine	8	34	33.37	8	38	60.75
	Hylobatid	5	32	85.9	5	28	115.63
	Hominid	5	40	1470.07	5	39	2657.30
Bi-Iliac Breadth	Platyrrhine	13	53	855.96	15	56	713.32
	Cercopithecine	15	57	669.57	15	54	1215.96
	Colobine	8	34	126.51	8	38	332.01
	Hylobatid	5	32	261.57	5	28	335.39
	Hominid	5	40	4107.92	5	39	8308.67
Lumbar Vertebral Column Length	Platyrrhine	12	52	322.56	15	61	166.87
	Cercopithecine	15	55	330.08	15	52	432.53
	Colobine	8	34	142.05	8	38	236.51
	Hylobatid	4	30	25.67	5	26	35.81
	Hominid	5	38	112.96	5	38	191.18

NSp = Number of species
NInd = Number of individuals

Limitations

Some researchers have suggested that time-based estimates of diet, such as the percent feeding time/observation data utilized throughout this dissertation, can misrepresent the importance of this food item in a species' diet (e.g., Chivers, 1998; Aristizabal et al., 2017; Righini, 2017). For example, Chivers (1998) reviews data on diet for several species and suggests that feeding time underestimates fruit consumption, but

also presents data indicating that percent time feeding for some taxa (e.g., *Presbytis*, *Hylobates*) is equivalent to estimated food intake by weight. The primary benefit of using time-based estimates of diet is that they allow comparisons across a large sample of primates, as data on percent time devoted to feeding on specific food items are readily available for many species and food categories are well-defined in the literature. Weight-based estimates or estimates of nutrient and energy intake may be preferable, but these data are not available for many species and methods can vary between studies, which makes comparisons difficult (Chivers, 1998). Until comparable data on diet based on weight and nutrient intake are available for more species, and specifically those species well-represented in museum skeletal collections, analyses testing how torso form relates to these dietary proxies across primates cannot be performed.

Additionally, the analyses in this chapter use ratios of torso variables to acetabular diameter (Analyses A and C) or the geometric mean (Analysis B) to adjust for body size. The utility of "size-correcting" ratios in statistical analyses has been criticized (e.g., Packard and Boardman, 1999), as these ratios rarely remove the effects of body size completely and can introduce artificial differences in group means that 1) do not accurately reflect the relationship between body size and the physiological variable of interest and 2) lead researchers to misinterpret their data. For these reasons, it may be preferred to rely on regression-based methods (such as multiple regression, ANCOVA, or residual analysis) to remove the effects of body size when analyzing the effect of a treatment/phenomenon on a body-size related physiological variable. However, eliminating the effects of body size entirely is not the goal of the analyses presented in this chapter. It is well-documented that the torso variables of interest for this dissertation

do not scale with isometry in anthropoids (e.g., Lewton, 2015; Middleton et al., 2017; Ward et al., 2018). These scaling relationships contribute to meaningful differences in torso shape across the body size range of the taxa represented by the sample of anthropoids in this dissertation. By using ratios of each torso variable divided by body size proxy, I am able to test whether torso shape varies according to differences in diet.

Conclusions

The analyses presented in this chapter indicate that among clades of anthropoid primates, diet has no relationship with the torso after accounting for phylogeny, body size, and locomotion. This is the case for Analysis A, which evaluates torso elements in isolation, and Analyses B and C, which considers the elements of the torso together. Results from Analysis A show that while some best-fitting PGLS models are ones that include diet variables as predictors, often these predictors are not significant (i.e. changes in the diet predictor are not associated with changes in the torso variables) or these predictors are significant because of the association between diet and body size. Analysis B confirms that torso variables are related to body size and locomotion, but not with diet variables. Furthermore, Analysis C demonstrates that the torso variables are better at distinguishing among locomotor groups than dietary groups.

Altogether, these results suggest that variation in torso shape in anthropoid primates does not show a clear relationship with percentage of time spent feeding on different food items, nor with gut size. These analyses do not provide support for the hypotheses that differences in torso form in fossil hominins can be used to infer differences in diet (Schmid, 1991; Aiello and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010). While the analyses featured in this chapter—which test

if diet is related to the torso in *large* samples of anthropoids—do not demonstrate a consistent relationship with diet, it is possible that pairwise comparisons between closely-related, similarly-sized species with similar locomotor repertoires could reveal diet-related differences in the torso. This line of research is pursued in Chapter 3.

Chapter 3: Do comparisons among pairs of species reveal a consistent relationship between diet and the torso?

Introduction

In the previous chapter, I tested whether there is a relationship between diet and the torso across a large sample of anthropoid primates. Both individual torso features (Appendix; Chapter 2, Analysis A), and several torso features considered altogether (Chapter 2, Analyses B and C), appear to be more closely related to locomotion and body size than to diet or gut size. When testing relationships across a large sample of anthropoids, the strong influences of body size and locomotion on torso form may make it difficult to identify diet-related differences in torso form between species within smaller taxonomic subgroups (platyrrhines, cercopithecoids, and hominoids) that are similar in body size and locomotor repertoire.

I examine this possibility by making narrow comparisons of torso shape among closely-related, similarly-sized species that have different diets, as well as among closely-related, similarly-sized species with similar diets. I selected pairs of species from each taxonomic subgroup and tested for differences between species means in relative torso variables, which include upper ilium width, bi-iliac breadth, iliac flare, and lumbar spine length. These comparisons are particularly relevant with respect to fossil hominins because differences in torso form in *Australopithecus* and early *Homo* have been interpreted as indicating differences in diet.

Specifically, researchers have suggested that species with diets rich in leaves and other green plants will have wider, more capacious torsos than more faunivorous species in order to accommodate relatively larger digestive tracts, or guts (Elftman, 1929; Aiello

and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010). Based on these assumptions, I hypothesize the following about the pairwise comparisons:

H1. Within each pair, the more folivorous of the two will have more iliac flaring, relatively longer lumbar spines, and relatively wider bi-iliac breadths, upper ilium widths, and ribcage breadths compared to the more faunivorous taxon (Figure 10, top panel).

H2. Pairs of species with similar diets will show no significant differences in relative torso dimensions (Figure 10, bottom panel).

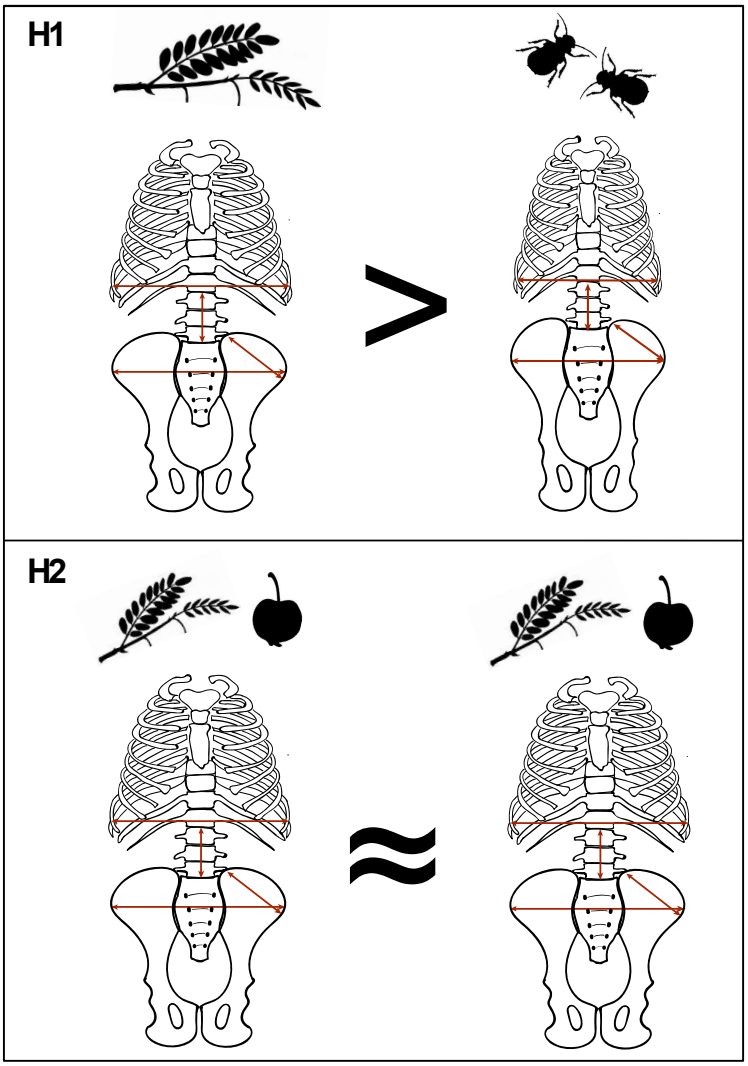

Figure 10. Hypotheses for the analyses in this chapter. The hypothesis about how species with different diets should differ in torso dimensions (H1) is illustrated in the top panel. The hypothesis about how species with similar diets should differ in torso dimensions (H2) is illustrated in the bottom panel.

Materials and Methods

Species selection

For the first analysis, species within each taxonomic subgroup of anthropoid primates (platyrrhines, cercopithecoids, hominoids) were matched into pairs. Pairs were matched by minimizing differences in body size (as approximated by the acetabular diameter) and differences in sample size (ensuring that sample sizes were relatively equal), as well as maximizing differences in diet composition (determined by percent feeding time on different food categories). Comparisons were made among seven pairs of species that met these criteria (Table 21).

Table 21. Species pairs for comparisons between species that have different diets.

Group	**Species that consumes more green plants**		**Species that consumes less green plants and/or more prey**
Platyrrhines	*Callicebus moloch*	vs.	*Saimiri bolivensis*
Platyrrhines	*Allouatta palliata*	vs.	*Lagothrix lagotricha*
Cercopithecoids	*Macaca mulatta*	vs.	*Lophocebus ugandae*
Cercopithecoids	*Theropithecus gelada*	vs.	*Papio hamadryas*
Cercopithecoids	*Colobus guereza*	vs.	*Macaca sylvanus*
Hominoids	*Gorilla beringei*	vs.	*Gorilla gorilla*
Hominoids	*Pongo pygmaeus*	vs.	*Pongo abelii*

In the second analysis, species were matched to minimize differences in body size (determined by acetabular diameter) and diet composition. Four pairs of species, whose sample sizes were similar, met these criteria (Table 22). Table 23 summarizes diet data for the species in both analyses.

Table 22. Species pairs for comparisons between species that have similar diets.

Comparisons among species that rely on green plants			
Group	**Species 1**		**Species 2**
Platyrrhines	*Allouatta palliata*	vs.	*Alouatta seniculus*
Cercopithecoids	*Colobus guereza*	vs.	*Macaca mulatta*
Comparisons among species that rely on fruit			
Cercopithecoids	*Cercopithecus cephus*	vs.	*Chlorocebus aethiops*
Hominoids	*Hylobates lar*	vs.	*Hylobates muelleri*

Table 23. Diet composition for species included in pairwise comparisons.

Taxon	Seeds	Fung	FG	RT	GP	Fruit	Prey	NSite
Alouatta seniculus	0	0	5.28	0	48.75	44.7	0.5	4
Alouatta palliata	0	0	12.7	0	50.83	36.43	0	3
Lagothrix lagotricha	2.37	0.03	3.92	0	12.63	71.22	8.64	5
Callicebus moloch	0	0	0	0	26	70	0	1
Saimiri boliviensis	0	0	28.07	0	0	18.18	52.67	1
Cercopithecus cephus	6.85	0	6.3	0	14.3	64.55	8	2
Chlorocebus aethiops	13	1	16	0	7	50	13	1
Lophocebus ugandae	0	0	3.4	0	12.2	60.3	24.1	1
Macaca mulatta	0	0	4.8	2.2	84.4	8.5	0	1
Colobus guereza	0.12	0	1.26	0	83.53	10.22	0	2
Macaca sylvanus	29.45	10.85	3.05	7.3	37.7	2.55	8.05	2
Papio hamadryas	15.39	0	11.88	4.64	18.06	49	0.25	1
Theropithecus gelada	5	0	0.8	0.5	91.8	1.9	0	1
Hylobates lar	0	0	2.82	0	21.49	64.86	8.83	9
Hylobates muelleri	0	0	4	0	32	62	8	1
Gorilla gorilla	3.3	0	0.37	0.37	42.65	51.32	0	3
Gorilla beringei	0	0	2.3	3.3	92.7	1.7	0	1
Pongo abelii	0	0	1.75	0	17.95	66.75	11.1	2
Pongo pygmaeus	0	0	1.6	0	38.6	57.9	1.9	2

Note: Data categorized following Pineda-Munoz and Alroy (2014). See Table 3 for diet references. Rounding to two decimal places for these values does not reflect the precision of the feeding time estimates but result from averaging these data across multiple field sites.
Seeds = % of seeds and nuts in diet; Fung = % of fungi in diet
FG = combined % of flowers, nectars, and gums in diet
RT = combined % of roots and tubers in diet
GP = combined % of leaves, stalks, grass, and other green plants in diet
Fruit = % of fruits in diet
Prey = combined % of invertebrate and vertebrate prey in diet
NSite = Number of field sites from which feeding time data were sourced

Statistical analyses

Upper-ilium width (UIW), bi-iliac breadth (BIB), lumbar vertebral column length (LSL), iliac fossa width, false pelvis length, and ribcage breadths were collected from these 14 species using digital calipers as described in Chapter 2. As in Chapter 2, these measurements were chosen for analyses in this chapter because they have each been hypothesized to relate to diet-induced differences in gut size among hominins (e.g., Aiello and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010), and because all four measurements are available for the species of interest. Ribcage breadths are also provided when available, but statistical tests were not performed on these measurements, due to very low sample sizes (see below). Sex-specific species averages for the raw measurements are listed in Table 2. These measurements were divided by acetabular diameter to adjust for any subtle differences in body size within species pairs. Relative iliac flare is calculated as the ratio of false pelvis length to iliac fossa width (inverse of the measurements calculated in Hammond et al., 2013a). Differences in relative torso variable means between the species in each pair were determined with Welch's t-tests. Welch's t-tests were preferred over Student's t-tests here as Welch's t-test adjusts the degrees of freedom when the variances are thought to be unequal, while the Student's t-test assumes equal variances. Analyses were performed separately for males and females.

Ribcages breadths are only listed in the tables below for a species in cases where ribcage breadths were also available for the species it was compared to (e.g., although I collected ribcage breadths for *A. palliata* these are not provided in Table 25, as none are available for *L. lagotricha*). Since the sample sizes for ribcage breadths for most species

are extremely low (one or two individuals per sex) summary statistics are provided but Welch's t-tests were not performed.

Results

Sex-specific means, standard deviations (SD), ranges, sample sizes (N), and t-test p-values for each of the relative torso variables are listed in Table 24 (*C. moloch* vs. *S. boliviensis*), Table 25 (*A. palliata* vs. *L. lagotricha*), Table 26 (*Lo. ugandae* vs. *M. mulatta*), Table 27 (*Co. guereza* vs. *M. sylvanus*), Table 28 (*T. gelada* vs. *P. hamadryas*), Table 29 (*G. beringei* vs. *G. gorilla*), Table 30 (*Po. abelii* vs. *Po. pygmaeus*), Table 31 *(A. palliata* vs. *A. seniculus*), Table 32 (*Ce. cephus* vs. *Ch. aethiops*), Table 33 (*Co. guereza* vs. *M. mulatta*) and Table 34 (*H. lar* vs. *H. muelleri*). Significant differences between species means are bolded and noted with asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**). Only significant differences between pairs will be discussed in the text for the results section.

Boxplots showing the ranges of the relative torso values by sex for each pair of species are illustrated in Figure 11 (*C. moloch* vs. *S. boliviensis*), Figure 12 (*A. palliata* vs. *L. lagotricha*), Figure 13 (*Lo. ugandae* vs. *M. mulatta*), Figure 14 (*Co. guereza* vs. *M. sylvanus*), Figure 15 (*T. gelada* vs. *P. hamadryas*), Figure 16 (*G. beringei* vs. *G. gorilla*), Figure 17 (*Po. abelii* vs. *Po. pygmaeus*), Figure 18 *(A. palliata* vs. *A. seniculus*), Figure 19 (*Ce. cephus* vs. *Ch. aethiops*), Figure 20 (*Co. guereza* vs. *M. mulatta*) and Figure 21 (*H. lar* vs. *H. muelleri*). Figures 11 through 17 compare taxa with different diets and the taxon represented by green boxes is the more folivorous of the pair. Figures 18 through 21 compare taxa with similar diets and boxes for folivorous species are colored with the

same shade of green, while those for frugivorous species are colored with the same shade of blue. For all plots, species are ordered alphabetically.

Among platyrrhines, *Saimiri boliviensis* females are relatively more flared than *Callicebus moloch* females and *C. moloch* females have relatively longer lumbar spines than *S. boliviensis* females (Table 24, Figure 11). There are no significant differences in relative torso measurements between the males of these species. Though no t-tests were performed, relative ribcage breadth across ribs seven through eleven in *C. moloch* males are wider than in *S. boliviensis*. *Alouatta palliata* females have relatively wider bi-iliac breadths and longer lumbar spines than *Lagothrix lagotricha* females, and *A. palliata* males are relatively more flared and have longer lumbar spines than *L. lagothrix* males (Table 25, Figure 12).

Table 24. Comparisons of relative torso variables in *C. moloch* and *S. boliviensis*.

Callicebus moloch					***Saimiri boliviensis***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	3	1.47	0.16	1.29 - 1.59	5	1.66	0.13	1.5 - 1.85	0.16
rel.BIB	3	3.55	0.35	3.16 - 3.84	5	3.95	0.40	3.3 - 4.26	0.2
rel.Flare	3	0.22	0.02	0.2 - 0.24	5	0.27	0.04	0.24 - 0.31	**0.044***
rel.Lumbar	3	11.27	0.54	10.72 - 11.8	5	9.37	0.51	8.81 - 9.97	**0.008****
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.48	0.23	1.22 - 1.72	6	1.66	0.15	1.5 - 1.87	0.25
rel.BIB	4	3.54	0.60	3.03 - 4.24	6	4.00	0.35	3.67 - 4.64	0.24
rel.Flare	4	0.23	0.07	0.17 - 0.33	6	0.25	0.05	0.18 - 0.3	0.7
rel.Lumbar	4	10.34	1.70	8.18 - 12.22	6	9.63	0.68	8.8 - 10.8	0.48
rel.Rib7	2	4.91	0.51	4.55 - 5.27	1	4.62	-	-	-
rel.Rib8	2	5.13	0.35	4.88 - 5.38	1	4.67	-	-	-
rel.Rib9	2	5.24	0.30	5.024 - 5.45	1	4.62	-	-	-
rel.Rib10	2	5.25	0.00	5.25 - 5.25	1	4.31	-	-	-
rel.Rib11	2	4.52	0.44	4.2 - 4.83	1	4.11	-	-	-

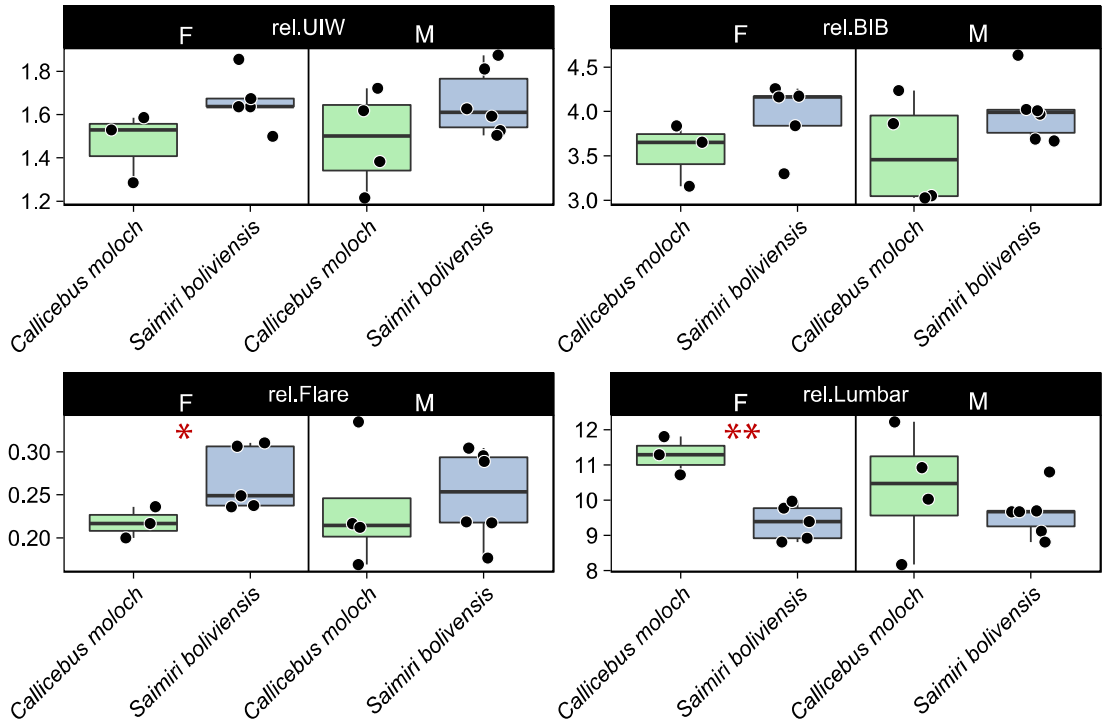

Figure 11. Boxplots with data points comparing relative torso variables in frugivorous/folivorous *C. moloch* (green) and faunivorous *S. boliviensis* (blue). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Table 25. Comparisons of relative torso variables in *A. palliata* and *L. lagotricha*.

Alouatta palliata					***Lagothrix lagotricha***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.80	0.19	1.58 - 2.04	5	1.57	0.11	1.45 - 1.73	0.09
rel.BIB	4	4.81	0.29	4.6 - 5.24	5	4.24	0.39	3.92 - 4.91	**0.04***
rel.Flare	4	1.41	0.22	1.18 - 1.65	5	1.24	0.28	0.95 - 1.58	0.35
rel.Lumbar	4	5.46	0.19	5.23 - 5.68	4	3.28	0.97	2.43 - 4.32	**0.019***
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	6	1.69	0.15	1.47 - 1.92	4	1.65	0.18	1.43 - 1.81	0.7
rel.BIB	6	4.40	0.35	3.87 - 4.9	4	4.12	0.37	3.65 - 4.51	0.28
rel.Flare	6	1.21	0.18	1.02 - 1.49	4	1.00	0.06	0.92 - 1.05	**0.036***
rel.Lumbar	6	4.78	0.20	4.55 - 5.05	4	3.46	0.49	2.94 - 3.9	**0.009****

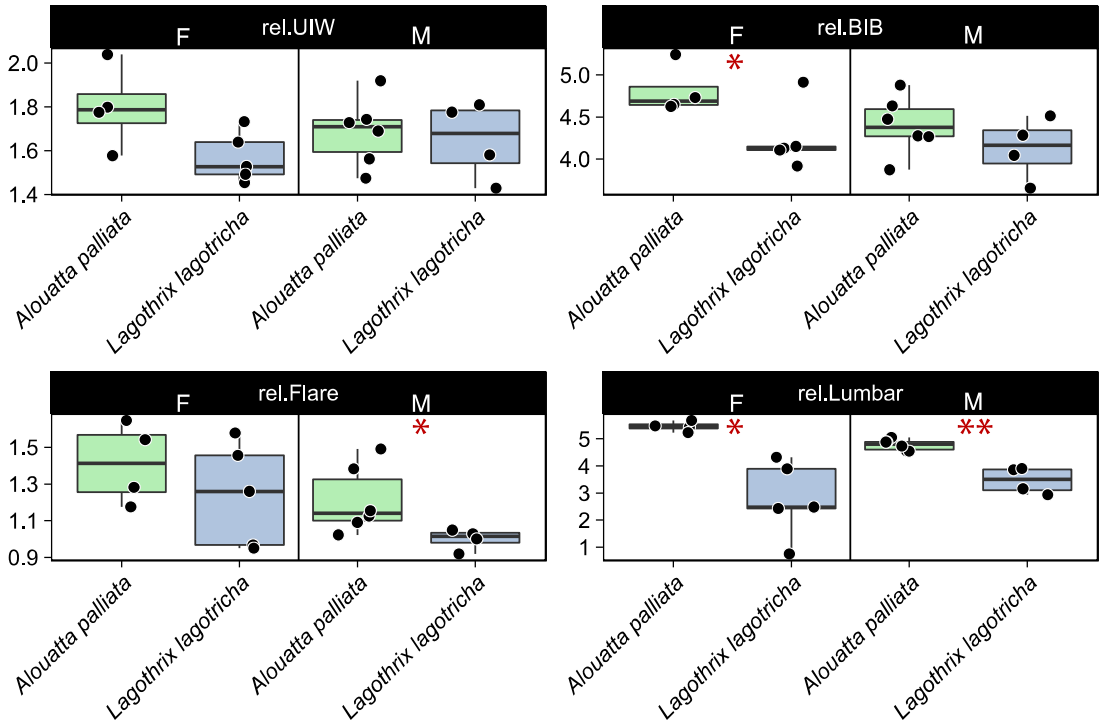

Figure 12. Boxplots with data points comparing relative torso variables in folivorous *A. palliata* (green) and frugivorous *L. lagotricha* (blue). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Among cercopithecines, torso form in *Lophocebus ugandae* is not significantly different than that in *Macaca mulatta*. Relative ribcage breadths are wider in *Lo. ugandae* males than in *M. mulatta* males (Table 26, Figure 13), but no t-tests were performed. *Macaca sylvanus* males have relatively wider ilia than *Colobus guereza*, but there are no significant differences between the females of these species (Table 27, Figure 14). *Theropithecus gelada* females have relatively wider bi-iliac breadths and longer lumbar spines than *Papio hamadryas* females, but there are no significant differences between the males of these species (Table 28, Figure 15). Though no t-tests were performed, relative ribcage breadth across ribs seven through eleven for both sexes are wider in *T. gelada* are than in *P. hamadryas*.

Table 26. Comparisons of relative torso variables in *Lo. ugandae* and *M. mulatta*.

Lophocebus ugandae					***Macaca mulatta***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	2	1.83	0.08	1.77 - 1.89	5	1.89	0.22	1.71 - 2.17	0.58
rel.BIB	2	4.05	0.30	3.83 - 4.26	5	4.83	0.52	4.16 - 5.37	0.08
rel.Flare	2	0.79	0.09	0.72 - 0.85	5	0.88	0.14	0.68 - 1.0	0.39
rel.Lumbar	2	7.51	0.60	7.09 - 7.93	5	6.24	0.76	5.34 - 7.3	0.12
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	3	1.87	0.33	1.58 - 2.23	5	2.07	0.14	1.85 - 2.18	0.4
rel.BIB	3	4.22	0.20	4.07 - 4.44	5	4.67	0.39	4.08 - 5.18	0.08
rel.Flare	3	0.63	0.05	0.57 - 0.67	5	0.76	0.17	0.53 - 0.93	0.17
rel.Lumbar	3	7.27	1.41	6.01 - 8.79	5	6.43	0.54	5.93 - 7.24	0.42
rel.Rib7	1	5.69	-	-	2	5.02	0.44	4.7 - 5.33	-
rel.Rib8	1	5.97	-	-	2	5.14	0.66	4.68 - 5.60	-
rel.Rib9	1	6.36	-	-	2	5.31	0.65	4.85 - 5.78	-
rel.Rib10	1	6.70	-	-	2	5.26	0.50	4.9 - 5.61	-
rel.Rib11	1	7.04	-	-	2	4.76	0.29	4.55 - 4.96	-

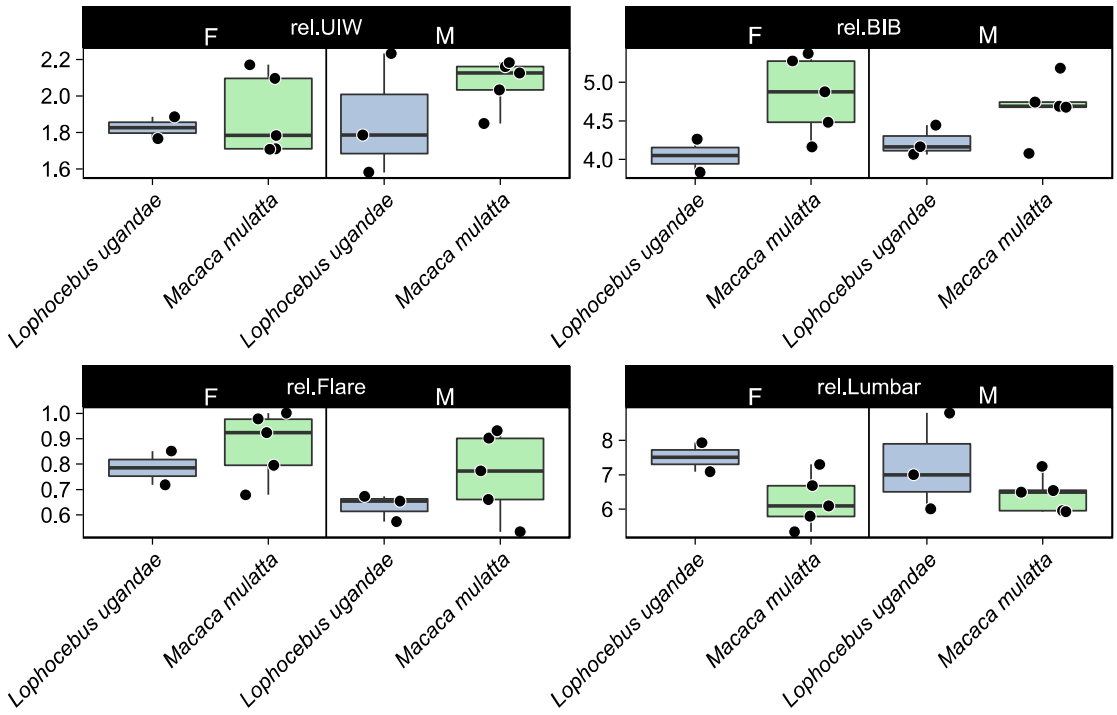

Figure 13. Boxplots with data points comparing relative torso variables in frugivorous/faunivorous *Lo. ugandae* (blue) and folivorous *M. mulatta* (green). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Table 27. Comparisons of relative torso variables in *Co. guereza* and *M. sylvanus*.

Colobus guereza					***Macaca sylvanus***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	3	1.85	0.18	1.68 - 2.05	3	2.01	0.09	1.91 - 2.07	0.29
rel.BIB	3	4.35	0.22	4.13 - 4.57	3	4.47	0.62	3.98 - 5.18	0.78
rel.Flare	3	0.71	0.22	0.5 - 0.93	3	0.70	0.20	0.58 - 0.93	0.96
rel.Lumbar	3	6.92	0.56	6.32 - 7.42	3	6.40	0.11	6.31 - 6.52	0.25
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.71	0.18	1.61 - 1.98	3	2.03	0.11	1.96 - 2.15	**0.033***
rel.BIB	4	4.22	0.28	3.9 - 4.59	3	4.65	0.30	4.47 - 5.0	0.12
rel.Flare	4	0.68	0.15	0.53 - 0.84	3	0.75	0.11	0.68 - 0.87	0.47
rel.Lumbar	4	7.21	0.56	6.54 - 7.88	3	6.08	0.80	5.16 - 6.62	0.12

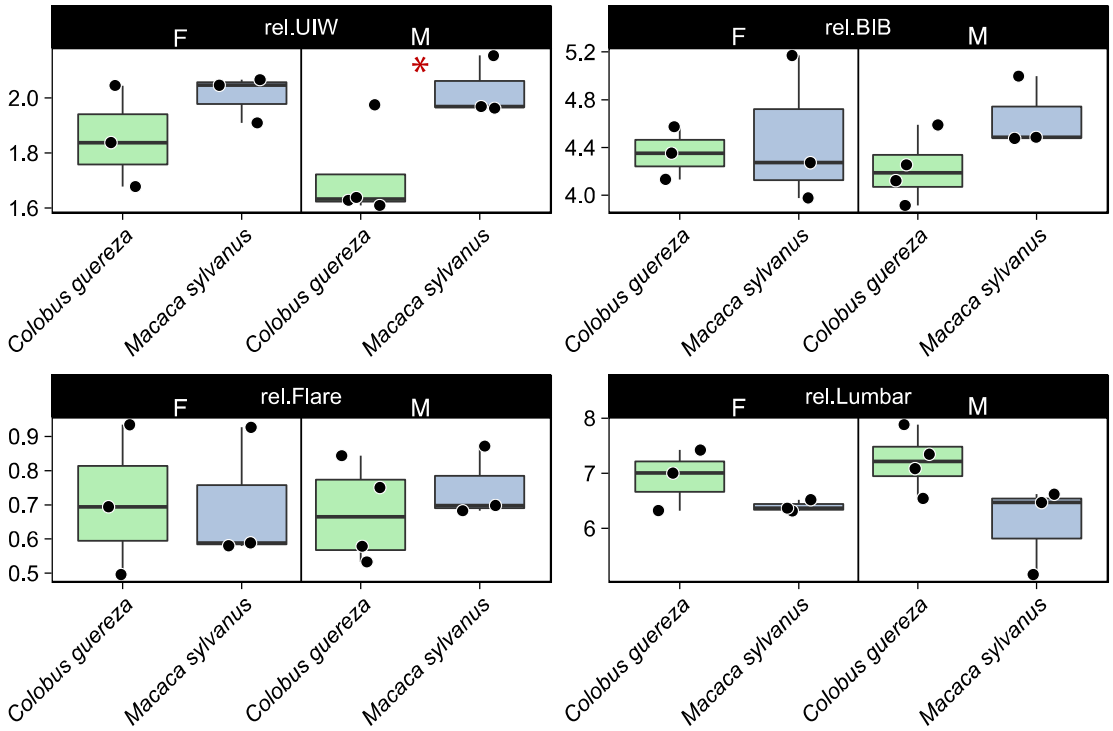

Figure 14. Boxplots with data points comparing relative torso variables in folivorous *Co. guereza* (green) and generalist *M. sylvanus* (blue). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Table 28. Comparisons of relative torso variables in *P. hamadryas* and *T. gelada*.

Papio hamadryas					***Theropithecus gelada***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	5	2.02	0.19	1.85 - 2.34	4	2.32	0.20	2.05 - 2.51	0.06
rel.BIB	5	4.91	0.28	4.51 - 5.31	4	5.52	0.15	5.35 - 5.72	**0.005****
rel.Flare	5	1.00	0.23	0.74 - 1.22	4	1.07	0.03	1.03 - 1.1	0.52
rel.Lumbar	5	4.70	0.41	4.01 - 5.04	4	5.80	0.42	5.21 - 6.17	**0.007****
rel.Rib7	1	5.61	-	-	1	6.55	-	-	-
rel.Rib8	1	6.14	-	-	1	7.35	-	-	-
rel.Rib9	1	6.89	-	-	1	7.39	-	-	-
rel.Rib10	1	7.29	-	-	1	7.44	-	-	-
rel.Rib11	1	7.82	-	-	1	NA	-	-	-
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	5	2.27	0.11	2.14 - 2.43	4	2.22	0.10	2.08 - 2.31	0.52
rel.BIB	5	5.12	0.26	4.83 - 5.42	4	5.03	0.15	4.81 - 5.34	0.63
rel.Flare	5	1.07	0.11	0.95 - 1.22	4	1.18	0.14	1.02 - 1.35	0.23
rel.Lumbar	5	4.70	0.44	4.23 - 5.35	4	4.65	0.55	3.96 - 5.3	0.89
rel.Rib7	1	5.42	-	-	1	5.61	-	-	-
rel.Rib8	1	5.66	-	-	1	6.00	-	-	-
rel.Rib9	1	5.74	-	-	1	6.51	-	-	-
rel.Rib10	1	6.07	-	-	1	6.58	-	-	-
rel.Rib11	1	5.77	-	-	1	6.54	-	-	-

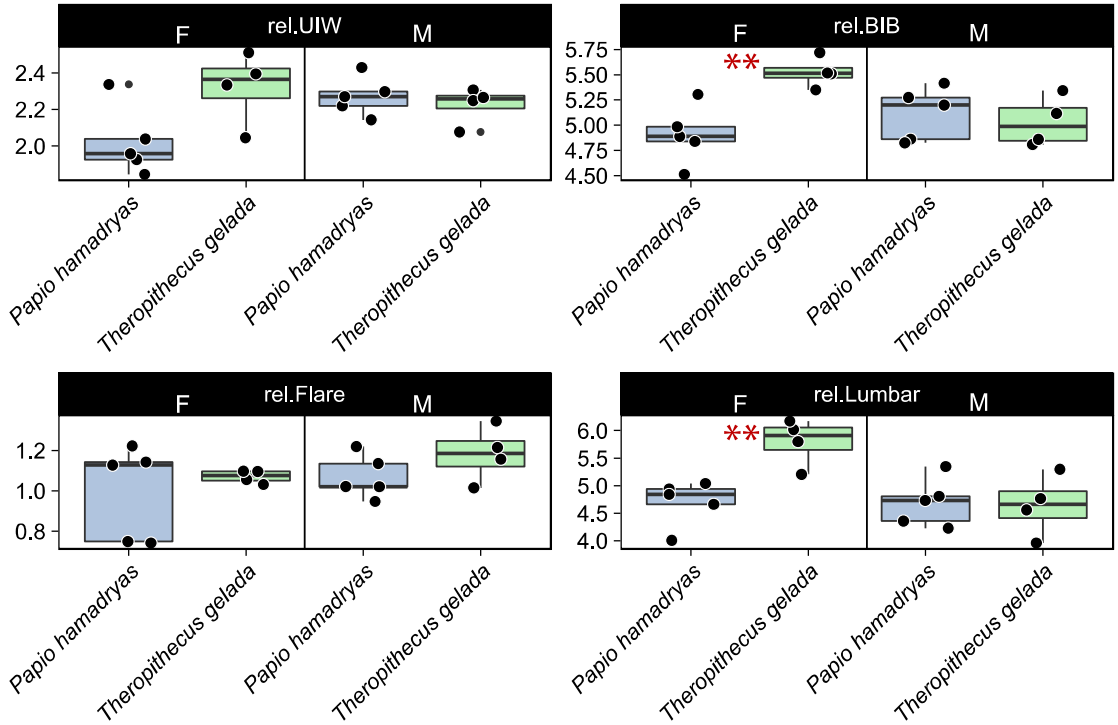

Figure 15. Boxplots with data points comparing relative torso variables in generalist *P. hamadryas* (blue) and graminivorous (grass-eating) *T. gelada* (green). Boxes span the

interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Among apes, there are no differences in relative torso form between female gorillas, but *G. beringei* males have relatively wider ilia, wider bi-iliac breadths, and longer lumbar spines than *G. gorilla* males (Table 29, Figure 16). *Pongo pygmaeus* females have relatively wider bi-iliac breadths than *Pongo abelii* females, but there are no significant differences between *Pongo* males (Table 30, Figure 17).

Table 29. Comparisons of relative torso variables in *G. beringei* and *G. gorilla*.

Gorilla beringei					***Gorilla gorilla***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	2	3.97	0.12	3.88 - 4.06	8	3.72	0.31	3.19 - 4.13	0.14
rel.BIB	2	7.96	0.23	7.79 - 8.13	8	7.36	0.64	6.23 - 8.15	0.08
rel.Flare	2	6.50	0.06	6.46 - 6.54	8	6.12	1.07	4.58 - 7.59	0.35
rel.Lumbar	2	2.20	0.05	2.16 - 2.23	8	1.96	0.31	1.35 - 2.27	0.08
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	6	3.90	0.12	3.7 - 4.03	9	3.62	0.13	3.38 - 3.77	**0.0013****
rel.BIB	6	7.92	0.40	7.51 - 8.54	9	6.99	0.44	6.59 - 8.06	**0.0014****
rel.Flare	6	6.22	0.48	5.56 - 6.99	9	6.16	0.60	5.24 - 7.33	0.8
rel.Lumbar	6	1.98	0.29	1.6 - 2.19	9	1.65	0.27	1.31 - 2.05	**0.048***

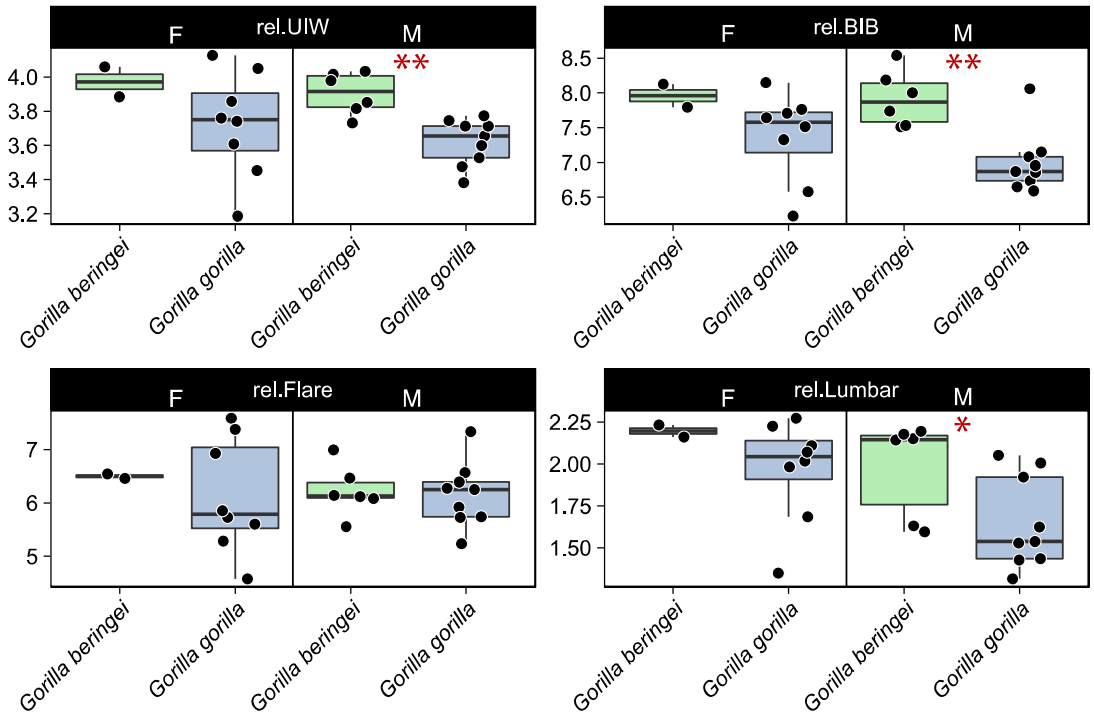

Figure 16. Boxplots with data points comparing relative torso variables in highly folivorous *G. beringei* (green) and frugivorous/folivorous *G. gorilla* (blue). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Table 30. Comparisons of relative torso variables in *Po. abelii* and *Po. pygmaeus.*

Pongo abelii					***Pongo pygmaeus***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	8	2.83	0.14	2.65 - 3.04	7	2.99	0.18	2.79 - 3.3	0.1
rel.BIB	8	6.24	0.38	5.73 - 6.78	7	6.64	0.28	6.37 - 7.19	**0.038***
rel.Flare	8	3.70	0.66	2.95 - 5.09	7	3.87	0.33	3.19 - 4.17	0.52
rel.Lumbar	7	2.17	0.30	1.54 - 2.46	7	2.18	0.30	1.75 - 2.7	0.93
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	2.75	0.15	2.61 - 2.95	8	2.86	0.13	2.65 - 3.0	0.24
rel.BIB	4	6.01	0.17	5.77 - 6.12	8	6.22	0.24	5.85 - 6.5	0.1
rel.Flare	4	3.36	0.32	3.12 - 3.8	8	3.29	0.48	2.63 - 3.92	0.75
rel.Lumbar	4	2.10	0.25	1.86 - 2.45	7	1.97	0.28	1.46 - 2.25	0.43

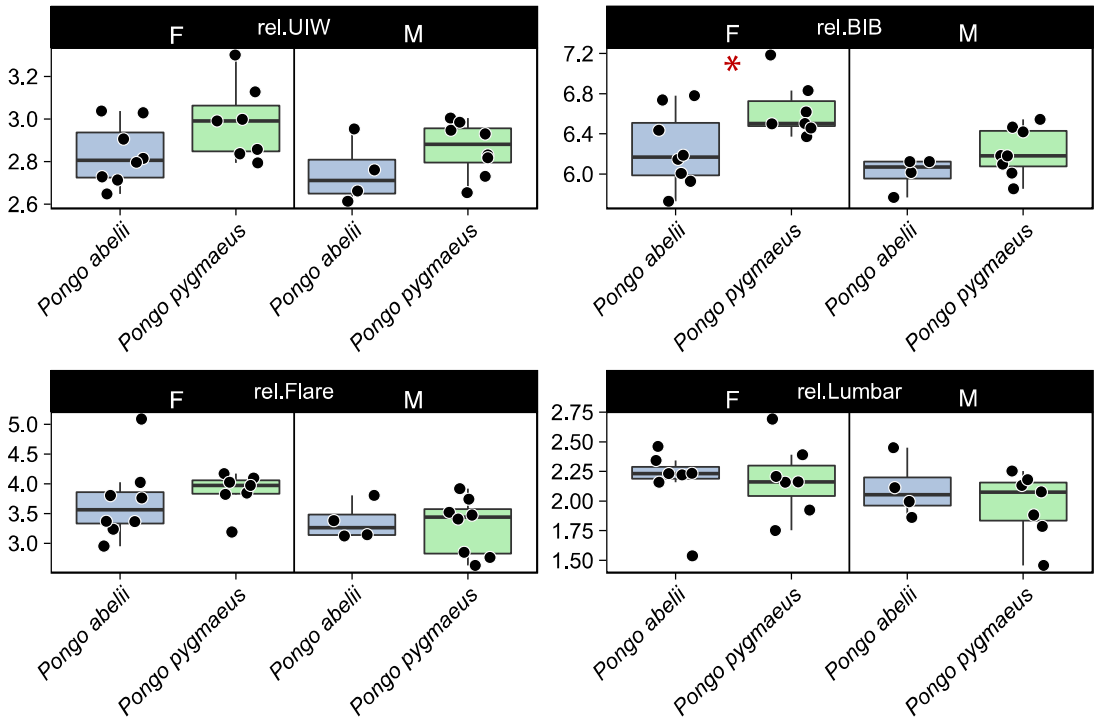

Figure 17. Boxplots with data points comparing relative torso variables in frugivorous/faunivorous *Po. abelii* (blue) and frugivorous/folivorous *Po. pygmaeus* (green). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

There are also significant differences in some relative torso variables between species that are closely-related, similarly-sized, and have similar diets. *Alouatta palliata* females have relatively wider bi-iliac breadths and relatively longer lumbar spines than *Alouatta seniculus* females (Table 31, Figure 18). There are no significant differences between the males of these species. Although a t-test was not performed, mean relative ribcage breadth at rib level 7 for male *A. palliata* is close to this measurement in one individual of *A. seniculus*.

Table 31. Comparisons of relative torso variables in *A. palliata* and *A. seniculus.*

Alouatta palliata					***Alouatta seniculus***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.80	0.19	1.58 - 2.04	6	1.59	0.14	1.44 - 1.76	0.11
rel.BIB	4	4.81	0.29	4.6 - 5.24	6	4.09	0.08	4.0 - 4.18	**0.013***
rel.Flare	4	1.41	0.22	1.18 - 1.65	6	1.09	0.11	0.98 - 1.28	0.056
rel.Lumbar	4	5.46	0.19	5.23 - 5.68	6	4.88	0.11	4.73 - 5.03	**0.004****
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	6	1.69	0.15	1.47 - 1.92	7	1.48	0.21	1.22 - 1.71	0.07
rel.BIB	6	4.40	0.35	3.87 - 4.9	7	4.00	0.32	3.6 - 4.5	0.06
rel.Flare	6	1.21	0.18	1.02 - 1.49	7	1.07	0.18	0.8 - 1.4	0.21
rel.Lumbar	6	4.78	0.20	4.55 - 5.05	7	4.78	0.15	4.57-4.93	0.99
rel.Rib7	2	5.47	0.59	5.05-5.89	1	5.45	-	-	-

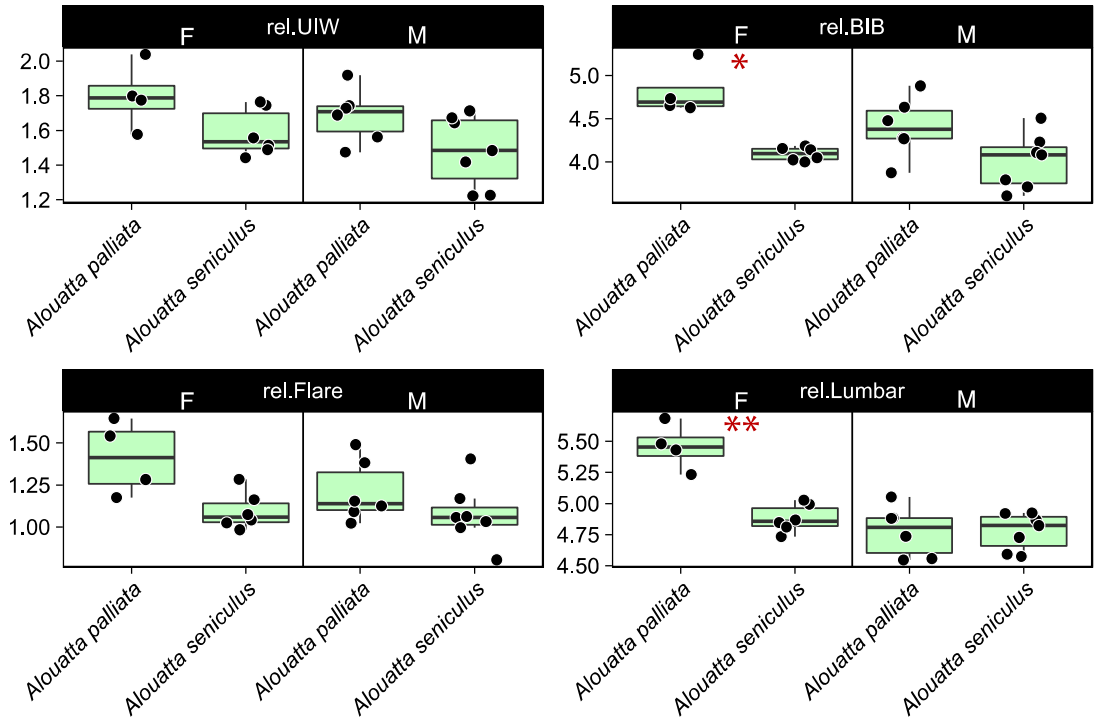

Figure 18. Boxplots with data points comparing relative torso variables in *A. palliata* (dark green) and *A. seniculus* (light green). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Among cercopithecines, relative lumbar spine length is greater in *Cercopithecus cephus* males than in *Chlorocebus aethiops* males, but there are no significant differences between the females of these species (Table 32, Figure 19). *Macaca mulatta* males have relatively wider ilia than males of *Colobus guereza*, but there are no significant differences between the females of these species (Table 33, Figure 20). Although t-tests were not performed between relative ribcage breadths, ribcage breadths are generally wider in *Co. guereza.*

Table 32. Comparisons of relative torso variables in *Ce. cephus* and *Ch. aethiops.*

Cercopithecus cephus					***Chlorocebus aethiops***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.97	0.41	1.62 - 2.56	5	1.92	0.09	1.85 - 2.06	0.80
rel.BIB	4	4.59	0.29	4.38 - 5.02	5	4.67	0.20	4.53 - 5.0	0.65
rel.Flare	4	0.50	0.12	0.43 - 0.68	5	0.87	0.34	0.49 - 1.27	0.07
rel.Lumbar	2	8.91	1.14	8.1 - 9.71	5	7.08	0.29	6.74 - 7.54	0.26
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.90	0.15	1.73 - 2.05	4	1.83	0.09	1.71 - 1.91	0.48
rel.BIB	4	4.25	0.38	3.68 - 4.49	4	4.36	0.39	3.84 - 4.75	0.69
rel.Flare	4	0.42	0.04	0.38 - 0.47	4	0.47	0.06	0.42 - 0.55	0.24
rel.Lumbar	3	8.43	0.40	7.98 - 8.71	4	7.51	0.55	7.01 - 8.19	**0.05***

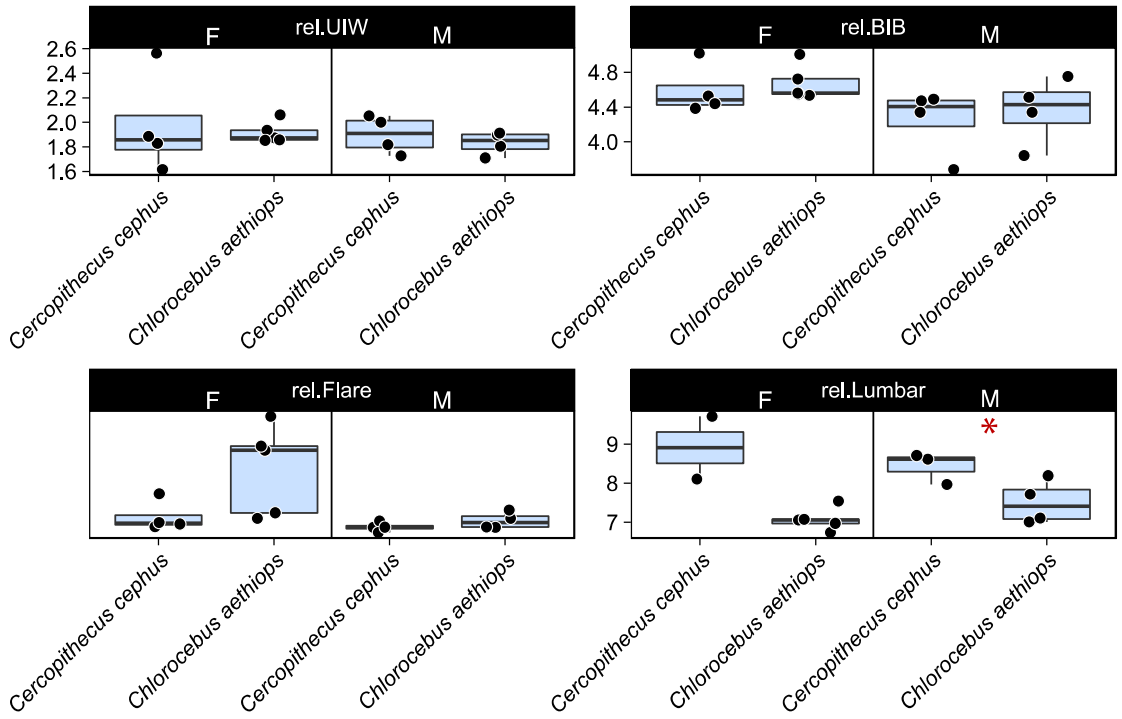

Figure 19. Boxplots with data points comparing relative torso variables in *Ce. cephus* (dark blue) and *Ch. aethiops* (light blue). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Table 33. Comparisons of relative torso variables in *Co. guereza* and *M. mulatta.*

Colobus guereza					***Macaca mulatta***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	3	1.85	0.18	1.68 - 2.05	5	1.89	0.22	1.71 - 2.17	0.79
rel.BIB	3	4.35	0.22	4.13 - 4.57	5	4.83	0.52	4.16 - 5.37	0.12
rel.Flare	3	0.71	0.22	0.5 - 0.93	5	0.88	0.14	0.68 - 1.0	0.32
rel.Lumbar	3	6.92	0.56	6.32 - 7.42	5	6.24	0.76	5.34 - 7.3	0.2
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	4	1.71	0.18	1.61 - 1.98	5	2.07	0.14	1.85 - 2.18	**0.017***
rel.BIB	4	4.22	0.28	3.9 - 4.59	5	4.67	0.39	4.08 - 5.18	0.08
rel.Flare	4	0.68	0.15	0.53 - 0.84	5	0.76	0.17	0.53 - 0.93	0.45
rel.Lumbar	4	7.21	0.56	6.54 - 7.88	5	6.43	0.54	5.93 - 7.24	0.08
rel.Rib7	2	6.06	0.01	6.05 - 6.06	2	5.02	0.44	4.7 - 5.33	-
rel.Rib8	2	6.17	0.35	5.92 - 6.41	2	5.14	0.66	4.68 - 5.60	-
rel.Rib9	2	5.87	0.4	5.59 - 6.15	2	5.31	0.65	4.85 - 5.78	-
rel.Rib10	2	5.75	0.35	5.51 - 6.0	2	5.26	0.50	4.9 - 5.61	-
rel.Rib11	2	5.76	0.42	5.46 - 6.05	2	4.76	0.29	4.55 - 4.96	-

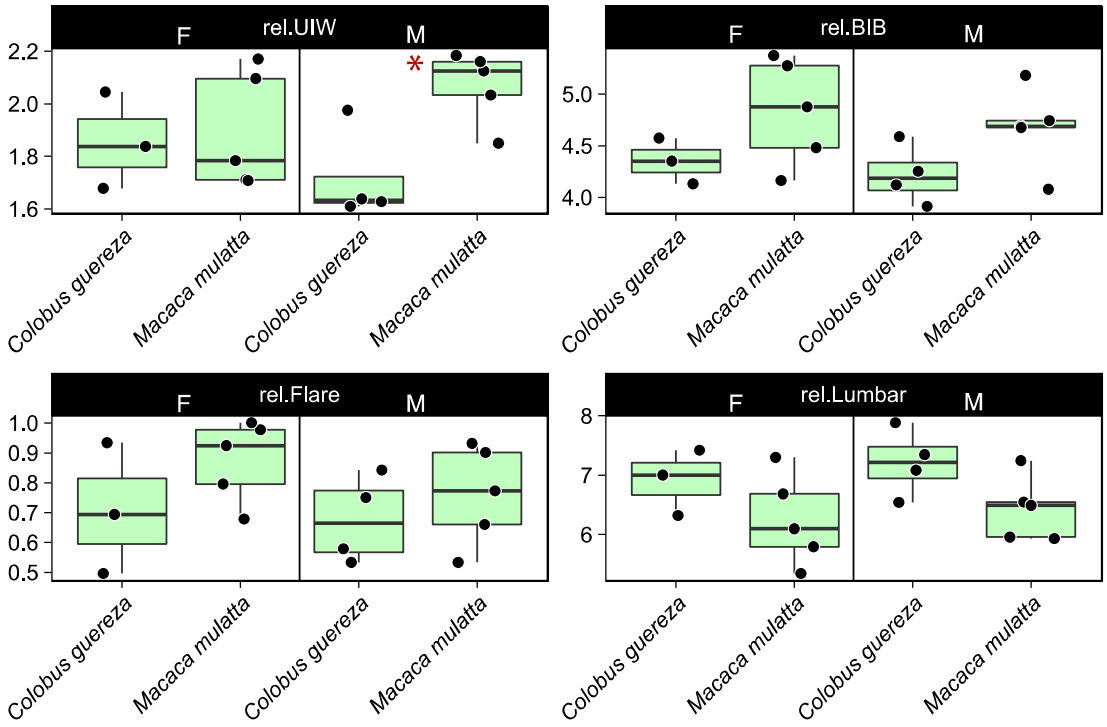

Figure 20. Boxplots with data points comparing relative torso variables in *Co. guereza* (dark green) and *M. mulatta* (light green). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

Among apes, relative iliac flare is greater in *Hylobates muelleri* males than in *Hylobates lar* males, but there are no significant differences between the females of these species (Table 34, Figure 21). Although t-tests were not performed between relative ribcage breadths, ribcage breadths are generally wider in *H. muelleri*.

Table 34. Comparisons of relative torso variables in *H. lar* and *H. muelleri.*

Hylobates lar					***Hylobates muelleri***				
Females									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	14	1.98	0.21	1.72 - 2.37	8	2.17	0.26	1.74 - 2.5	0.10
rel.BIB	14	4.84	0.28	4.42 - 5.39	8	5.13	0.44	4.57 - 5.67	0.12
rel.Flare	14	2.01	0.24	1.56 - 2.38	8	2.19	0.35	1.59 - 2.55	0.23
rel.Lumbar	14	3.40	0.32	2.85 - 4.14	8	3.08	0.45	2.32 - 3.55	0.10
rel.Rib7	5	5.81	0.355	5.31 - 6.23	1	6.3252	-	-	-
rel.Rib8	5	5.86	0.396	5.45 - 6.36	1	6.8013	-	-	-
rel.Rib9	5	6.02	0.387	5.55 - 6.38	1	7.0733	-	-	-

rel.Rib10	5	5.77	0.44	5.24 - 6.23	1	7.1413	-	-	-
rel.Rib11	5	5.48	0.425	4.92 - 6.04	1	7.4389	-	-	-
Males									
Variables	**N**	**Mean**	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**p-value**
rel.UIW	12	1.94	0.16	1.69 - 2.29	8	2.02	0.17	1.76 - 2.35	0.29
rel.BIB	12	4.74	0.24	4.39 - 5.16	8	4.82	0.27	4.4 - 5.15	0.49
rel.Flare	12	1.92	0.27	1.57 - 2.31	8	2.25	0.19	2.0 - 2.46	**0.005****
rel.Lumbar	12	3.16	0.38	2.42 - 3.89	7	3.05	0.24	2.79 - 3.4	0.43
rel.Rib7	2	5.83	0.31	5.61 - 6.05	2	6.29	0.06	6.25 - 6.33	-
rel.Rib8	2	5.92	0.31	5.7 - 6.13	2	6.54	0.02	6.53 - 6.56	-
rel.Rib9	2	5.97	0.44	5.66 - 6.28	2	6.61	0.03	6.59 - 6.63	-
rel.Rib10	2	5.99	0.47	5.66 - 6.32	2	6.61	0.24	6.44 - 6.78	-
rel.Rib11	2	5.85	0.54	5.47 - 6.23	2	6.86	0.45	6.54 - 7.17	-

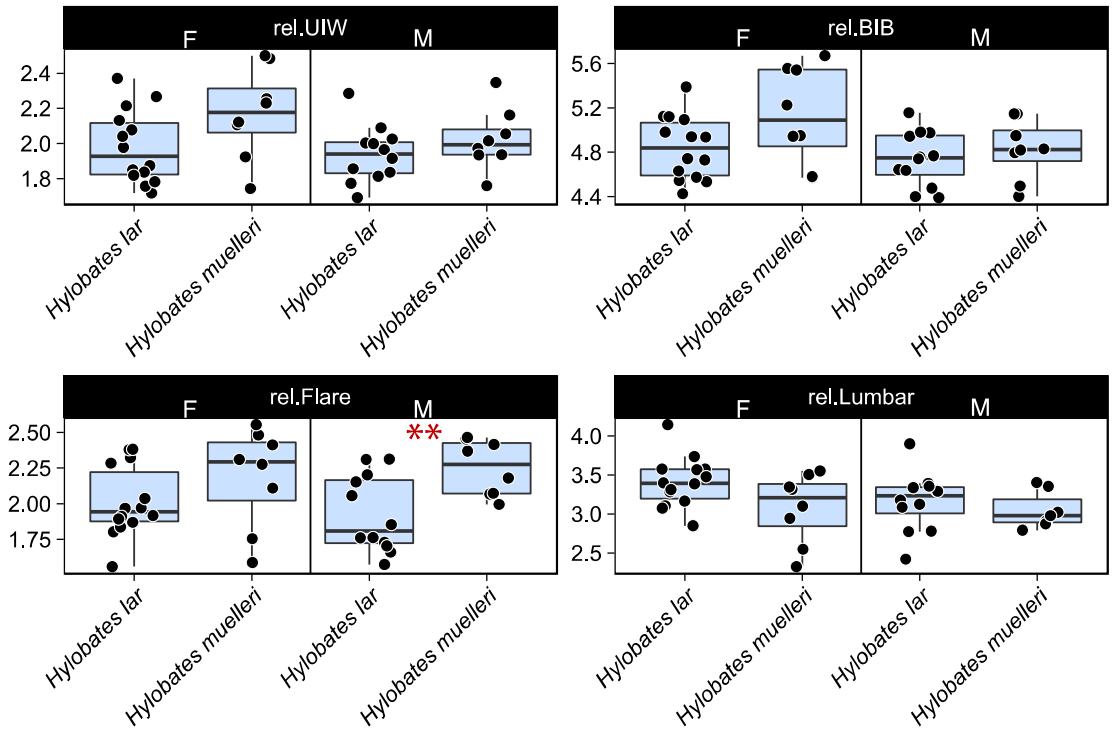

Figure 21. Boxplots with data points comparing relative torso variables in *H. lar* (dark blue) and *H. muelleri* (light blue). Boxes span the interquartile ranges, with the horizontal center lines indicating median values. For each measurement, results for females are on the left (F) and results for males are on the right (M). Whiskers indicate sample range, excluding outliers. Significant differences between species means are noted with red asterisks corresponding to significance level ($p < 0.05$*, $p < 0.01$**).

In summary, of the 11 pairwise comparisons, four comparisons were consistent with the expectation that torso form is influenced by diet, but 1) only one of these comparisons shows significant differences in torso form in both sexes, and 2) the number

and type of relative torso variables that differ between species are not the same across these comparisons.

The remaining seven comparisons were not consistent with the expectation that torso form is influenced by diet. One comparison yields conflicting results as the more faunivorous species was relatively more flared while the more folivorous species had a relatively longer lumbar vertebral column. In another, the more faunivorous species had values for relative upper ilium width that indicate a more capacious abdominal cavity. One comparison shows no significant differences in relative torso dimensions between species with different diets. Four comparisons show differences in these dimensions between species with similar diet compositions. Therefore, there is no consistent support for H1, and no support for H2.

Discussion

If differences in diet are linked to differences in torso morphology among primates, we would expect more folivorous primates to have relatively wider, more flared pelves with longer lumbar spines, while species that consume higher amounts of prey will have relatively narrower, less flared pelves with shorter lumbar spines (Elftman, 1929; Aiello and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010). The analyses presented in this chapter indicate that there is no morphological pattern that consistently conforms to these expectations across pairs of closely-related, similarly-sized anthropoids.

In some cases, primates that consume higher amounts of green plants do have broader/longer relative torso dimensions than species with higher-quality diets that are richer in fruits and prey. There is at least one example of this in each taxonomic

subgroup. *Alouatta palliata* has four-fold more green plants in its diet than *L. lagotricha*, and *A. palliata* females have relatively wider bi-iliac breadths and longer lumbar spines than *L. lagotricha* females, and *A. palliata* males are relatively more flared and have longer lumbar spines than *L. lagothrix* males (Table 25, Figure 12). *Theropithecus gelada* has five-fold more green plants in its diet than *Papio hamadryas*, and *T. gelada* females have relatively wider bi-iliac breadths and longer lumbar spines than *P. hamadryas* females (Table 28, Figure 15). *Gorilla beringei* has two-fold more green plants in its diet than *G. gorilla*, and *G. beringei* males have relatively wider ilia and bi-iliac breadths, and longer lumbar spines than *G. gorilla* males (Table 29, Figure 16). *Pongo pygmaeus* has two-fold more green plants in its diet than *Po. abelii*, and female *Po. pygmaeus* have relatively wider bi-iliac breadths than *Po. abelii* (Table 30, Figure 17).

Although these results conform to predictions and provide partial support for H1, there are confounding factors that prevent accepting these results as conclusive evidence that differences in relative torso dimensions could be linked to diet. First, there are different results among the sexes. Only the *A. palliata* vs. *L. lagothrix* comparison yields differences in relative torso variables for both males and females, while in each of the other comparisons there are only significant differences in relative torso variables for one sex. Second, there is no consistency in which, and how many, relative torso variables are significantly different between more and less folivorous species. For example, while only relative bi-iliac breadth differs among *Pongo* females, three relative torso variables are significantly different among *Gorilla* males. As 1) diets do not differ between the sexes (as reported by publications from which the diet data are derived), and 2) there is no consistent number/type of torso features that differ between more folivorous species and

less folivorous species, these suggest that other variables are likely driving differences in torso form between the species in each pair.

The results of the remaining comparisons between species with different diets further challenge the hypotheses that diet influences torso form. The comparison between *S. boliviensis* and *C. moloch* yields one result that supports H1, and another that conflicts it. Though females of *S. boliviensis*, a primarily faunivorous primate (~53% prey in diet), have relatively shorter lumbar spines than frugivorous *C. moloch* (0% prey in diet), *S. boliviensis* females are relatively more flared than *C. moloch* (Table 24, Figure 11), which is opposite of what is expected. Similarly, *M. sylvanus* males (~38% green plants in diet, ~8% prey in diet) have relatively wider ilia than *Co. guereza* males (~84% green plants in diet, 0% prey in diet) (Table 27, Figure 14), which is also the opposite of what is expected. Lastly, contra to expectations, there are no significant differences in the relative torso variables between either sex of *Lo. ugandae* (12.2% green plants in diet, 24.1% prey in diet) and *M. mulatta* (84.4% green plants in diet, 0% prey in diet) (Table 26, Figure 13). Thus, species that have lower percentages of green plants and higher percentages of prey in their diets can have relatively broader ilia or greater iliac flaring than their more frugivorous or folivorous comparators, and *L. ugandae* and *M. mulatta*, two species that have substantially different diets, have similar relative torso dimensions.

Comparisons between species with similar diets reveal other unexpected significant differences in relative torso variables and do not support H2. The same relative torso variables that differ among female *A. palliata* and *L. lagothrix*—bi-iliac breadth and lumbar spine length—also differ among female *A. palliata* (~51% green plants in diet) and *A. seniculus* (~49% green plants in diet) (Table 31, Figure 18). So,

regardless if there is a ~2% difference (*A. palliata* vs. *A. seniculus*) or ~ 40% difference (*A. palliata* vs. *L. lagothrix*) in feeding time on green plants, female *A. palliata* have relatively wider bi-iliac breadths and lumbar spine lengths than these other atelids. Similarly, relative upper ilium widths in both *M. sylvanus* (~38% green plants in diet) and *M. mulatta* (~84% green plants in diet) males are significantly broader than in *Co. guereza* males (also ~84% green plants in diet) (Table 33, Figure 20). So, whether there is a ~ 47% difference (*Co. guereza* vs. *M. sylvanus*) or a <1% difference (*Co. guereza* vs. *M. mulatta*) in feeding time on green plants, male macaques have relatively wider ilia than *Co. guereza*.

In the remaining comparisons between species with similar diets, only males show differences in relative torso dimensions. Relative lumbar spine length is longer in *Ce. cephus* males than in *Ch. aethiops* males, though both are primarily frugivorous and consume foods from nearly each diet item category (Table 32, Figure 19), and relative iliac flare is higher in *H. muelleri* males than in *H. lar* males, although their diet compositions are similar (Table 34, Figure 21). Altogether, these four comparisons indicate that species with similar diet compositions can show significant differences in relative torso dimensions.

The torso differences revealed between the species in some of these comparisons are likely due to influences (besides diet) from phylogeny, locomotion, or some combination of these factors. For example, the relatively wider ilia of macaques compared to *Co. guereza* is likely related to differences in locomotion, with *Co. guereza* leaping more often than macaques (see locomotion data in Table 6). It is also possible that some of the torso differences are due to the influence of altitude. *Gorilla beringei*

live at altitudes ranging between ~2200 to ~4000 meters (m), while *G. gorilla* occupy habitats at sea level up to ~ 2000 m (Groves, 1970; Sarmiento et al., 1996), and skeletal differences in these species have been attributed to this altitudinal variation (e.g., Sarmiento et al., 1996; Jabbour and Pearman, 2016). Similarly, though *P. hamadryas* are known to occupy habitats from sea level up to ~ 3300 m (Crook and Aldrich-Blake, 1968; Yalden et al., 1996), *T. gelada* has been observed at even higher altitudes, from ~1700 m up to 4600 m (Yalden et al., 1977, 1996; Iwamoto 1993; Hunter, 2001). The relatively wider torsos in *G. beringei* and *T. gelada*, as well as the potentially wider ribcages in *T. gelada*, therefore could reflect thermoregulatory adaptations in these species.

While it is possible that locomotion and altitude could be influencing differences in relative torso dimensions between species, the sex differences in the results presented in this chapter pose a challenge to accepting these explanations. Only in the *A. palliata* vs. *L. lagothrix* comparison is one of the measurements, relative lumbar spine length, significantly different between both males and females of these species. In the ten remaining comparisons, significant differences in relative torso variables are only captured in one of the sexes. One potential explanation could be because of differences in pelvic growth relative to body size between the sexes and between species. Though Leutenegger and Larson (1985) focused on whether postcranial metrics in four platyrrhine species were different between males and females of the *same* species, they found that in some dimensions males were significantly larger than females, while in others females were significantly larger than males. Furthermore, there was not one metric in the limbs or pelvis that was significantly different between sexes in all four

species. They attribute these differences to differences in both growth period and growth rate between the sexes, and differences in growth period and growth rate across regions of the postcranial skeleton.

Extrapolating these results to this chapter, where I test for significant differences within the same sex of two different species, it is possible that the disparity between sexes is due to sex-specific differences in how relative torso dimensions relate to body size. So, for example, we found above that bi-iliac breadth is significantly greater in *Po. pygmaeus* than *Po. abelii*. In both subspecies, male orangutans are about twice the size of females, and body size growth rate in females is lower and occurs over a shorter duration of time than in males (Leigh and Shea, 1995). Effects of this sex difference in growth rate could potentially be compounded with subspecific differences in growth rate, as indicated by differences in life history between Bornean and Sumatran orangutans (Wich et al., 2004). There thus may be significant differences in how the pelvis grows relative to overall body size between *Pongo* sp. females, which leads to significant differences in relative bi-iliac breadth, while there may be no detectable differences in how this pelvic dimension grows with body size in *Pongo* sp. males.

Furthermore, while lumbar spine length is known to vary with locomotion across primates (e.g., Schultz, 1930, 1961; Napier and Napier, 1967; Ward, 1993; Williams and Russo, 2015; Hunt, 2016), the analyses in this chapter suggest that this variable significantly differs between species that engage in generally similar locomotor behaviors (e.g., *Saimiri* vs *Callicebus*). Phylogeny may be influencing this difference in some comparisons, in others it may be influenced by differences in the number of lumbar vertebrae within some species (e.g., *A. palliata, Gorilla sp.*, *Ce. cephus*). Lumbar spine

length in individuals with a non-modal number of lumbar vertebrae can be anywhere between ~15 to ~30 mm longer or shorter than is typical of other individuals in that species, depending on the vertical height of each lumbar vertebrae. Such individuals would contribute to differences in the sex-specific means that may not be functionally relevant.

The results presented here suggest that differences in relative torso dimensions between similarly-sized, closely-related anthropoids are not reliable indicators of diet., There is no conclusive evidence that lumbar vertebral column length and ilium width (Lovejoy et al., 2009), nor bi-iliac breadth and iliac flare (Elftman, 1929; Aiello and Wheeler, 1995) are relatively broader in species that consume higher proportions of green plants in their diets. Because there is no consistent pattern of how torso variables vary between more folivorous and more faunivorous primates, researchers should be wary of assuming that differences in torso form among fossil hominins reflect dietary differences.

Conclusions

Comparisons between closely-related and similarly-sized species with different diets, as well as species with similar diets, reveal that differences in relative upper ilium width, bi-iliac breadth, iliac flare, and lumbar spine length cannot be reliably used to infer diet among anthropoids. Although some torso variables are relatively broader or longer in species that primarily feed on leaves and other green plants, there are also some instances of species that feed on higher percentages of prey having relatively broader/longer torso dimensions. This chapter provides examples where species that differ substantially in diet *do not* differ in relative torso dimensions, and other examples where species that have

similar diets *do* differ in these dimensions. These results do not support the practice of using torso form to infer shifts in diet among fossil hominin species.

Chapter 4: Is lower torso volume related to diet in anthropoid primates?

Introduction

The previous two chapters tested whether and how torso shape and size, as captured by linear measurements based on skeletal landmarks, relate to diet in platyrrhines, cercopithecines, colobines, and hominoids. Results from these chapters suggest that variation in ilium width, bi-iliac breadth, iliac flare, and lumbar spine length across anthropoids are mainly influenced by body size and locomotion and do not show any consistent relationship with diet. This is the case for analyses that test for a diet effect on the torso across both a large sample of anthropoids (Chapter 2) and in pairwise comparisons between similarly-sized, closely-related species (Chapter 3). These analyses (except Analysis B, Chapter 2) test for relationships between each individual torso feature and diet, but it is possible that measurements that capture information about torso form in its entirety may reveal a relationship with diet. One such variable is lower torso volume which is computed from the dimensions of the ribcage, lumbar vertebral column, and pelvis.

Researchers have suggested that differences in hominin torso dimensions reflect differences in lower torso volume, or abdominal volume (Robinson, 1972; Schmid, 1991), which may be associated with diet-related differences in gut size (Aiello and Wheeler, 1995; Lovejoy et al., 2009). Specifically, it has been suggested that species with diets rich in green plants will have more capacious torsos, and thus larger abdominal volumes, to accommodate larger digestive tracts adapted for fermenting and digesting fibrous plant materials (Elftman, 1929; Aiello and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010).

Lower torso volume, or abdominal volume, of vertebrates can be estimated from measurements taken *in vivo*, as well as from preserved specimens. Abdominal volume has been estimated for modern humans and lizards by modeling body form using simple shapes with known geometric formulae to derive volume estimates. With respect to the humans, Guerrero-Romero and Rodríguez-Morán (2003) used anthropometric measurements from the waist and hips and the volume formulas for a cylinder and vertical cone, to estimate abdominal volume in order to generate an index for obesity. For lizards, Shine (1992) used the volume of a cylinder to calculate abdominal cavity volume in preserved female lizards in order to offer an index of available space for internal organs and eggs. Although abdominal circumferences from captive and free-ranging populations are provided in the literature for a few primate species, not enough data exist to calculate lower torso volumes using volume formulas.

Torso volume can also be computed using built-in functions in software used for processing information from three-dimensional (3D) models of articulated skeletons. For example, the convex hull method can measure the volume of skeletal sections by fitting the smallest-possible 3D polyhedron to a point cloud or suite of x, y, z coordinates that represent the surface of skeletal sections (Sellers et al., 2012; Brassey and Sellers, 2014; Brassey et al., 2017; Clauss et al., 2017). Using the "convhulln" function in MATLAB (Mathworks, USA), Brassey and Sellers (2014) calculate and sum volumes of body segments to explore how total body volume of mounted skeletons scale with body mass in primates, non-primate mammals, and birds. Brassey et al. (2017) also use this protocol to calculate a total convex hull volume of the skeleton of A.L. 288-1 (*Australopithecus afarensis*), which they use to generate a body mass estimate for this individual.

Clauss et al. (2017) use the convex hull method to test if torso volume and diet are related among a large sample of terrestrial tetrapods, which includes early synapsids, mammals, birds, non-avian dinosaurs, and reptiles. The authors estimate torso volume from models of mounted skeletons using Point Cloud Library (Aldoma et al., 2012). Torso volume here refers to the minimum volume of the body cavity that is bounded caudally by the ischium and cranially by the first ribs. The authors found that torso volume in herbivores is about 1.5 larger than in carnivores. The only primates included in their dataset, *Gorilla gorilla* and *Nasalis larvatus*, are classified as herbivorous.

Here, I use the convex hull filter in Geomagic (version 2017) to calculate lower torso volumes (volume of the torso caudal to rib level 6) in a sample of 44 anthropoid primates representing 20 taxa, with the goal of testing whether lower torso volume covaries with diet. Based on the assumptions of how lower torso volume relates to diet in hominins (described above; Aiello and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010) and on the findings of Clauss et al. (2017), I hypothesize the following:

H1. More folivorous primates will have relatively larger lower torso volumes than frugivorous and faunivorous primates (Figure 22, top panel).

H2. Taxa with relatively larger guts will also have relatively larger lower torso volumes (Figure 22, middle panel).

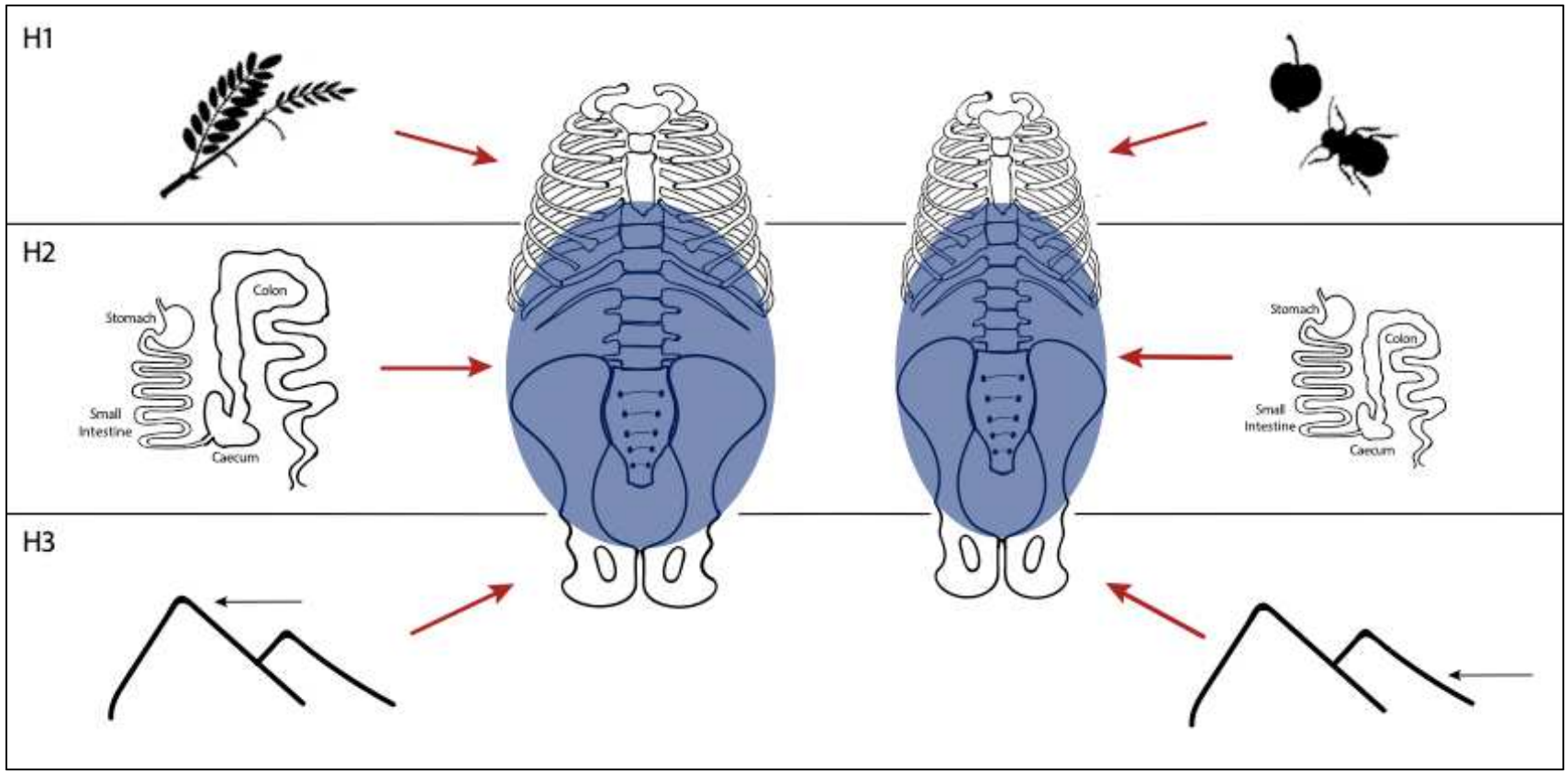

Figure 22. Hypotheses for the analyses in this chapter. The hypothesis about how diet is related to lower torso volume (H1) is illustrated in the top panel. The hypothesis about how gut size is related to lower torso volume (H2) is illustrated in the middle panel. The hypothesis about how maximum habitat altitude is related to lower torso volume (H3) is illustrated in the bottom panel.

Furthermore, as mentioned in the introductory chapter, some researchers have suggested that wider, more voluminous torsos of some hominin populations reflect thermoregulatory adaptations to occupying higher altitudes (Ruff, 1994; Weinstein, 2008). I applied this notion to non-human primates in Chapter 3, where I discuss the possibility that relatively wide lower torsos in *G. beringei* and *T. gelada* could reflect thermoregulatory adaptations in these species, as they occupy colder, higher altitude climates than other gorillas and baboons (Groves, 1970; Yalden et al., 1977, 1996; Iwamoto 1993; Sarmiento et al., 1996; Hunter, 2001). It is possible that large torso volumes in the sample analyzed here reflect adaptations to living in higher-altitude habitats. I therefore also test the following hypothesis:

H3. Relative lower torso volume will be larger in species that occupy habitats at a greater maximum altitude (Figure 22, bottom panel).

Lastly, it is important to acknowledge the potential confounding factor that, in life, the abdominal viscera protrude beyond the torso skeleton, which suggests that the convex hull method underestimates true abdominal volume (Clauss et al., 2017). But since the researchers who are investigating the diets of fossil hominins only have access to skeletal remains of the torso to infer abdominal volume, it is important to test if there is any relationship between diet and estimates of lower torso volume based on the skeletal elements that are related to the torso. For these reasons, the volume estimates of the lower torso presented in this chapter should be considered minimum estimates of actual lower torso volume.

Materials and Methods

Sample

3D models of fully articulated primate torsos were generously provided by Dr. Carol Ward and Dr. Daniel García-Martínez. The models from the Ward sample were produced from computed tomography (CT) scans of fresh, frozen, and fluid-preserved cadavers. CT scans were obtained from the Arizona State University, the University of Minnesota, and the University of Zurich. Torsos from the García-Martínez sample were scanned with an Artec Space Spider scanner at the Swedish Museum of Natural History. Additional 3D models of primate torsos produced from CT scans were obtained from the Kyoto University Primate Research Institute's (KUPRI) Digital Morphology Museum. Care was taken to exclude specimens with vertebral columns that were excessively curved in the sagittal and coronal planes or were otherwise warped in such a way that would prevent reliable comparisons with other individuals.

Table 35 lists the taxa represented by the final 3D torso sample (N = 44) and includes values for lower torso volume, acetabular diameter, and relative lower torso volume for each individual, and species averages. Genus averages are provided when species identifications are not indicated for that genus. Unfortunately, as sex is only available for eight individuals in the sample, it is likely that species and genus averages include values from both sexes—this is certainly the case for *H. moloch* and *S. syndactylus*.

Table 35. Lower torso volumes, acetabular diameters, and relative lower torso volumes for 44 individuals. Species or genus averages are provided where applicable.

Group	Specimen ID	Acet	Volume	Rel Vol	Source	Sex
Platyrrhine	*Aotus*-1	9.6	212.95	0.62	W	
Platyrrhine	*Aotus*-2	8.8	255.9	0.72	K	M
Platyrrhine	*Aotus* sp. average	9.2	234.43	0.67	-	

Platyrrhine	*Ateles*	22	1618.37	0.53	W	
Platyrrhine	*Cebus*-1	11.95	709.66	0.75	W	
Platyrrhine	*Cebus*-2	11.35	605.06	0.75	W	
Platyrrhine	*Cebus*-3	13.71	666.7	0.64	W	
Platyrrhine	*Cebus*-4	11.15	686.57	0.79	W	
Platyrrhine	*Cebus*-5	11.78	623.35	0.73	W	
Platyrrhine	*Cebus* sp. average	11.99	658.27	0.73	-	
Platyrrhine	*Lagothrix*	20.5	1370.86	0.54	W	
Platyrrhine	*Saimiri sciureus*-1	9.03	213.56	0.66	K	M
Platyrrhine	*Saimiri sciureus*-2	8.42	202.96	0.70	K	M
Platyrrhine	*Saimiri sciureus* average	8.73	208.26	0.68	-	
Cercopithecine	*Cercopithecus mitis*	17	2001.31	0.74	G	
Cercopithecine	*Chlorocebus cynosurus*	14.9	978.91	0.67	G	
Cercopithecine	*Macaca fascicularis*-1	13.39	727.25	0.67	G	
Cercopithecine	*Macaca fascicularis*-2	14.04	889.34	0.68	G	
Cercopithecine	*Macaca fascicularis*-3	14.09	1004.93	0.71	G	
Cercopithecine	*Macaca fascicularis* average	13.84	873.84	0.69	-	
Cercopithecine	*Macaca mulatta*	17.34	1209.28	0.61	G	
Cercopithecine	*Mandrillus sphinx*-1	28.19	5060.91	0.61	W	
Cercopithecine	*Mandrillus sphinx*-2	21.75	1364.4	0.51	G	F
Cercopithecine	*Mandrillus sphinx* average	24.97	3212.66	0.59	-	
Cercopithecine	*Papio*-1	27.08	1780.62	0.45	W	
Cercopithecine	*Papio*-2	26.67	1603.05	0.44	W	
Cercopithecine	*Papio* sp. average	26.88	1691.84	0.44	-	
Cercopithecine	*Theropithecus gelada*-1	25.6	4300.83	0.64	W	
Cercopithecine	*Theropithecus gelada*-2	21.93	3373.32	0.68	W	
Cercopithecine	*Theropithecus gelada*-3	24.14	2679.12	0.58	W	
Cercopithecine	*Theropithecus gelada* average	23.89	3451.09	0.63	-	
Colobine	*Colobus guereza*-1	22.89	2456.11	0.59	W	
Colobine	*Colobus guereza*-2	20.14	2121.77	0.64	W	
Colobine	*Colobus guereza* average	21.52	2288.94	0.61	-	
Colobine	*Presbytis melalophos*-1	18.45	2477.71	0.73	G	
Colobine	*Presbytis melalophos*-2	17.33	2392.02	0.77	G	
Colobine	*Presbytis* melalophos average	17.89	2434.87	0.75	-	
Colobine	*Trachypithecus*-1	17.6	1591.59	0.66	W	
Colobine	*Trachypithecus*-2	17.73	1403.06	0.63	W	
Colobine	*Trachypithecus* sp. average	17.67	1497.33	0.65	-	
Lesser Ape	*Hylobates muelleri*	20.51	1620.25	0.57	G	
Lesser Ape	*Hylobates moloch*-1	17.75	854.99	0.53	G	
Lesser Ape	*Hylobates moloch*-2	19.73	1751.58	0.61	G	
Lesser Ape	*Hylobates moloch*-3	19.34	1714.44	0.62	G	M

Lesser Ape	*Hylobates moloch*-4	16.72	952.25	0.59	G	F
Lesser Ape	*Hylobates moloch* average	18.81	1441.06	0.60	-	
Lesser Ape	*Symphalangus syndactylus*-1	26.46	3403.57	0.57	W	
Lesser Ape	*Symphalangus syndactylus*-2	24.2	2922.95	0.59	W	
Lesser Ape	*Symphalangus syndactylus*-3	23.9	2939.17	0.60	G	F
Lesser Ape	*Symphalangus syndactylus*-4	26.89	3422	0.56	K	M
Lesser Ape	*Symphalangus syndactylus* average	25.36	3088.56	0.57	-	
Ape	*Pan*-1	36.04	4701.33	0.46	W	
Ape	*Pan*-2	42.82	6548.82	0.44	W	
Ape	*Pan*-3	38.42	6374.92	0.48	W	
Ape	*Pan* sp. average	39.09	5875.02	0.46	-	
Ape	*Pongo*-1	38.2	4204.73	0.42	W	
Ape	*Pongo*-2	42.04	15047.56	0.59	W	
Ape	*Pongo* sp. average	40.12	9626.15	0.53	-	

Acet = Acetabular diameter (mm)
Volume = Volume of the lower torso (cm^3)
Rel Vol = Relative volume; cubed root of volume divided by acetabular diameter
Source = Data provided by C. Ward (W), D. García-Martínez (G), and KUPRI (K)

Scan preparation

Avizo (version 7.1.0) was used to convert raw CT scan files into 3D models, which were stored as PLY files that were cleaned with Geomagic (version 2017). Upper and lower limbs, clavicle, scapula, tail, and first five superior ribs and vertebrae were removed, isolating the lower torso, which is comprised of the caudal thorax beginning at rib level 6, the lumbar spine and sacrum, and the pelvis (Figure 23A). Ribs 1 through 5 were not included as Bastir et al. (2013) demonstrates the cranial thorax is responsive to respiratory system development in humans and suggests that caudal thorax (rib level 6 and below) differences among primates could potentially be related to diet-related differences in abdominal organ volume. The interior surface of the lower torso was produced by selecting the anterior surface of the vertebral column, interior surface of the ribs and sternum, anterior surface of the iliac blades, anterior surface of the sacrum until the first set of sacral foramina, and the superior surface of the pubis. Any remaining

surfaces of the ribs sitting posterior to the anterior surface of the vertebral column were deleted.

Volume calculation

In MeshLab (Cignoni et al., 2008), first the 'remove unreferenced vertices' filter was applied to the interior surface file. Then, the 'convex hull' filter was used to generate the convex manifold (Figure 23B), which is a water-tight polygon fitted by the hulling operation. The convex hull (Figure 23C) was then exported back to Geomagic where the volume (cm^3) was computed using the 'compute volume' function.

Statistical analyses

Acetabular diameter was measured from the pelves in Geomagic (version 2017) and used as a proxy for body size. Phylogenetic generalized least squares (PGLS) regressions based on genus and species averages were used to test if there is a relationship between natural log-transformed lower torso volume (LTV) and natural log-transformed acetabular diameter, to test how lower torso volume scales with body size after accounting for phylogenetic relatedness. Relative lower torso volume (RLTV) was obtained by dividing the cubed root of lower torso volume by acetabular diameter. PGLS regressions were also used to test the relationships between 1) RLTV and each diet variable, 2) LTV and absolute gut size for the 11 taxa for which these data are available, 3) RLTV and relative gut size, and 4) RLTV and maximum habitat altitude.

After averaging the volume data by genus or species, 20 taxa are represented in the sample. A phylogenetic tree was obtained for these taxa from 10ktrees version 3 (Figure 24; Arnold et al., 2010). All PGLS analyses were conducted in R version 3.3.1 (R Core Development Team 2015) using the caper package version 1.0.1 (Orme et al. 2011).

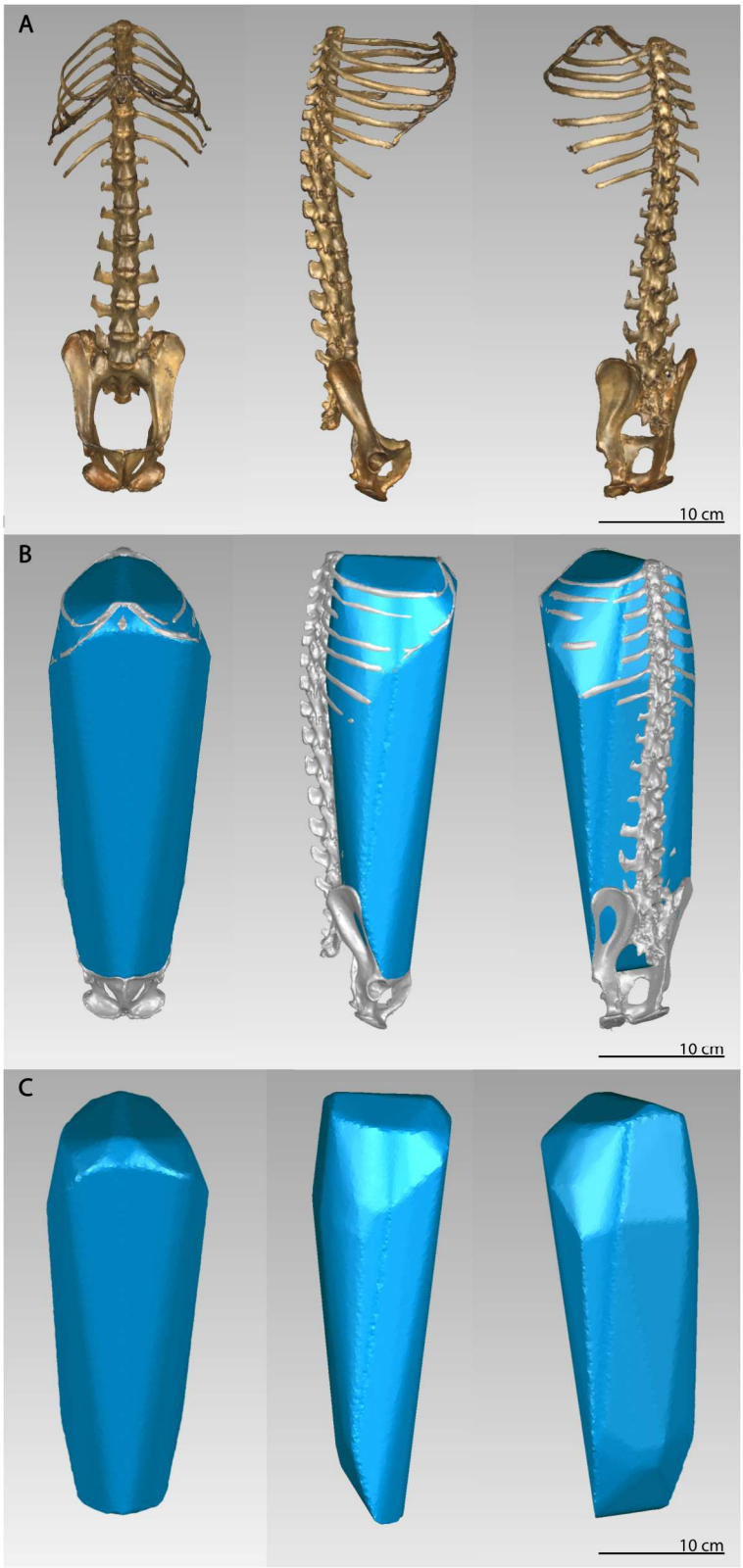

Figure 23. Lower torso of *Presbytis melalophos* in anterior (left), lateral (middle), and posterolateral (right) views. A) Lower torso skeleton. B) Convex manifolds fitted to the skeleton. C) Isolated convex hull from which volume was computed.

Phylogenetic signal for lower torso volume and relative lower torso volume values were calculated using the 'phylosig' function in the phytools package version 0.5-64 (Revell, 2012). This analysis provides an estimate for both Blomberg's K (Blomberg et al., 2003) and Pagel's lambda (Pagel, 1999). For both test statistics, values closer to 0 indicate no phylogenetic signal (trait evolution is independent of phylogeny) and values closer to 1 indicate trait evolution according to Brownian motion. When K is greater than 1, this suggests that close relatives are more similar to each other than expected under Brownian motion, while values for K less than 1 indicate that close relatives are less

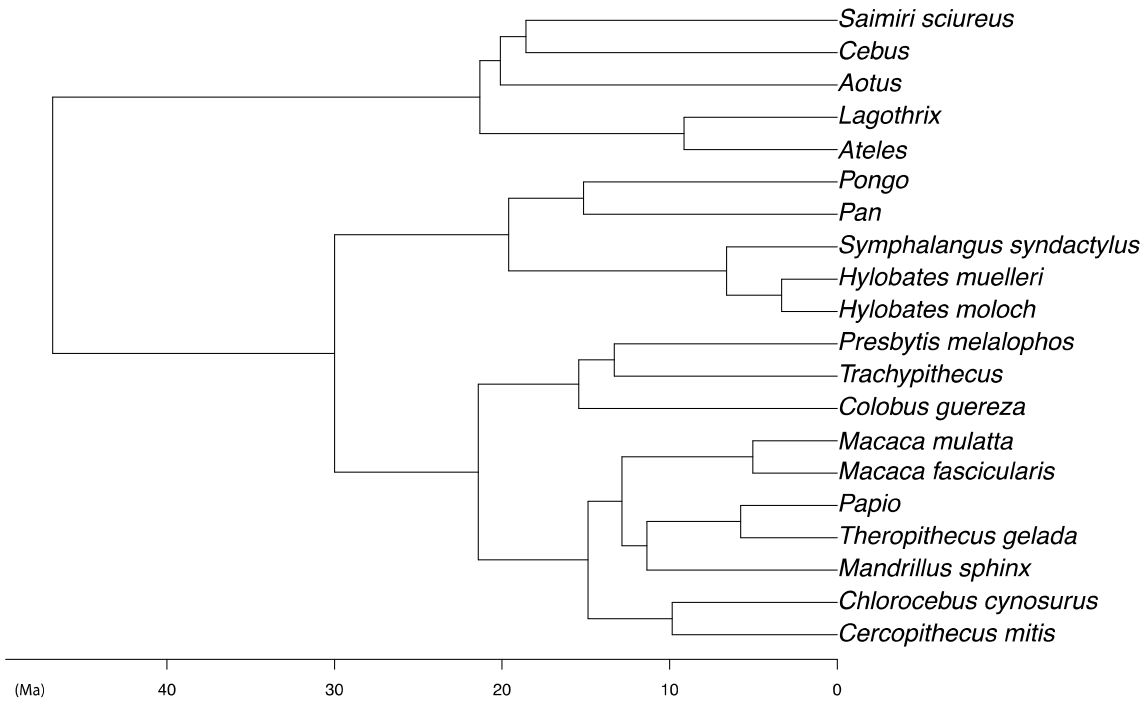

Figure 24. Time-calibrated phylogenetic tree showing the relationships among the 20 taxa sampled in this chapter.

Diet

As in Chapters 2 and 3, diet is defined as percent feeding time on different food item categories. Table 36 summarizes diet data for all taxa represented in the sample. Among the individuals included in analyses for this chapter, 18 individuals representing 8 genera do not have a species designation. Diet data for these individuals were obtained by averaging the diet data in Table 4 from the species within their genus. So, for example, the values provided in Table 36 for *Ateles* is the average of data for *A. belzebuth* and *A. geoffroyi*.

Table 36. Diet composition for the 20 taxa represented in the 3D torso sample.

Taxon	Seeds	Fung	FG	RT	GP	Fruit	Prey	NSite
Aotus	0	0	0	0	10	75	15	1
Ateles	0	0	4.58	0	15.17	74.69	0	7
Cebus	3.43	0	2.69	0.19	14.68	62.58	16.6	5
Lagothrix	2.37	0.03	3.92	0	12.63	71.22	8.64	5
Saimiri sciureus	0	0	7.4	0	0	92.6	0	1
Cercopithecus mitis	2.5	0	5.6	0	20	54.6	16.8	1
Chlorocebus cynosurus	13	1	16	0	7	50	13	1
Macaca fascicularis	0	0.5	3.6	0	16.9	75.95	2.8	2
Macaca mulatta	0	0	4.8	2.2	84.4	8.5	0	1
Mandrillus sphinx	30.2	0	1.75	0	13.2	48.7	4.5	2
Papio	12.98	0.09	7.94	16.86	22.33	34.6	2.02	8
Theropithecus gelada	5	0	0.8	0.5	91.8	1.9	0	1
Colobus guereza	0.12	0	1.26	0	83.53	10.22	0	2
Presbytis melalophos	32.4	0	11.5	0	35.2	17.1	0	1
Trachypithecus	0	0	8.1	0	58.95	32.95	0	2
Hylobates moloch	0	0	5.9	0	31.3	61.75	0.6	2
Hylobates muelleri	0	0	4	0	32	62	8	1
Symphalangus syndactylus	0	0	5.8	0	32.24	51.66	10.31	7
Pan	0	0	5.8	0.3	32.24	51.66	10.31	3
Pongo	0	0	1.68	0	28.28	62.33	6.5	4

Note: Data categorized following Pineda-Munoz and Alroy (2014). See Table 3 for diet references. Rounding to two decimal places for these values does not reflect the precision of the feeding time estimates but result from averaging these data across multiple field sites.
Seeds = % of seeds and nuts in diet; Fung = % of fungi in diet; FG = combined % of flowers, nectars, and gums in diet; RT = combined % of roots and tubers in diet; GP = combined % of leaves, stalks, grass, and other green plants in diet; Fruit = % of fruits in diet; Prey = combined % of invertebrate and vertebrate prey in diet; NSite = Number of field sites from which feeding time data were sourced
Diet data for *Aotus* from *A. trivirgatus*; for *Ateles* from *A. belzebuth* (6 sites) and *A. geoffroyi* (1 site); for *Cebus* from *C. apella* (4 sites) and *C. capucinus* (1 site); *Chlorocebus cynosurus* for *C. aethiops* (1 site); for *Papio* from *P. anubis* (4 sites), *P. cynocephalus* (3 sites), and *P. hamadryas* (1 site); for *Trachypithecus* from *T. cristatus* (1 site) and *T. obscurus* (1 site); for *Pan* from *Pan troglodytes* (3 sites in West Africa); for *Pongo* from *P. abelii* (2 sites) and *P. pygmaeus* (2 sites).

Gut size

As in Chapter 2, gut size is defined as the summed surface area of the stomach, small intestine, caecum, and colon. Relative gut size for each taxon was calculated by dividing the square root of gut size by the average acetabular diameter for each taxon derived from the 3D torsos. Table 37 summarizes gut size data for the 11 taxa in the sample for which these data are available. Data from *Aotus trivirgatus* were used for *Aotus*; from *Ateles belzebuth* for *Ateles*; from *Lagothrix lagotricha* for *Lagothrix*; from *Pongo pygmaeus* for *Pongo*. Data from *Cebus apella* and *C. capucinus* were averaged for *Cebus*, and data for *Trachypithecus cristatus* and *T. obscurus* were averaged for *Trachypithecus*. Data for *Symphalangus syndactlyus* and *Lagothrix* are from captive individuals.

Table 37. Gut sizes and relative gut sizes for 11 taxa.

Group	Taxon	Gut	Rel Gut	Ref	Notes
Platyrrhine	*Aotus*	539	2.52	1	Data from one female individual.
Platyrrhine	*Ateles*	2338	2.2	1	Sex not listed.
Platyrrhine	*Cebus*	1014.5	2.66	1	Data averaged from one female *C. capucinus* and three male *C. apella*.
Platyrrhine	*Lagothrix*	3248	2.78	1	Data averaged from from one captive female and one captive male.
Platyrrhine	*Saimiri sciureus*	359.2	2.17	2	Data averaged from one female and four males.
Cercopithecine	*Macaca fascicularis*	2394.5	3.54	1	Data averaged from one female and three males.
Cercopithecine	*Mandrillus sphinx*	4317.33	2.63	1	Data averaged from two females and one male.
Colobine	*Trachypithecus*	4320	3.72	1,2	Data averaged from one female *T. obscurus*, two male *T. obscurus*, and one female *T. cristatus*.
Lesser Ape	*Symphalangus syndactylus*	2725	2.06	1	Data from two captive males.
Ape	*Pan troglodytes*	7662	2.28	1	Data from one male.
Ape	*Pongo pygmaeus*	9176	2.39	2	Data from one female.

Gut = summed surface area of the stomach, small intestine, caecum, and colon (cm^2); Rel Gut = Relative gut size = square root of gut size divided by acetabular diameter. Rounding to two decimal places for these

values does not reflect the precision of the gut size estimates but result from averaging these data across multiple individuals. References: 1. Chivers and Hladik (1980); 2. Chivers personal communication (2016).

Altitude

Data on the maximum altitudes at which populations of each taxon have been observed were collected from the literature and are summarized in Table 38. Altitude values are estimates for the highest elevation above sea level occupied by these taxa.

Table 38. Maximum habitat altitude estimates for 20 taxa.

Taxon	Altitude	Ref	Notes
Aotus	3200	1	Genus-level estimate from the reference.
Ateles	1950	2,5	Estimate for *A. belzebuth* and *A. chamek* from the eastern slopes of the Andes mountains in Bolivia, Colombia, Ecuador, and Peru.
Cebus	2150	3	Genus-level estimate from the reference.
Lagothrix	2800	4	Estimate for a montane forest-dwelling population of *L. lagotricha* in Colombia.
Saimiri sciureus	1400	5	Estimate for a montane forest-dwelling population in Peru.
Cercopithecus mitis	2100	6	Estimate for a montane forest-dwelling population in Tanzania.
Chlorocebus cynosurus	1850	7	Estimate for a high-elevation population in the Democratic Republic of the Congo.
Macaca fascicularis	1470	8	Species-level estimate from museum specimen provenance.
Macaca mulatta	4500	8	Species-level estimate from museum specimen provenance.
Mandrillus sphinx	2000	9	Species-level estimate from the reference.
Papio	3300	10	Genus-level estimate from the reference.
Theropithecus gelada	4600	11-14	Species-level estimates from montane grasslands in Ethiopia.
Colobus guereza	3300	15	Species-level estimate from montane forests in Ethiopia.
Presbytis melalophos	2500	16	Species-level estimate from the reference.
Trachypithecus	3000	17	Genus-level estimate from montane forests in Bhutan.
Hylobates moloch	1750	18	Species-level estimate from montane forests in Indonesia.
Hylobates muelleri	1600	19	Species-level estimate from montane forests in Indonesia.
Symphalangus syndactylus	2300	20	Species-level estimate from montane forests in Indonesia.
Pan	1170	21	Estimate for *P. troglodytes verus* from a montane forest in Guinea.
Pongo	1300	22	Estimate for *P. pygmaeus* from forests in Malaysia.

Altitude = elevation in meters (m) above sea level.
References: 1. Defler and Bueno (2007); 2. Shanee (2009); 3. Dow and Poirier (1977), 4. Ramírez et al. (2013); 5. Shanee et al. (2013); 6. Marshall et al. (2005); 7. Sarmiento (2013); 8. Weinstein (2011); 9. Hongo et al. (2018); 10. Jolly (2013); 11. Yalden et al. (1977); 12. Yalden et al. (1996); 13. Iwamoto (1993); 14. Hunter (2001); 15. Dunbar and Dunbar (1974b); 16. Yu et al. (2011); 17. Choudhury (2008);

18. Nijman (2004); 19. Cheyne et al. (2016); 20. Yanuar (2009); 21. Koops et al. (2012); 22. Ancrenaz et al. (2004).

Results

Relationships between LTV, RLTV, and acetabular diameter

LTV has a significant positive relationship with logged acetabular diameter (Figure 25; $p < 0.001$, adjusted $r^2 = 0.88$, maximum likelihood lambda estimate = 0.102), and scales with negative allometry (slope = 2.16). This suggests that relative lower torso volume (RLTV), or the cubed root of lower torso volume divided by acetabular diameter, is greater in smaller anthropoids. Only three taxa have significantly large LTV for their body size (above the regression line and outside of the 95% confidence interval), and include *Cercopithecus mitis*, *Presbytis melalophos*, and *Theropithecus gelada*.

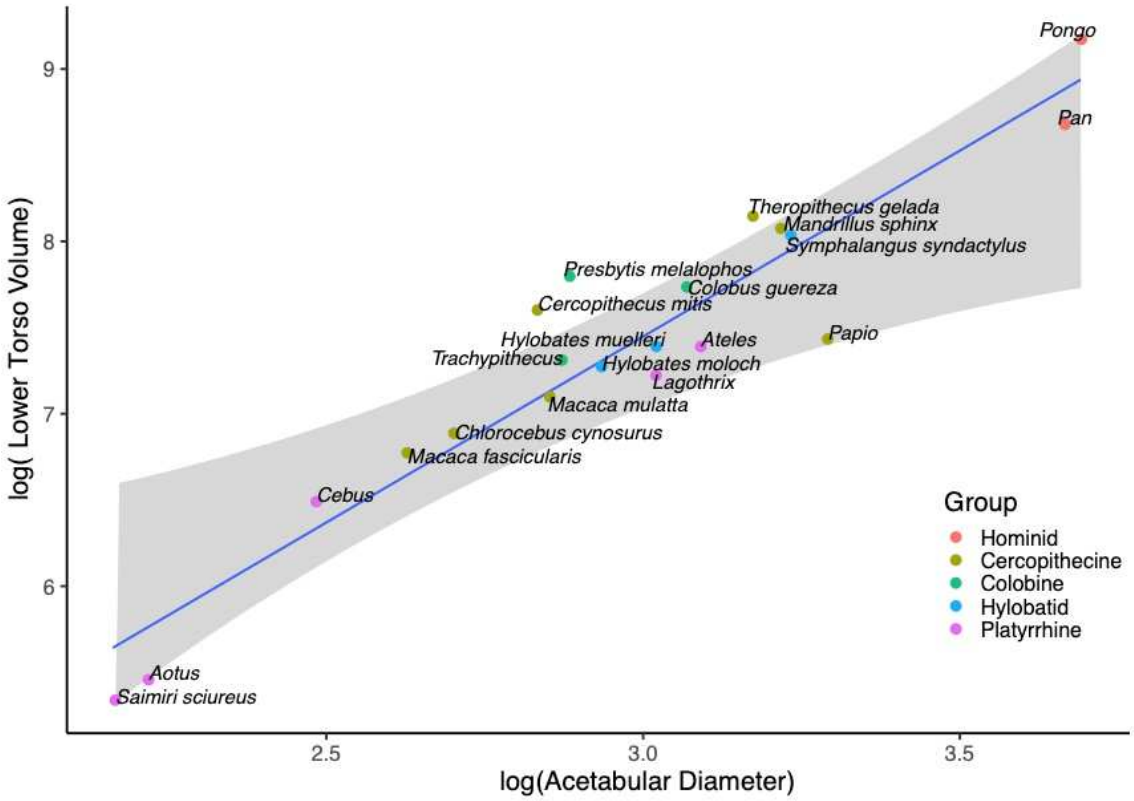

Figure 25. Relationship between logged acetabular diameter and logged lower torso volume in 20 taxa.

Phylogenetic signal in LTV and RLTV

There is strong phylogenetic signal in LTV for the taxa sampled in this chapter (K = 0.86, lambda = 1). Phylogenetic signal present for RLTV, but lower (K = 0.49, lambda = 0.00006), likely because of the influence of the variation in body size (and acetabular diameter) within clades.

Relationships between RLTV and the diet variables

There is a significant negative relationship between percent roots and tubers in diet and RLTV ($p = 0.036$, adjusted $r^2 = 0.18$, maximum likelihood lambda estimate = 0). In other words, as relative lower torso volume increases, percent roots and tubers in diet decreases (Figure 26). As only five taxa in the sample have a value above 0% for roots and tubers in their diets, this result is driven by the relationship between percent roots and tubers in *Papio*, which has a small RLTV but ~17% roots and tubers in diet. When *Papio* is excluded from the sample, there is no relationship between percent roots and tubers in diet and RLTV ($p = 0.72$). There is not a relationship between RLTV and any of the other diet variables.

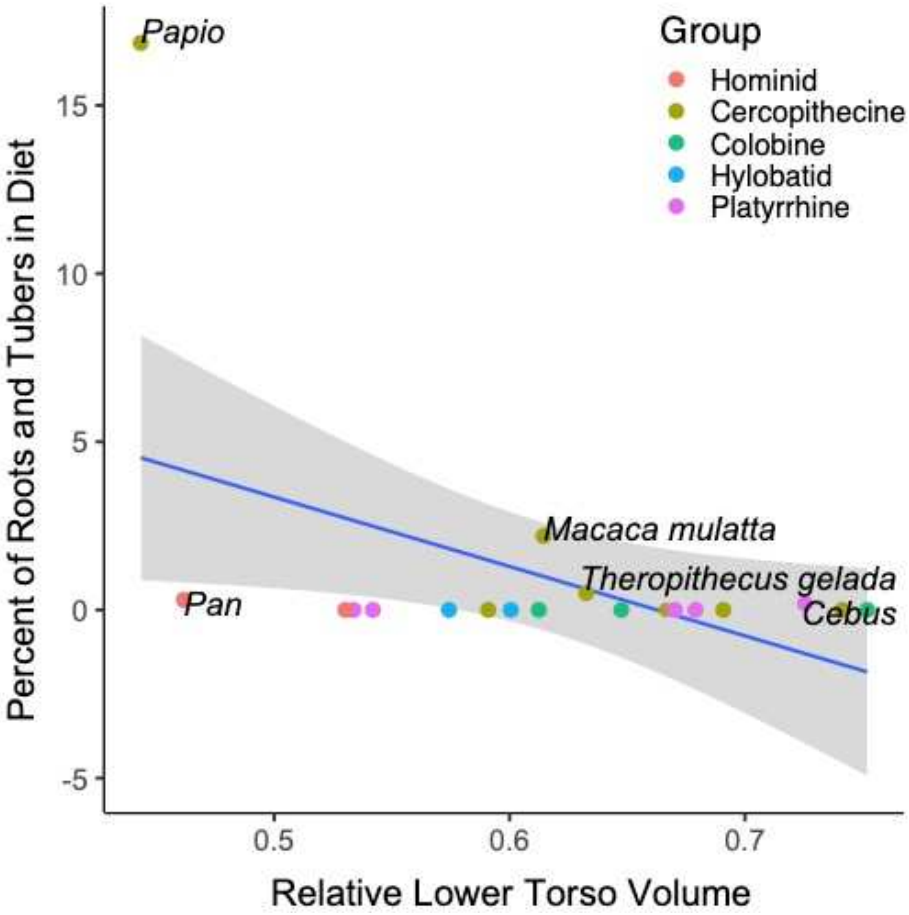

Figure 26. Relationship between relative lower torso volume and percent roots and tubers in diet for 20 taxa. Taxa with values above 0 for percentage of roots and tubers in diet are labeled.

Relationship between LTV, RLTV, and gut size

LTV has a significant positive relationship with gut size (Figure 27; $p < 0.001$, adjusted $r^2 = 0.89$, maximum likelihood lambda estimate = 0, slope = 1.12, intercept = -1.45). There is no relationship between RLTV and relative gut size (Figure 28; $p = 0.15$).

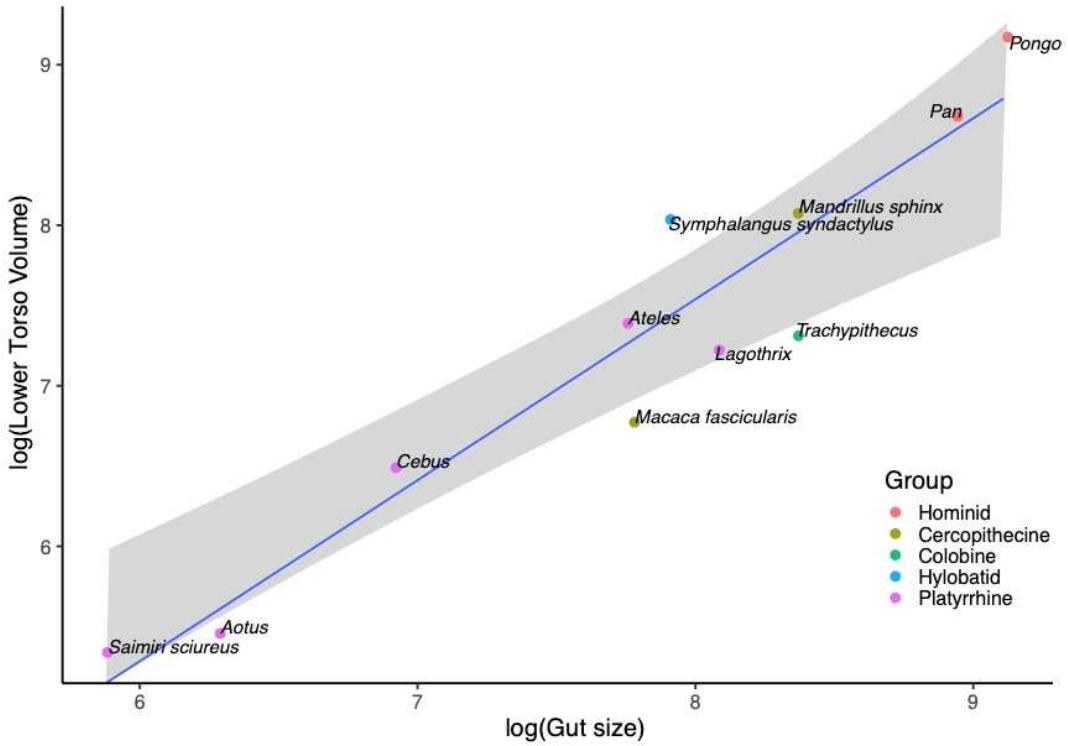

Figure 27. Relationship between logged gut size and logged lower torso volume in 11 taxa.

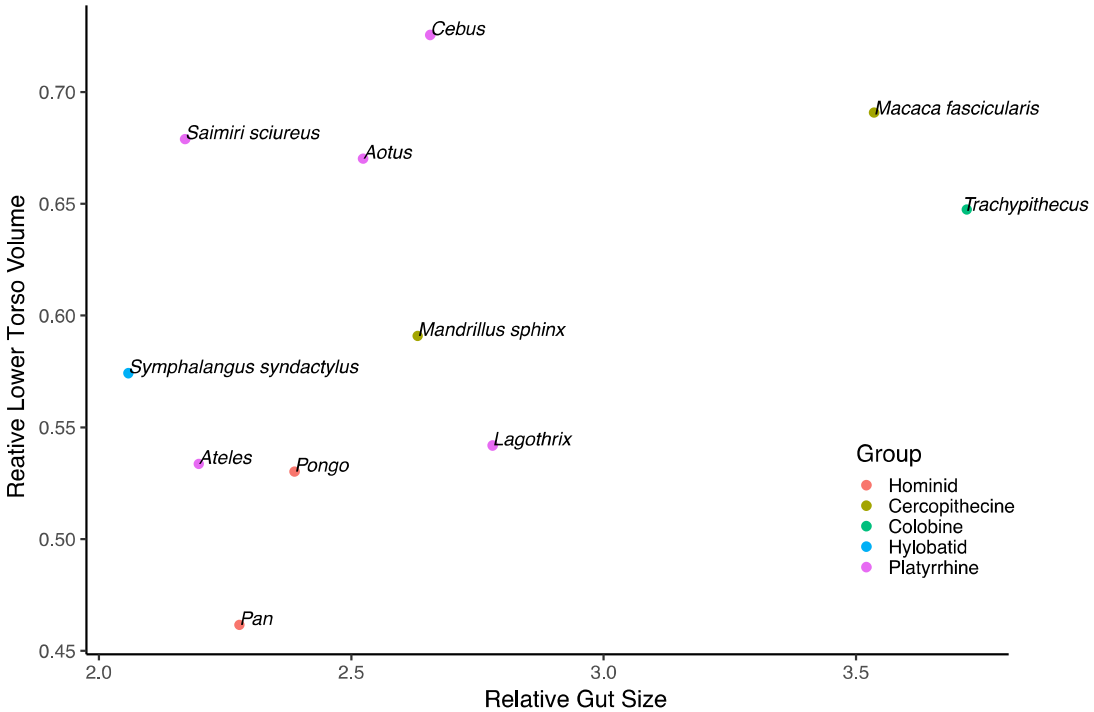

Figure 28. RLTV plotted against relative gut size for 11 taxa. There is no statistically significant relationship between these variables.

Relationship between RLTV and altitude

There is no relationship between RLTV and maximum habitat altitude (Figure 29; $p = 0.84$).

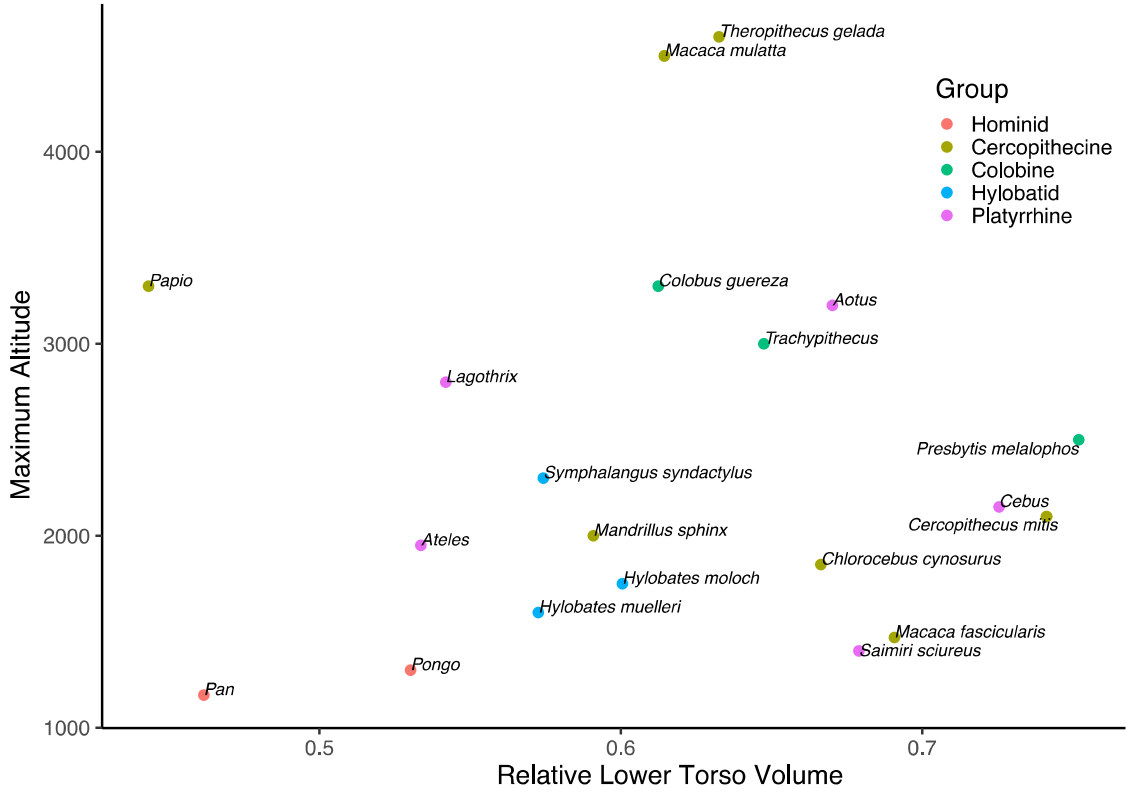

Figure 29. RLTV plotted against maximum habitat altitude for 20 taxa. There is no statistically significant relationship between these variables.

Results summary

Lower torso volume (LTV) increases with acetabular diameter and there is a strong phylogenetic signal in LTV. Relative lower torso volume (RLTV) is greater in smaller anthropoids. There is a relationship only between relative lower torso volume and percent roots tubers in diet, but this result should be viewed with caution. As relative lower torso volume does not demonstrate a relationship between green plants in diet, there is no support for H1. Taxa with relatively larger guts do not have greater relative

lower torso volumes, so there is no support for H2. There is no relationship between maximum habitat altitude and relative lower torso volume, so there is no support for H3.

Discussion

The analyses in this chapter suggest that lower torso volume (LTV) and relative lower torso volume (RLTV) are more closely related to body size and phylogeny than to diet. LTV increases with acetabular diameter, so larger anthropoids (e.g., hominoids, large cercopithecines) have absolutely larger LTV than smaller anthropoids (e.g., platyrrhines). Blomberg's K (K = 0.86) and Pagel's lambda (lambda = 1) values for LTV confirm that lower torso volume in this sample is strongly influenced by phylogeny. Additionally, LTV scales with negative allometry, so relative lower torso volume (RLTV) is greatest in smaller anthropoids.

The taxa that have a significantly large LTV (above the regression line) or a significantly small LTV (below the regression line) for their body size do not consistently relate to differences in diet. The PGLS regression of LTV against acetabular diameter indicates that *Presbytis melalophos*, *Cercopithecus mitis*, and *Theropithecus gelada* have the largest lower torso volumes for their body sizes (Figure 25). *Theropithecus gelada* and *P. melalophos* primarily rely on green plants, with green plants comprising >90% of the diet in the former taxa and ~35% of the diet in the latter. This result is consistent with the expectation that primarily folivorous taxa have more voluminous lower torsos. However, *Cercopithecus mitis* feeds predominantly on fruit and has the largest percent of prey in its diet of all the taxa in the sample (~17% prey). Similarly, *Papio* individuals seem to have the smallest LTV for their size, although the genus average for green plants in diet is the same as that for *P. melalophos* (~35%).

Evidence that lower torso volume is not related to diet is further confirmed by analyses that test for relationships between the diet variables and RLTV. There is a significant negative relationship ($p = 0.036$) between percent roots and tubers in diet and RLTV (Figure 26). However, this result should be viewed with skepticism, as only four taxa in the sample have a value above 0% for roots and tubers in their diet. Furthermore, this result is certainly driven by *Papio* individuals, which have some of the smallest RLTV values but the highest value for percent roots and tubers in diet among the taxa in the sample (genus average = ~17%). There are no other statistically significant relationships between RLTV and the diet variables.

There is also no relationship between relative lower torso volume and relative gut size. Absolute gut size is larger in taxa that have absolutely larger lower torso volumes (Figure 27), which is expected because both of these variables scale positively with body size. However, RLTV is not related to relative gut size ($p = 0.15$, Figure 28), as the species with the largest RLTV values have either relatively small guts (*Aotus*, *Saimiri*, *Cebus*) or have relatively large guts (*Trachypithecus*, *Macaca fascicularis*). Lower torso volume therefore does not show a relationship with gut size after adjusting these measurements in relation to acetabular diameter.

This result likely reflects the disconnect between minimum lower torso volume—the volume of the lower torso that is delineated by the skeleton, like those computed in this chapter—and actual lower torso volume, which includes the gut and other soft tissues that protrude beyond the bounds of the ribcage and pelvis. Relative lower torso volume as it can be estimated from the skeleton alone is not an accurate indicator of relative gut size, but it is possible that *in vivo* measurements of the abdomen (e.g., circumference)

would better capture variation in relative gut size. It is also possible that collecting a ratio of abdominal protrusion relative to body length from photographs of wild primates, like the belly scores that are used to quantify prey consumption in carnivore research (e.g., Potgieter and Davies-Mostert, 2012), could provide a measure that is related to relative gut size and/or diet.

Lastly, there is no relationship between relative lower torso volume and maximum habitat altitude (Figure 29). The species that have been observed at the highest altitudes, *Theropithecus gelada* and *Macaca mulatta*, do not have high values for RLTV, while species that occupy habitats at lower altitudes exhibit a wide range of RLTV values. The overlap in altitude ranges among the taxa included in this sample could be driving this pattern. Therefore, comparing lower torso volume in a larger sample of primates that occupy exclusively high altitudes versus exclusively lowland species may yield a different result. It is also possible that the inclusion of information about the respiratory apparatus (via the inclusion of upper torso volume housed between ribs 1 and 5) would demonstrate a relationship with maximum habitat altitude, but testing hypotheses about this region of the torso is not the focus of this dissertation.

Limitations

The results in this chapter corroborate those of Chapters 2 and 3, suggesting that the torso is not a reliable indicator of differences in diet among anthropoids. However, unlike the previous two chapters, sex specification is not available for all of the individuals in the 3D torso sample. Averages for *S. syndactylus* and *H. moloch* include values for both sexes, and this is probably also the case for other taxa (e.g., *M. sphinx*, *Pongo*). Furthermore, I also averaged gut sizes from males and females to obtain species

averages to regress against the lower torso volume data. The analyses presented in the previous chapters demonstrate that there are sex differences in how torso form varies relative to ecological variables (diet, locomotion) and body size. So, the lack of information about sex in this chapter could be obscuring interesting differences in how lower torso volume differs between males and females of the same species. A larger sample of lower torso volumes from individuals with certain sex identification would resolve this issue.

Additionally, most of the specimens from museum collections that provided data for Chapters 2 and 3 also included information on recovery site or regional provenance. This allowed me to match diet and locomotion data to the same country/region that the specimens were collected for most species. Unfortunately, the sample of torsos that provide data for this chapter does not include information about the individual's countries or regions of origin. Moreover, as described above, genus-level averages for diet data were attributed to individuals without a species identification. Although I do not think this is likely, it is possible that the diet and altitude data are "mismatched" for this sample and that data from other sites/populations for these taxa would show different relationships with lower torso volume.

Lastly, it could be possible that slight differences in orientation of the pelvis and vertebral column between individuals can introduce error into the volume measurements, despite the care taken to exclude specimens that were positioned in such a way that prevented a reliable volume calculation. Methods for calculating error estimates for lower torso volume, as well as interobserver errors in orienting the skeletons and calculating the volumes, will be explored as this research continues.

Conclusions

This chapter presents lower torso volumes for 44 individuals representing 20 taxa. I found that lower torso volume scales with negative allometry, and smaller anthropoids (i.e., platyrrhines) have relatively large lower torso volumes for their body sizes. Variation in lower torso volume across the sample is closely related to body size and phylogeny. There is no consistent relationship between diet and relative lower torso volume, which is a result best exemplified by the comparison between *Presbytis melalophos* (largest RLTV) and *Papio* (smallest RLTV), which both have ~35% of green plants in their diet. There is also no relationship between relative gut size and relative lower torso volume, nor maximum habitat altitude and relative lower torso volume.

The analyses presented in this chapter do not provide support for the hypothesis that lower torso volume is related to differences in diet. As the gut protrudes past the bounds of the skeleton, variation in gut size independent of body size cannot be captured by lower torso volume calculated from the skeleton alone. These results do not support the practice of using estimated differences in torso volume to infer shifts in gut size and diet among fossil hominin species.

Chapter 5: Conclusions and significance

Summary

This dissertation tested whether extant anthropoid torso shape shows any consistent relationship with diet after considering the effects of phylogeny, body size, and locomotion. In Chapter 2, I first used multiple PGLS regressions with data from >40 species to test specific hypotheses put forth in the paleoanthropological literature about how five dimensions of the torso should relate to diet and gut size. I then considered several parts of the torso together and used multiple, multivariate PGLS regressions with data from 31 species to test whether variation in four of these features is best explained by variation in body size, diet, or locomotion. Lastly, I used discriminant function analyses to test whether four torso variables better discriminate among locomotor or dietary groups. These analyses utilized ratios of the torso measurements relative to either acetabular diameter or the geometric mean in order to test if there is a pattern in how torso 'shape' varies relative to diet, while accounting for phylogenetic relatedness and body size. Taken together, the results of these three analyses indicate that variation in anthropoid torso shape can be best explained by differences in body size and locomotion, not differences in gut size, percent feeding time on specific food items, nor differences in dietary group.

In the following chapter, I tested whether comparisons between pairs of similarly-sized, closely-related primates would reveal a link between diet and torso shape. I found that of 11 comparisons, only four support the hypothesis that more folivorous species are broader in torso dimensions than less folivorous species. The other comparisons yield results where: more folivorous primates are narrower in torso dimensions than less

folivorous primates, species with different diets show no differences in torso dimensions, or species with similar diets show significant differences in torso dimensions. These results indicate that differences in torso dimensions cannot be consistently used to infer differences in diet among pairs of anthropoid species.

In Chapter 4, I tested whether differences in lower torso volume can be linked to differences in diet, body size, and maximum habitat altitude in 20 taxa, and with gut size in 11 taxa. I found that lower torso volume is closely correlated with body size and phylogenetic history, and there is no reliable link between this variable and diet, gut size, or altitude. These results suggest that estimates of lower torso volume generated from the bony skeleton do not provide accurate information about diet-related differences in gut size.

Relevance for paleoanthropology

The results of this dissertation indicate that differences in torso shape cannot be used to reliably infer differences in diet or gut size among extant anthropoid species. There is no consistent relationship between diet and ribcage breadth, bi-iliac breadth, upper ilium width, iliac flare, lumbar vertebral column length, or lower torso volume beyond the broad relationship these variables have because of their connections to body size. More folivorous species are not always broader in torso dimensions than less folivorous species, and species that belong to different dietary groups show significant overlap in torso dimensions. Locomotion and body size are better predictors of torso shape than diet.

We can use these results to establish a framework that we can apply to the hominin fossil record. The results of this dissertation suggest that differences in torso

form between *Australopithecus* and *Homo* do not reflect a grade shift in diet. Rather, these differences are more likely due to differences in locomotor capabilities, body size, and/or phylogenetic history, or could even be due to issues with fossil reconstruction. Although the broad *Australopithecus* torso and narrower *Homo* torso have become iconic in paleoanthropology, recent research and evidence from recently recovered skeletons indicates that the *Australopithecus* ribcage may not have been funnel-shaped (Latimer et al., 2016), and the *Homo* pelvis may be wider than previously thought (Simpson et al., 2008; Fornai and Haeusler, 2017). These findings add to evidence from recent analyses of endocranial volume (Du et al., 2018), tooth crown area (Gómez-Robles et al., 2017), and stable carbon isotopes (Sponheimer et al., 2013), which all cast doubt on the hypothesis that there was any distinct transition in diet between these hominin genera (see also Kimbel and Villmoare, 2016).

The presumed relationship between diet and hominin torso form (Aiello and Wheeler, 1995) has influenced descriptions of recently recovered partial hominin torso skeletons, including those of *Ardipithecus ramidus* (Lovejoy et al., 2009), *Australopithecus sediba* (Schmid et al., 2013), and *Homo naledi* (Williams et al., 2017), and has contributed to new interpretations of well-studied hominin skeletal material, such as the Neanderthal torso (Ben-Dor et al., 2016). This hypothesis has also been influential oustide of the primary literature, and is referenced in sections of biological anthropology textbooks that explain differences in hominin postcranial skeletons (e.g., Stanford et al., 2011, pg. 322), as well as museum exhibits that summarize milestones in human evolutionary history, such as the Human Origins Hall at the Smithsonian National Museum of Natural History.

The findings of this dissertation challenge this conventional wisdom, which has been influential beyond the paleoanthropological literature and has had an impact on the teaching and understanding of hominin skeletal evolution in the classroom and beyond. The results of this dissertation are important because they provide the first tests of whether there is a dietary signal in torsos of a large sample of anthropoid primates. There is currently no comparative basis for suggesting that differences in the torso form of fossil primates reflect dietary differences, and researchers should take caution when attempting to infer diet from the postcranial skeleton of hominins.

Future directions

This thesis is focused on testing the relationship between diet and the anthropoid torso, given the availability of anthropoid torso skeletons in the museum collections accessible to the author, and the close phylogenetic relationship of extant anthropoids to fossil hominins. Performing tests of whether diet relates to the torso in the lemurs and indriids that engage in bipedal hopping is a natural next step for this research, as this analysis would provide a particularly relevant comparison to bipedal hominins. Furthermore, given the proposed relationship between diet in the torso in extant non-primate mammals (e.g., Elftman, 1929), studies that quantitatively test these hypotheses would be a useful comparative reference to the analyses performed here.

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Appendices

Appendix A

With all the data I collected on torsos, and the data compiled from the literature on diet and locomotion, I initially conducted an exploratory series of sex-specific phylogenetic least squares regressions (PGLS). This exploratory analysis identified relationships between torso variables and measures of diet, locomotion, and body size. Sex-specific body mass averages from Smith and Jungers (1997) were used to control for overall size by including logged body mass (log.BM) as a covariate in each model. Logged bi-iliac breadth, logged upper ilium width, logged iliac flare, and logged lumbar vertebral column length were included as response variables in a series of regressions. Ribcage breadth at rib level 7 was excluded because of the small sample size for this measurement.

Males and females are separated in the analyses because not all of the torso variables are available for both of the sexes for all of the taxa (e.g., data for *Cebus capucinus* and *Pithecia irrorata* are only available for males, and lumbar vertebral column length is only available for *Hylobates agilis* and *Cacajao calvus* females). Data on diet and torso form are available for males for 48 species and for females for 46 species (with lumbar vertebral column length only for 44 species of females). Each torso variable was first included as a response variable in a regression with body mass as the only predictor variable, and then in models with body mass and diet variables included as predictors.

So, for example, logged bi-iliac breadth (abbreviated log.BIB) was tested as a function of log.BM (log.BIB ~ log.BM), as a function of log.BM plus each diet variable

alone (e.g., log.BIB ~ log.BM + Green Plants), and as a function of log.BM plus the diet variables included in a stepwise fashion (e.g., log.BIB ~ log.BM + Green Plants + Fruit, etc.). Model fit for each torso measurement were compared using the Akaike Information Criterion (AIC), with the effect of body mass and diet determined by the significance of p-value for each covariate.

Data on torso form, diet, *and* locomotion are only available for males for 34 species and for females for 33 species. If any diet variables had an effect on the regressions with the larger sample sizes, or if a model with the lowest AIC included a diet covariate (or a combination of diet variables), only these diet variables were included as covariates in the models that included locomotion data (e.g., log.BIB ~ Green Plants + Quadrupedalism). Species for which locomotion are available are indicated in Table 2 and listed in Table 6.

Results

For the expanded sample (48 species of males, 46 or 44 species of females), a total of 104 PGLS regressions were conducted (13 regressions per torso measurement, 52 regressions per sex). For females, most models were significant ($p < 0.05$), and this appears to be driven by the inclusion of body mass as a covariate, which has a significant effect ($p < 0.05$) in all of the models except for ten models, two of which have log.UIW as a response variable and eight of which have log.Lumbar as a covariate. The models with the lowest AIC values for each torso measurement are those that include at least one diet variable. However, diet variables only have a significant effect ($p < 0.05$) in seven models. Percentage of flowers and gums in diet has a small, positive effect in models where logged flare, upper ilium width, and bi-iliac breadth are response variables. Fruits

and the dietary quality index have small, negative effects in models where logged lumbar vertebral column length is the response variable. A list of the best-fitting models for each torso measurement for both sexes, as well as models with a significant diet effect are listed in Table A1.

For males, all models are also significant ($p < 0.05$) and this is again driven by the inclusion of log.BM as a covariate, which has a significant effect ($p < 0.05$) in all 52 models. The best-fitting models for log.Lumbar and log.UIW are the simplest, i.e., each measurement ~ log.BM. For log.Flare and log.BIB, the best-fitting models are models which include only one diet variable (Table A1). Diet variables have a significant effect ($p < 0.05$) in five models. Percentage of seeds in diet has a small, negative effect on logged flare, and percentage of green plants has a small, positive effect on logged flare. Percentage of green plants in diet has a small, positive effect on logged bi-iliac breadth, while percentage of fruits and the dietary quality index have small, negative effects on logged bi-iliac breadth.

Table A1. Best-fitting models, and models with a significant diet effect for the expanded species sample.

Torso var	N	Model	λ	Slopes	Rsq	Best-fitting ?	Effect of diet coefficients
Females							
Flare	46	log.flare ~ log.BM + Flowers/Gums	1	log.BM = 0.41; Flowers/Gums = 0.01	0.47	Yes	Flowers/Gums (p = 0.047)
Flare	46	log.flare ~ log.BM + Green Plants + Fruits + Flowers/Gums + Prey + Seeds	1	log.BM = 0.47; Green Plants = 0.0009; Fruits = 0.003; Flowers/Gums = 0.02; Prey = -0.002; Seeds = -0.003	0.51	No	Green Plants (p = 0.78), Fruits (p = 0.34), Flowers/Gums (p = 0.007), Prey (p = 0.62), Seeds (p = 0.37)
UIW	46	log.UIW ~ log.BM + Flowers/Gums	0.93	log.BM = 0.49; Flowers/Gum = 0.004	0.86	Yes	Flowers/Gums (p = 0.12)

UIW	46	log.UIW ~ log.BM + Green Plants + Fruits + Flowers/Gums + Prey + Seeds	0.95	log.BM = 0.48; Green Plants = 0.0001; Fruits = 0.0005; Flowers/Gums = 0.009; Prey = -0.003; Seeds = -0.0008	0.87	No	Green Plants (p = 0.48), Fruits (p = 0.76), Flowers/Gums (p = 0.015), Prey (p = 0.22), Seeds (p = 0.71)
BIB	46	log.BIB ~ log.BM + Green Plants + Fruits + Flowers/Gums + Prey + Seeds	0.94	log.BM = 0.45; Green Plants = 0.002; Fruits = 0.001; Flowers/Gums = 0.012; Prey = -0.004; Seeds = 0.0006	0.89	Yes	Green Plants (p = 0.22), Fruits (p = 0.42), Flowers/Gums, (p = 0.0006), Prey (p = 0.08), Seeds (p = 0.76)
Lumbar	44	log.Lumbar ~ log.BM + Green Plants + Fruits + Flowers/Gums	1	log.BM = 0.05; Green Plants = -0.0002; Fruits = -0.003; Flowers/Gums = -0.008	0.23	Yes	Green Plants (p = 0.89), Fruits (p = 0.026), Flowers/Gums (p = 0.08)
Lumbar	44	log.Lumbar ~ log.BM + Fruits	0.995	log.BM = 0.07; Fruits = -0.001	0.19	No	Fruits (p = 0.027)
Lumbar	44	log.Lumbar ~ log.BM + DQ	1	log.BM = 0.07; DQ = -0.001	0.17	No	DQ (p = 0.04)
Males							
Flare	48	log.Flare ~ log.BM + Seeds	1	log.BM = 0.39 Seeds = -0.005	0.49	Yes	Seeds (p = 0.03)
Flare	48	log.Flare ~ log.BM + Green Plants + Fruits	1	log.BM = 0.36; Green Plants = 0.004; Fruits = 0.002	0.47	No	Green Plants (p = 0.04), Fruits (p = 0.15)
UIW	48	log.UIW ~ log.BM	0.7	log.BM = 0.48	0.89	Yes	NA
BIB	48	log.BIB ~ log.BM + Green Plants	1	log.BM = 0.41; Green Plants = 0.002	0.88	Yes	Green Plants (p = 0.005)
BIB	48	log.BIB ~ log.BM + Fruits	1	log.BM = 0.41; Fruits = -0.001	0.88	No	Fruits (p = 0.02)
BIB	48	log.BIB ~ log.BM + DQ	0.98	log.BM = 0.41; DQ = -0.0009	0.88	No	DQ (p = 0.035)
Lumbar	48	log.Lumbar ~ log.BM	0.89	log.BM = 0.11	0.17	Yes	NA

Torso var = Torso variables: Lumbar = lumbar vertebral column length, Flare = ratio between false pelvis length and iliac fossa width, UIW = upper ilium width, BIB = bi-iliac breadth
N = Total number of species included in the PGLS regression
Model = Function included in the PGLS regression; λ = Pagel's lambda estimate of phylogenetic signal in the residuals (Pagel, 1999); Slope = slope of the model, indicating the direction of the interaction of the relationship between the predictor variables and the response variables; Rsq = adjusted R^2 value; Best-fitting? = Indicates whether the model has the lowest AIC value among the models for each torso variable; Effect of diet coefficients = Indicates p-values of diet covariates. $p < 0.05$ indicates the diet variables have a significant effect on the model after controlling for body size and phylogenetic relatedness.

Diet variables that appear to correlate to each torso measurement were further explored in the subsample that includes locomotion data to see if including locomotion variables in the repressions improve model fit. Each logged torso variable was first included as a response in regressions against the locomotor variables, (e.g., log.Flare ~ log.BM + Quadrupedalism), and then in a series of regressions as a function of the significant diet variable and the locomotor variables (e.g., log.Flare ~ log.BM + Quadrupedalism + Flowers/Gums; log.Flare ~ log.BM + Quadrupedalism + Climbing + Flowers/Gums). For males, since log.lumbar and log.UIW showed no relationship with diet in the expanded sample, these variables were included as responses in regressions with only the locomotion variables as predictors, to see if including locomotion data yielded an AIC value lower than log.lumbar ~ log.BM and log.UIW ~ log.BM.

A total of 260 PGLS regressions were conducted: 86 for 33 species of female individuals, 39 that included lumbar vertebral column length as a response variable for 31 species of females, and 135 regressions for 34 species of male individuals. The best-fitting models (lowest AIC value) for each torso measurement for both sexes are listed in Table A2.

For females, all models including pelvic measurements as response variables were significant ($p < 0.05$), likely because of the inclusion of log.BM as a covariate, which has a significant effect ($p < 0.05$) in all 86 models. The best-fitting models that explored the relationship between each logged pelvis measurement, flowers/gums, and locomotion data are ones that include 5 out of 6, or all 6 (in the case of flare) locomotor variables and percentage flowers/gums. In these best-fitting models, even though body size and locomotion have significant effects on the model ($p < 0.05$), percentage flowers/gums in

diet still has small, positive, but statistically significant effects ($p < 0.05$). None of the models including logged lumbar vertebral column length as a response variable are significant.

For males, all models are significant ($p < 0.05$). For all torso measurements, except measures of iliac flare, the best-fitting models are those that include body size and locomotion data, *only*. In other words, most diet variables no longer have a relationship with the logged torso measurements when controlling for locomotion. The best-fitting model where log.Flare is a response, however, is log.Flare ~ log.BM + Leap + Seeds, and percentage of seeds in diet has a small, negative but statistically effect (slope = -0.008; $p = 0.01$).

Table A2. Best-fitting models for each torso measurement in the locomotion subsample, according to the diet variable of interest (

Torso var	Diet var of interest	N	Model	λ	Slopes	Rsq	Effect of coefficients	Still a diet effect ?	Loco effect ?
Females									
Flare	Flowers /Gums	33	log.Flare ~ log.BM + Quad + Climb + Susp + Leap + Biped + Bridg + Flowers/ Gums	0	log.BM = 0.6; Quad = 0.02; Climb = 0.03; Susp = 0.03; Leap = 0.02; Biped = 0.07; Bridg = 0.05; Flowers/ Gums = 0.02	0.94	log.BM ($p < 0.001$), Quad ($p = 0.17$), Climb ($p = 0.05$), Susp ($p = 0.06$), Leap ($p = 0.21$), Biped ($p = 0.007$), Bridg ($p = 0.01$), Flowers/ Gums ($p = 0.025$)	Yes	Yes
UIW	Flowers /Gums	33	log.UIW ~ log.BM + Quad + Climb + Susp + Leap + Biped + Flowers/ Gums	0	log.BM = 0.55; Quad = 0.02; Climb = 0.02; Susp = 0.02; Leap = 0.02; Biped	0.98	log.BM ($p < 0.001$), Quad ($p < 0.001$), Climb ($p < 0.001$), Susp ($p < 0.001$), Leap ($p =$	Yes	Yes

					= 0.04; Flowers/ Gums = 0.009		0.001), Biped (p < 0.001), Flowers/ Gums (p = 0.043)		
BIB	Flowers /Gums	33	log.BIB ~ log.BM + Quad + Climb + Susp + Leap + Biped + Flowers/ Gums	0	log.BM = 0.51; Quad = 0.008; Climb = 0.01; Susp = 0.01; Leap = 0.007; Biped = 0.02; Flowers/ Gums = 0.008	0.98	log.BM (p < 0.001), Quad (p = 0.04), Climb (p = 0.02), Susp (p = 0.01), Leap (p = 0.07), Biped (p = 0.01), Flowers/ Gums (p = 0.046)	Yes	Yes
Lumb	Fruits	31	No model is significant	-	-	-	-	-	-
Lumb	DQ	31	No model is significant	-	-	-	-	-	-
Males									
Flare	Seeds	34	log.Flare ~ log.BM + Leap + Seeds	0.96	log.BM = 0.45; Leap = -0.005; Seeds = -0.008	0.66	log.BM (p < 0.001), Leap (p = 0.16), Seeds (p = 0.01)	Yes	No
Flare	Green Plants	34	log.Flare ~ log.BM	0.98	log.BM = 0.45	0.59	log.BM (p < 0.001)	No	No
UIW	NA	34	log.UIW ~ log.BM + Quad + Climb + Susp + Leap + Biped	0	log.BM = 0.49; Quad = 0.01; Climb = 0.02; Susp = 0.02; Leap = 0.01; Biped = 0.04	0.98	log.BM (p < 0.001), Quad (p = 0.004), Climb (p = 0.001), Susp (p = 0.004), Leap (p = 0.01), Biped (p < 0.001)	NA	Yes
BIB	Green Plants	34	log.BIB ~ log.BM + Quad + Climb + Susp + Leap + Biped + Green Plants	0	log.BM = 0.45; Quad = 0.006; Climb = 0.0088; Susp = 0.009; Leap = 0.005; Biped = 0.2; Green Plants = 0.001	0.98	log.BM (p < 0.001), Quad (p = 0.11), Climb (p = 0.04), Susp (p = 0.04), Leap (p = 0.2), Biped (p = 0.004), Green Plants (p = 0.1)	No	Yes
BIB	Fruits	34	log.BIB ~ log.BM +	0	log.BM = 0.46; Quad	0.98	log.BM (p < 0.001),	No	Yes

			Quad + Climb + Susp + Leap + Biped		= 0.007; Climb = 0.01; Susp = 0.01; Leap = 0.006; Biped = 0.03		Quad (p = 0.1), Climb (p = 0.02), Susp (p = 0.048), Leap (p = 0.14), Biped (p = 0.002)		
BIB	DQ	34	log.BIB ~ log.BM + Quad + Climb + Susp + Leap + Biped	0	log.BM = 0.46; Quad = 0.007; Climb = 0.01; Susp = 0.01; Leap = 0.006; Biped = 0.03	0.98	log.BM (p < 0.001), Quad (p = 0.1), Climb (p = 0.02), Susp (p = 0.048), Leap (p = 0.14), Biped (p = 0.002)	No	Yes
Lumb	NA	34	log.Lumbar ~ log.BM + Susp	0.79	log.BM = 0.08; Susp = -0.006	0.21	log.BM (p = 0.026), Susp (p = 0.024)	NA	Yes

Torso var = Torso variables: Lumb = lumbar vertebral column length, Flare = ratio between false pelvis length and iliac fossa width, UIW = upper ilium width, BIB = bi-iliac breadth
Diet var of interest = Diet variables that had showed a relationship with the torso variables in the expanded sample
N = Total number of species included in the PGLS regression
Model = Function included in the PGLS regression; Lamb= Pagel's lambda estimate of phylogenetic signal in the residuals (Pagel, 1999); Slope = slope of the model, indicating the direction of the interaction of the relationship between the predictor variables and the response variables; Rsq = adjusted R^2 value; Effect of diet coefficients = Indicates p-values of diet covariates. $p < 0.05$ indicates the diet variables have a significant effect on the model after controlling for body size and phylogenetic relatedness.

Nearly all PGLS regressions were statistically significant, and this was driven by the inclusion of body mass as a covariate, which had a significant effect in most models. In the first part of this analysis, when testing the relationship between lumbar vertebral column length and upper ilium width with diet variables in males, the best-fitting models were the ones that only included body mass (Table A1). In the second part of this analysis, the best-fitting models for all measurements (except iliac flare for males) were ones that included both body mass and locomotion data as covariates (Table A2).

For females, even though percentage of flowers and gums in diet seems to have a small, positive relationship with the logged pelvic variables even after including locomotion data, this result is still driven by body mass. In the second part of this

analysis, the best-fitting models in tests of how the female pelvis relates to body mass, diet, and locomotion all have a maximum likelihood Pagel's (1999) lambda estimate of 0 (Table A2). A linear regression (where lambda = 0) of percent flowers/gums in diet against both logged acetabular diameter and logged species-average body mass are statistically significant ($p < 0.001$ in both cases).

A body mass effect on percentage of flowers and gums in diet is consistent with the literature on primate diet. Primates over 5 kg are more likely to consume entire flowers whereas smaller primates are more likely to exploit nectar, and the combined consumption of both these resources increases with body size (Heymann, 2011). Furthermore, digesting flowers does not require a specialized gut, but digesting gums does. However, the taxa that feed on the greatest amounts of gums in the sample of primates included this chapter—*Saguinus*, *Papio*, and *Chlorocebus*—do not exhibit the gut specializations to digesting gums, which includes an expanded caecum (Nash, 1986). Therefore, it is not likely that percentage of flowers and gums in anthropoid diets is related to gut size-related differences in torso form.

The relationship between the torso and locomotion in the male subsample is particularly interesting. The only model that has a dietary effect is logged iliac flare as a function of logged body mass + percent leaping + percent seeds. However, the effect of seeds on the model is probably because taxa that engage in higher frequencies of leaping consume higher percentages of seeds (Figure A1, Table 3). For example, *Pithecia pithecia* exhibits low iliac flare, and a very high percentage of leaping in their locomotor repertoire, and also has a high percentage of seeds in their diets. Several species that leap

a moderate amount (in the cluster around 20% leaping), also feed frequently on seeds, including *Piliocolobus badius* and *Colobus polykomos*.

Second, the best-fitting model for logged lumbar vertebral column length, is this variable as a function of logged body mass and suspension (Table A2). This result reflects the reduction of lumbar vertebral column length in larger anthropoids that engage in fore-limb dominated locomotor behaviors, such as suspension (Benton, 1967; Schultz, 1961; Ward, 1993; Williams and Russo, 2015).

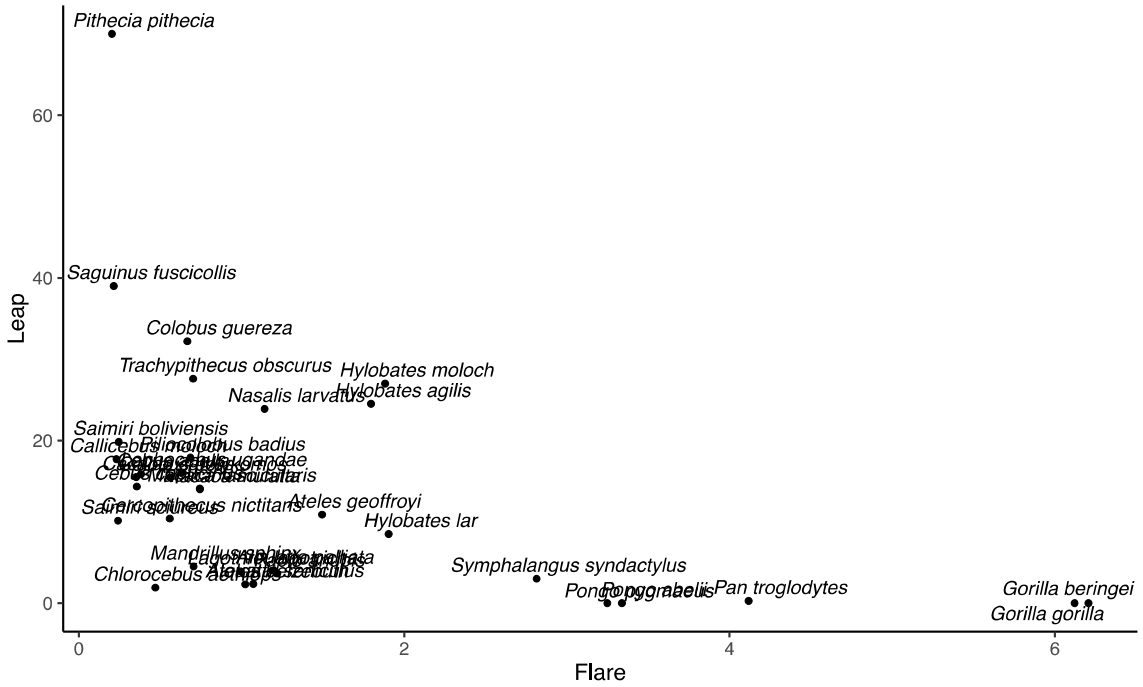

Figure A1. Relationship between leaping and iliac flare in males of 34 anthropoid species.

Appendix B

These analyses are similar to those presented in Analysis A of Chapter 2, in which I employ a targeted approach to test hypotheses from the literature about how the torso may be related to diet and gut size (Elftman, 1929; Schmid, 1991; Aiello and Wheeler, 1995; Lovejoy et al., 2009; Wrangham and Carmody, 2010). In those analyses, I divide ribcage breadth, lumbar vertebral column length, bi-iliac breadth, and upper ilium width by acetabular diameter. These ratios provide 'shape' metrics for each measurement, that I then use as response variables in PGLS regressions, where acetabular diameter and diet or gut size variables are the predictor variables. This approach provides a way of testing how differences in torso shape are related to differences in body size across the sample.

Here, I use raw linear measurement data (not divided by acetabular diameter) for these four torso variables to test the hypotheses put forth in the literature about how they relate to diet and raw data for gut size. The regressions where iliac flare is the measure of interest is not repeated here, as this measurement is a ratio. The hypotheses tested and the models that correspond to these hypotheses are listed in Table B1. The sample sizes and species used for the analyses presented here are the same as in Analysis A (Chapter 2).

Table B1. Hypotheses about how diet is related to the torso. These hypotheses are translated into functions for the PGLS regressions in this analysis.

Morphology	Link to diet	Ref	Functions for Appendix B analyses
Bi-iliac breadth	Related to gut volume and diet type. Wider bi-iliac breadths are associated with a folivorous, green plant-based diet (larger guts) while narrow bi-iliac breadths are associated with a higher-quality diet via cooking, eating more animal foods, prey, nuts and seeds, and underground storage organs (smaller guts).	1,2,3	log(Bi-iliac breadth) ~ log(Acetab) log(Bi-iliac breadth) ~ log(Acetab) + Green Plants log(Bi-iliac breadth) ~ log(Acetab) + Prey log(Bi-iliac breadth) ~ log(Acetab) + Seeds log(Bi-iliac breadth) ~ log(Acetab) + Roots/Tubers **Reduced sample size:** log(Bi-iliac breadth) ~ log(Acetab) log(Bi-iliac breadth) ~ log(Acetab) + log(Gut)

Ilium width	Related to gut volume and diet type. Wider ilia are associated with larger guts in frugivorous and folivorous anthropoids.	5	log(Ilium width) ~ log(Acetab) log(Ilium width) ~ log(Acetab) + Green.Plants log(Ilium width) ~ log(Acetab) + Fruits **Reduced sample size:** log(Ilium width) ~ log(Acetab) log(Ilium width) ~ log(Acetab) + log(Gut)
Ribcage breadth	Related to gut volume and diet type. Wider bi-iliac breadths are associated with a folivorous, green plant-based diet (larger guts) while narrow bi-iliac breadths are associated with a higher-quality diet via cooking, eating more animal foods, prey, nuts and seeds, and underground storage organs (smaller guts).	2,3	log(Ribcage breadth) ~ log(Acetab) log(Ribcage breadth) ~ log(Acetab) + Green.Plants log(Ribcage breadth) ~ log(Acetab) + Prey log(Ribcage breadth) ~ log(Acetab) + Seeds **Reduced sample size:** log(Ribcage breadth) ~ log(Acetab) log(Ribcage breadth) ~ log(Acetab) + log(Gut)
Lumbar vertebral column length	Related to gut volume and diet type. Longer lumbar spines are associated with larger guts in frugivorous and folivorous anthropoids.	5	log(Lumbar) ~ log(Acetab) log(Lumbar) ~ log(Acetab) + Green.Plants log(Lumbar) ~ log(Acetab) + Fruits **Reduced sample size:** log(Lumbar) ~ log(Acetab) log(Lumbar) ~ log(Acetab) + log(Gut)

Ref = References 1. Elftman (1929); 2. Aiello and Wheeler (1995); 3. Wrangham and Carmody (2010); 4. Schmid, 1991; 5. Lovejoy et al. (2009).

Model fit was compared using the Akaike Information Criterion (AIC). AIC is a model selection tool that quantifies goodness of fit, and a lower AIC value means the model is better-fitting, as a lower value indicates the model explains more of the variance after controlling for the number of terms in the model. After determining which model is best fitting, whether the predictors are having an effect on the response variables was determined from the predictor p-values. A significant p-value ($p < 0.05$) suggests that changes in the predictors, either diet variables or acetabular diameter, contribute to changes in the response. Insignificant predictors ($p > 0.05$) suggest that the predictors add net explanatory power to the models, though these variables themselves are not significant predictors of the response variables.

Table B2. Best-fitting models for largest sample sizes, where pelvic and lumbar measurements are response variables (analogous to Table 12).

Torso var	N	Model	Lambda	Slopes	Rsq	Effect of diet coefficients
Females						
UIW	45	log(adj.UIW) ~ log(Acetab) + Fruits	1	log(Acetab) = 1.19; Fruits = -0.001	0.89	Fruits (p = 0.02)
BIB	45	log(adj.BIB) ~ log(Acetab) + Green Plants	0.99	log(Acetab) = 1.1; Green Plants = 0.001	0.88	Green Plants (p = 0.019)
Lumbar	44	log(adj.Lumbar) ~ log(Acetab) + Fruits	1	log(Acetab) = 0.2; Fruits = -0.002	0.22	Fruits (p = 0.02)
Males						
UIW	45	log(adj.UIW) ~ log(Acetab) + Fruits	0.99	log(Acetab) = 1.25, Fruits = -0.001	0.91	Fruits (p = 0.06)
BIB	45	log(adj.BIB) ~ log(Acetab) + Roots/Tubers	0.84	log(Acetab) = 1.2; Roots/Tubers = 0.002	0.94	Roots/Tubers (p = 0.15)
Lumbar	44	log(adj.Lumbar) ~ log(Acetab)	0.91	log(Acetab) = 0.33	0.2	NA

Torso var = Torso variables: Lumbar = lumbar vertebral column length, Flare = ratio between false pelvis length and iliac fossa width, UIW = upper ilium width, BIB = bi-iliac breadth
N = Total number of species included in the PGLS regression; Model = Function included in the PGLS regression; Lambda = Pagel's lambda estimate of phylogenetic signal in the residuals (Pagel, 1999); Slopes = slopes of the model predictors, indicating the direction of the interaction of the relationship between the predictor variables and the response variables; Rsq = adjusted R^2 value; Effect of diet coefficients = Indicates p-values of diet covariates. $p < 0.05$ indicates the diet variables have a significant effect on the model after accounting for body size and phylogenetic relatedness

For the large sample sizes (45 or 44 species), the best-fitting models for both sexes are the same as those in Analysis A of Chapter 2 (Table B2). The only differences are 1) differences in the slopes of the predictor variables and 2) higher adjusted r-squared values for the models where pelvic measurements are the response variables, and lower r-squared values for the models where lumbar vertebral column length is the response variable. The p-values for the diet predictors are nearly identical between the two versions of this analysis, as well. These results confirm that 1) diet variables do not have an effect on the relationships between acetabular diameter and bi-iliac breadth, upper ilium width, or lumbar spine length in males and 2) the apparent diet effects on these

models in females are due to the relationship between fruit consumption and acetabular diameter in cercopithecoids, and the relationship between green plant consumption and acetabular diameter in hominoids (See Analysis A results in Chapter 2).

The relationship between the diet variables and logged ribcage breadth was tested in 21 species of males and 21 species of females (See Table 8 for the species included). All the models are significant, due to the inclusion of acetabular diameter as a covariate, which has a significant p-value in all models. The best-fitting model for females is ribcage breadth as a function of acetabular diameter. Diet variables do not have an effect on any of the models for females (green plants p-value = 0.42, prey p-value = 0.65; seeds p-value = 0.78). The best-fitting model for males is ribcage breadth as a function of acetabular diameter and green plants (adjusted r-squared = 0.91, $p < 0.001$, log(acetab) slope = 0.92, green plants slope = 0.0009) but green plants is not a significant predictor ($p = 0.17$). The other diet variables do not have an effect on the other models (prey p-value = 0.69; seeds p-value = 0.93).

The relationship between logged gut size and logged pelvic measurements was tested in 23 species for females and 23 species for males (See Table 9 for the species included). All models were significant for both sexes, but relative gut size has no effect on any of the models. The relationship between logged relative gut size and logged lumbar vertebral column length was tested in 22 species for females and 23 species for males (See Table 10 for the species included). These models were not significant for females, but both models were significant in males. Gut size, however, does not have an effect on the relationship between lumbar vertebral column length and acetabular diameter in males (gut p-value = 0.63).

The relationship between gut size and logged ribcage breadth was tested in 9 species for males and 9 species for females (See Table 11 for the species included). These models were significant, due to the inclusion of acetabular diameter as a covariate, which has a significant p-value in all models. Gut size does not have an effect in females ($p = -.33$) but gut size does have an effect in males ($p = 0.37$), but this is due to the relationship between gut size and acetabular diameter in males ($p = 0.0008$).

Altogether, these results are similar to those presented in Analysis A of Chapter 2. Diet variables and gut size do not show a relationship with torso variables on top of the relationship that these variables already share with acetabular diameter (and therefore, body size).

Appendix C

These analyses test whether torso variables can distinguish among diet categories in 44 species. For females, logged, size-adjusted upper ilium width has a strong negative loading on the first discriminant function and logged, size-adjusted bi-iliac breadth has a strong negative loading on the second discriminant function (Figure C1, Table C1). Together these first two discriminant functions account for ~95% of the among-group variation. There is substantial overlap of the diet categories (Figure C1); the generalists and folivores are almost fully subsumed by the range of frugivores, and the two granivores do not plot near each other. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is 51.2%.

Table C1. Variable loadings, from the DFA for torso variables of 44 species of female anthropoids.

	LD1	**LD2**	**LD3**	**LD4**
log.adj.BIB	0.98539	-11.107643	-15.306999	2.0013382
log.adj.Flare	3.9606	0.9798053	1.313527	-1.2342526
log.adj.UIW	-5.50294	4.5028219	10.622973	5.2390342
log.adj.Lumbar	3.89072	-1.613694	2.276391	-0.3739614

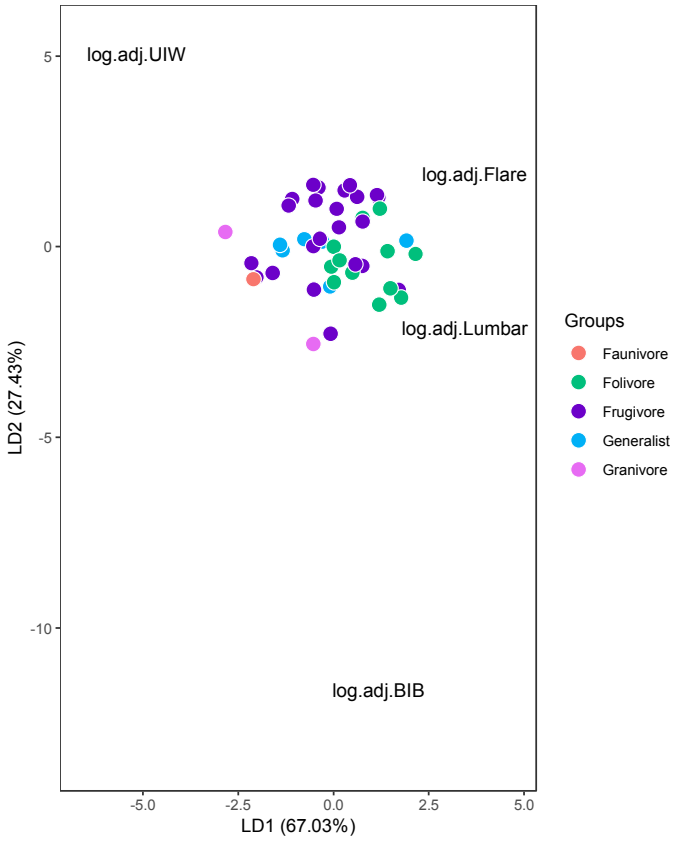

Figure C1. Scatter plot of the first two linear discriminants from the DFA for torso variables of 44 species of female anthropoids.

There are similar results for the males of these same 44 species. As in females, logged, size-adjusted upper ilium width has a strong negative loading on the first discriminant function. However, LD1 is more strongly influenced by logged, size-adjusted bi-iliac breadth, which has a high positive loading on this discriminant. Also, like females, logged, size-adjusted bi-iliac breadth has a strong loading on the second discriminant function (Figure C2, Table C2). Together these first two discriminant functions account for ~97% of the among-group variation. There is substantial overlap of the diet categories (Figure C2); the generalists and folivores are almost fully subsumed by the range of frugivores, and the two granivores do not plot near each other. Leave-

one-out cross-validation indicates that the predictive accuracy of this DFA is about 55.8%.

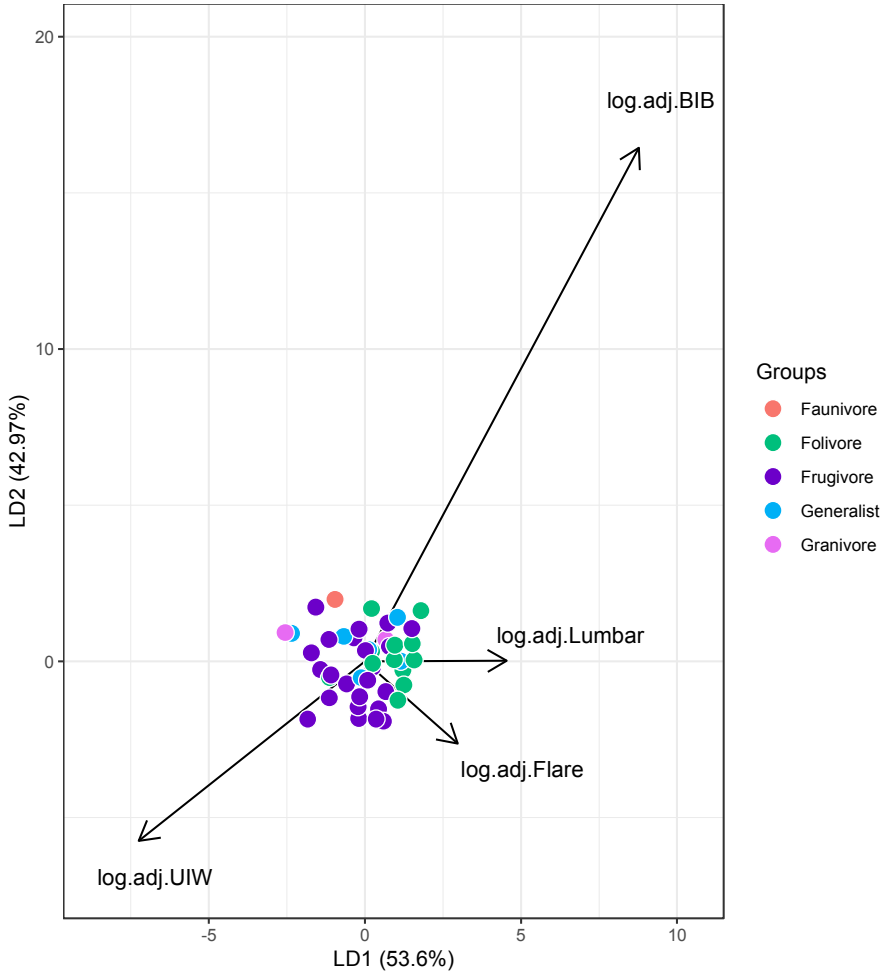

Figure C2. Scatter plot of the first two linear discriminants from the DFA for torso variables of 44 species of male anthropoids.

Table C2. Variable loadings, from the DFA for torso variables of 44 species of male anthropoids.

	LD1	LD2	LD3	LD4
log.adj.BIB	8.777329	16.4376444	-15.50175	15.07992
log.adj.Flare	2.975009	-2.6424592	2.672632	-1.009008
log.adj.UIW	-7.240465	-5.7525466	5.106031	-13.37541
log.adj.Lumbar	4.548476	0.01021438	2.925493	-1.982964

Appendix D

Four discriminant function analyses were conducted using logged, raw measurements. Two DFA test whether torso variables discriminate among diet categories, and two test whether torso variables discriminate among locomotor categories. These analyses differ from those included in Chapter 2, Analysis C, since those DFA relied on four logged torso variables that were divided by acetabular diameter.

The Wilk's lambda values for all four analyses were statistically significant ($p < 0.05$). Percent success of each DFA, resulting from the leave-one-out cross-validation tests, are summarized in Table D1. The DFA are illustrated in Figures D1 through D4. Tables D2 through D5 provide the variable loadings for these analyses.

Table D1. Success of each DFA as determined by leave-one-out cross validation.

	Sample Size	**% Success**
Females		
Diet Category ~ torso vars	31	53.3
Locomotor Category ~ torso vars	31	64.5
Males		
Diet Category ~ torso vars	31	46.7
Locomotor Category ~ torso vars	31	64.5

Torso vars = the five logged variables: bi-iliac breadth, upper ilium width, iliac flare, lumbar vertebral column length, and acetabular diameter.

For the diet DFA for females, logged upper ilium width has a strong positive loading on the first discriminant function, and a strong negative loading on the second discriminant function (Figure D1, Table D2). Logged acetabular diameter has a strong positive loading on the first discriminant function and logged bi-iliac breadth has a strong negative loading on the second discriminant function. Together these first two discriminant functions account for ~90% of the among-group variation. There is overlap of the diet categories (Figure D1), particularly between frugivores and folivores, and the

faunivore plots within the frugivore range. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 53% (Table D1).

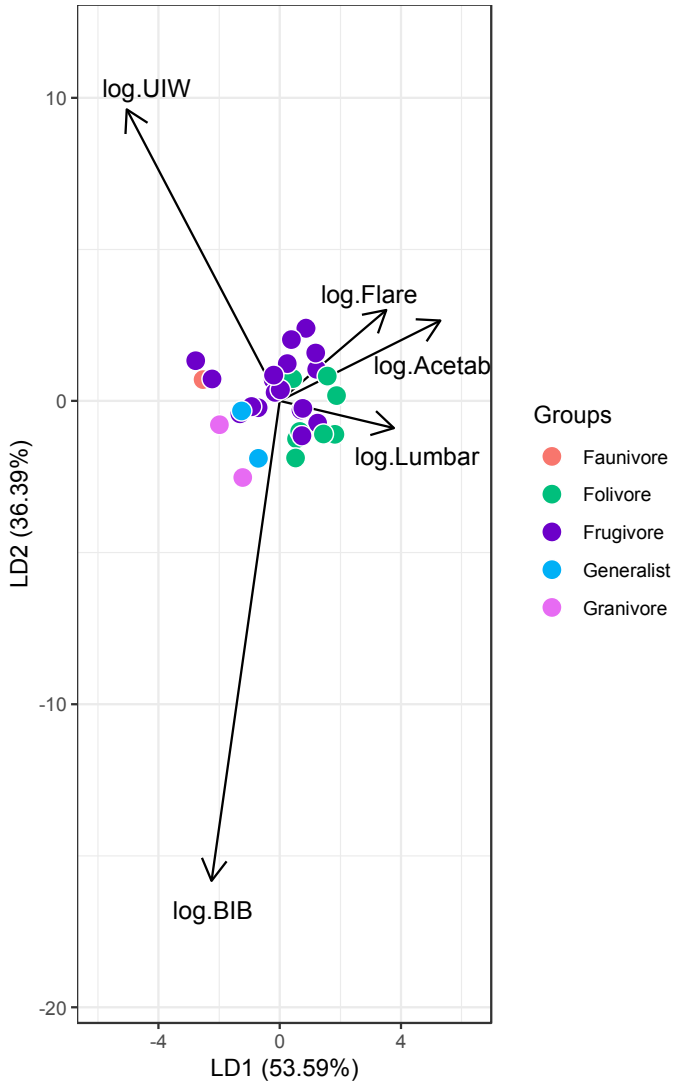

Figure D1. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among diet groups for 31 species of female anthropoids.

Table D2. Variable loadings, from the DFA testing how torso variables distinguish among diet groups for 31 species of female anthropoids.

	LD1	LD2	LD3	LD4
log.BIB	-2.255679	-15.82556	1.703495	13.5167412
log.Flare	3.513756	3.001418	-1.639164	0.1620983
log.UIW	-5.050306	9.6218953	-3.252115	-7.9636897
log.Lumbar	3.7675	-0.893436	-2.562032	-0.6444596
log.Acetab	5.298657	2.6505259	6.622277	-6.7932736

For the diet DFA for males, logged upper ilium width has a strong negative loading on the first discriminant function, while logged bi-iliac breadth has a strong positive loading on the first discriminant function (Figure D2, Table D3). Logged bi-iliac breadth also has a strong negative loading on the second discriminant function, and logged acetabular diameter has a strong positive loading on the second discriminant function. Together these first two discriminant functions account for ~86% of the among-group variation. As with females, there is overlap of the diet categories (Figure D2), and the frugivore range nearly encompasses all other diet groups. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 47% (Table D1).

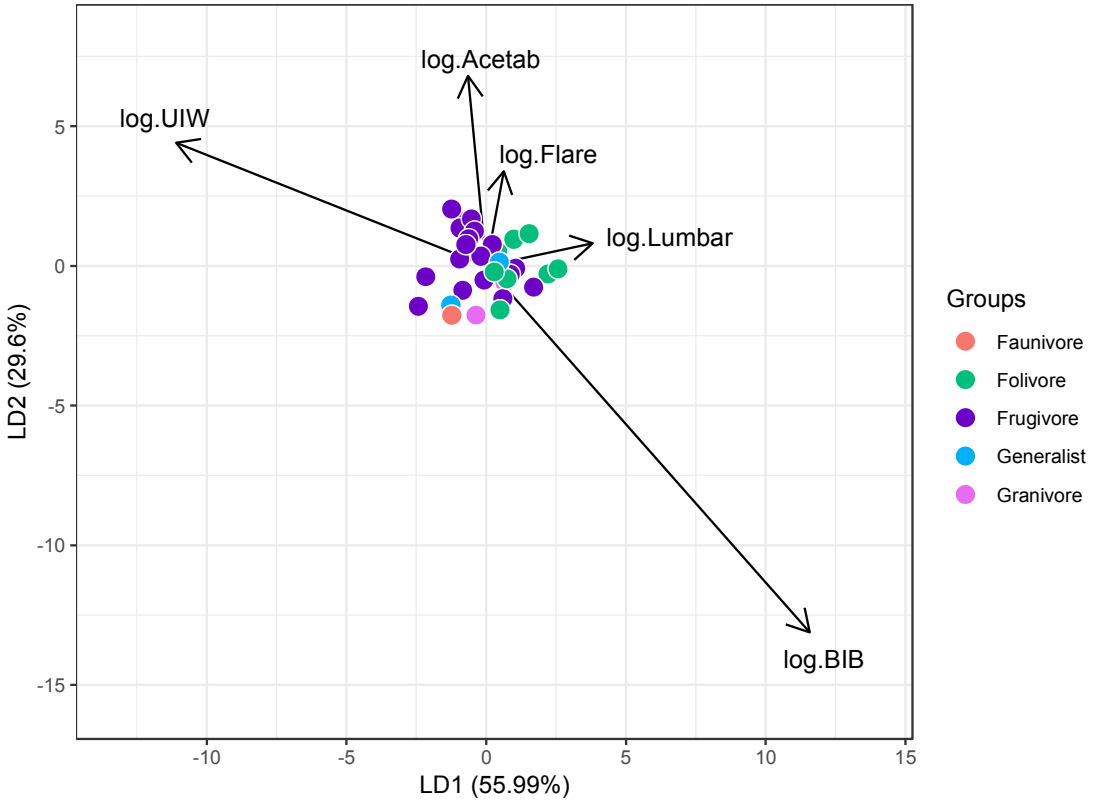

Figure D2. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among diet groups for 31 species of male anthropoids.

Table D3. Variable loadings, from the DFA testing how torso variables distinguish among diet groups for 31 species of male anthropoids.

	LD1	LD2	LD3	LD4
log.BIB	11.5783658	-13.11336	-10.76031	14.612797
log.Flare	0.6393493	3.3818875	-1.893364	-2.617002
log.UIW	-11.094058	4.4046628	4.996152	-3.842757
log.Lumbar	3.8174578	0.8093834	-2.006164	-1.722366
log.Acetab	-0.6490684	6.7975127	11.048593	-8.3329

For the locomotion DFA for females, logged bi-iliac breadth has strong negative loadings on the first two discriminant functions and logged upper ilium width has strong positive loadings on the first two discriminant functions (Figure D3, Table D4). Logged acetabular diameter has a strong positive loading on the first discriminant function. Together these first two discriminant functions account for ~98% of the among-group variation. There are more distinct groupings of the locomotor categories than there were for the diet groups (Figure D3). Leapers are subsumed within the arboreal quadruped cluster. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 65% (Table D1).

Table D4. Variable loadings, from the DFA testing how torso variables distinguish among locomotor groups for 31 species of female anthropoids.

	LD1	LD2	LD3
log.BIB	-8.370034	-3.973616	-3.551432
log.Flare	-1.355131	-1.993521	-2.532688
log.UIW	8.378801	7.723496	3.361369
log.Lumbar	-4.828244	1.511437	-2.814896
log.Acetab	5.619445	-2.070811	3.633502

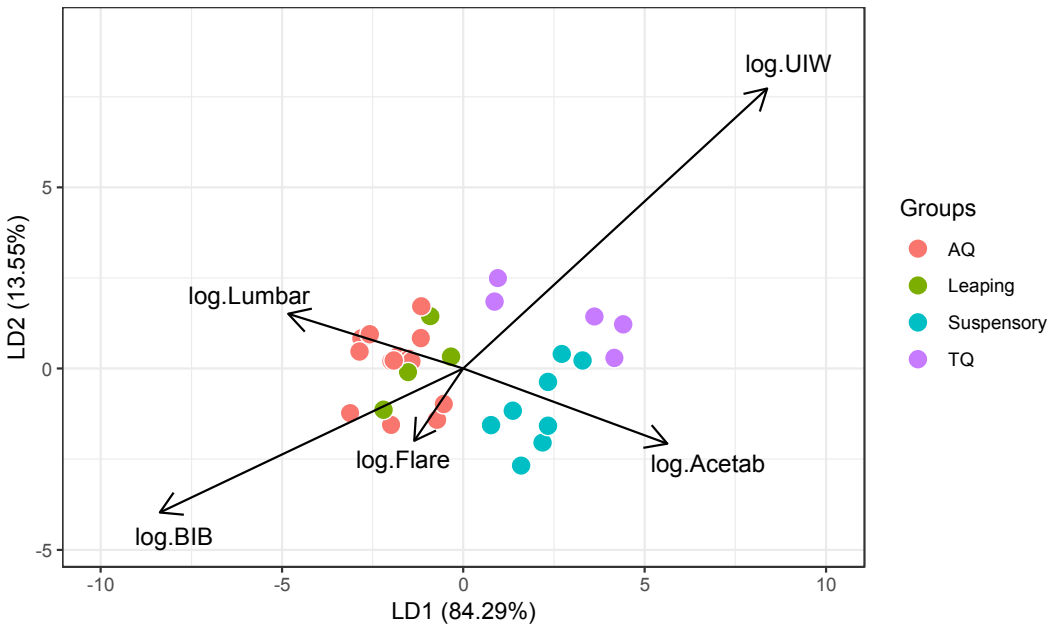

Figure D3. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among locomotor groups for 31 species of female anthropoids.

For the locomotion DFA for males, logged bi-iliac breadth has a strong negative loading on the first discriminant function, while logged upper ilium width has a strong positive loading on the first two discriminant functions (Figure D4, Table D5). Logged acetabular diameter has a strong positive loading on the first discriminant function and a strong negative loading on the second discriminant function. Together these first two discriminant functions account for ~99% of the among-group variation. Similar to the results for females, there are more distinct groupings of the locomotor categories than there were for the diet groups (Figure D4). Leapers are subsumed within arboreal quadrupeds. Leave-one-out cross-validation indicates that the predictive accuracy of this DFA is about 65% (Table D1).

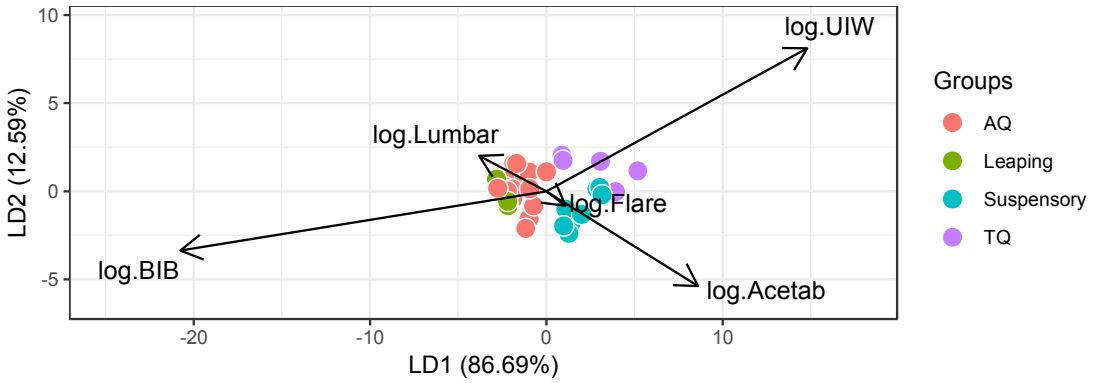

Figure D4. Scatter plot of the first two linear discriminants from the DFA testing how torso variables distinguish among locomotor groups for 31 species of male anthropoids.

Table D5. Variable loadings, from the DFA testing how torso variables distinguish among locomotor groups for 31 species of male anthropoids.

	LD1	LD2	LD3
log.BIB	-20.75936	-3.372724	-19.74526
log.Flare	1.09006	-0.818687	4.741288
log.UIW	14.801317	8.0975292	8.440873
log.Lumbar	-3.815141	2.0116102	3.806233
log.Acetab	8.619578	-5.376053	5.916508

Altogether, these results are extremely similar to those presented in Analysis C in Chapter 2 of this dissertation. Logged acetabular diameter (the body size proxy) has a clear effect on the distribution of the data points, as it has strong loadings on at least one of the first two discriminant functions in each of these analyses. The DFA in Analysis C of Chapter 2 perform a bit better for males as they have higher predictive accuracies, but only slightly higher. The DFA analyses for females are similar in both cases, but the locomotor DFA presented here in Appendix D has a slightly higher predictive accuracy than that in Analysis C. Overall, Appendix D and Analysis C demonstrate that torso variables, whether divided by acetabular diameter or not, are better at distinguishing among locomotor categories than dietary categories.