



Strategies for the Use of Fallback Foods in Apes

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Received: 8 April 2010 / Accepted: 24 August 2010 / Published online: 7 January 2011
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Abstract Researchers have suggested that fallback foods (FBFs) shape primate food processing adaptations, whereas preferred foods drive harvesting adaptations, and that the dietary importance of FBFs is central in determining the expression of a variety of traits. We examine these hypotheses in extant apes. First, we compare the nature and dietary importance of FBFs used by each taxon. FBF importance appears greatest in gorillas, followed by chimpanzees and siamangs, and least in orangutans and gibbons (bonobos are difficult to place). Next, we compare 20 traits among taxa to assess whether the relative expression of traits expected for consumption of FBFs matches their observed dietary importance. Trait manifestation generally conforms to predictions based on dietary importance of FBFs. However, some departures from predictions exist, particularly for orang-utans, which express relatively more food harvesting and processing traits predicted for consuming large amounts of FBFs than expected based on observed dietary importance. This is probably due to the chemical, mechanical, and phenological properties of the apes' main FBFs, in particular high importance of figs for chimpanzees and hylobatids, compared to use of bark and leaves—plus figs in at least some Sumatran populations—by orang-utans. This may have permitted more specialized harvesting adaptations in chimpanzees and hylobatids, and required enhanced processing adaptations in orang-utans. Possible intercontinental differences in the availability and quality of preferred and FBFs may also be important. Our analysis supports previous hypotheses suggesting a critical influence of the dietary importance and quality of FBFs on ape ecology and, consequently, evolution.

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Keywords Adaptation · Ape · Diet · Fallback foods · Feeding ecology

Introduction

Fallback foods (FBFs) are generally regarded as foods of relatively poor nutritional quality and high abundance that are eaten when preferred foods are unavailable. Although the term has been widely used, it has been inconsistently defined in the literature (Lambert 2007; Marshall *et al.* 2009b). This has led to confusion, particularly regarding the distinction between staple/important foods (i.e., foods eaten in large amounts year-round or at specific times of year) and FBFs, which have generally been regarded as distinct types of food resources (Marshall and Wrangham 2007). Marshall and Wrangham (2007) operationally define FBFs as “foods whose use is negatively correlated with the availability of preferred foods” (p. 1220) and preferred foods as foods “selected disproportionately often relative to their abundance within the population’s habitat” (p. 1221). Notably, the preceding definitions imply nothing about a food item’s level of consumption, i.e., its importance. Accordingly, preferred foods need not necessarily comprise a large portion of the diet, if they are rare in the environment, and an FBF can also be a staple/important food, if preferred foods are frequently unavailable. This leads Marshall and Wrangham to propose 2 types of FBF: staple, which is available and eaten year-round and can be up to 100% of the diet; and filler, which may not be eaten for long periods, and is never 100% of the diet.

Further, based on these definitions, some foods may be neither preferred nor FBFs. For example, some fruits eaten by orang-utans (*Pongo pygmaeus wurmbii*) in Sabangau, Indonesian Borneo have very low preference rankings, but consumption does not correlate with the environmental availability of more preferred fruits, indicating that these fruits are neither avoided nor preferred (Harrison 2009).

FBFs are generally widely available but difficult to process and, hence, offer lower energetic returns. Preferred foods are generally nutrient/energy-rich and, hence, are less abundant in the environment, as they are expensive for plants to produce, but easy to process and offer high energetic returns. Based on this distinction, Marshall and Wrangham (2007) suggest that FBFs tend to shape processing adaptations, whereas preferred foods tend to shape harvesting adaptations, and that reliance on the 2 different classes of FBF has different effects on primate socioecology.

In an alternative scheme (Lambert 2007), FBFs are viewed as lying along a spectrum from relatively abundant and low quality, e.g., leaves and bark, to relatively rare and high quality, e.g., fruit. The former are argued to be more difficult to process and, hence, to drive specialized adaptations toward processing, whereas the latter are expected to drive behavioral adaptations, such as fission–fusion social systems and tool use. Though this framework approaches the problem from a slightly different perspective than that of Marshall and Wrangham (2007), the 2 approaches are largely complementary: both hypothesise that relatively high-quality foods require a long search time, but short handling time and, hence, drive harvesting adaptations, while relatively low-quality foods have a high processing time and low searching time and, hence, drive processing adaptations (Marshall *et*

al. 2009b). Further, in both frameworks, low-quality foods are hypothesized to be disproportionately important in determining anatomical traits, i.e., traits that can be inferred directly from the fossil record, while high-quality foods are generally more implicated in behavioral adaptations (Marshall *et al.* 2009b).

Here, we consider these ideas using data from wild ape populations. Although the terminology follows that of Marshall and Wrangham (2007) and it is primarily their predictions that are tested, the high complementarity of this scheme and Lambert's (2007) means that this analysis is relevant to both frameworks. Our analysis builds on previous analyses of apes (Lambert 2007; Marshall *et al.* 2009b) in that 1) a greater number of traits are analyzed in a more systematic, comparative manner and 2) the smallest apes, the Hylobatidae, which differ substantially in their biology from the Hominidae, are included. Apes are an appropriate group for testing these predictions, as they all share similar broad dietary preferences—ripe fruit—but differ morphologically and live in habitats of differing food availability and, hence, vary in their dietary profiles and FBFs (Conklin-Brittain *et al.* 2001; Ghiglieri 1987; Knott 2005; Lambert 2007). They have also been studied widely and so the necessary data are more available than for many other primate groups. We treat siamangs (*Symphalangus syndactylus*) as a separate category from the smaller hylobatids, as their larger size and distinct behavior makes their grouping under gibbons (used herein to refer to all other hylobatids) inappropriate. Similarly, the ecological differences between species demand that bonobos (*Pan paniscus*) be treated separately from common chimpanzees (*Pan troglodytes*). Cross river gorillas (*Gorilla gorilla diehli*) are excluded, as data are sparse for this species.

Fallback Foods Used by Apes

Despite substantial interest in the concept of FBFs in primates in general and apes in particular, quantitative comparisons of FBF use by apes are lacking and are complicated by several limitations. First, few authors present quantitative data on changes in the relative use and relative availability of ape foods over time (Marshall *et al.* 2009b). Second, several methods for calculating diet composition are commonly used, e.g., percent feeding time, diet composition by weight, and these methods are not always strictly comparable (Kurland and Gaulin 1987). Further, different computational methods and sample sizes may also generate small differences in results, even when using the same observation method (Harrison *et al.* 2009). Third, substantial variations within a taxon have been reported over both space (Morrogh-Bernard *et al.* 2009; Rogers *et al.* 2004) and time (Chapman and Chapman 1990; Doran-Sheehy *et al.* 2009; Harrison *et al.* 2010). We therefore follow previous researchers (Conklin-Brittain *et al.* 2001) in assuming that, regardless of the method or time frame used, the most important foods will emerge from the data. Similarly, to produce a manageable comparison, we do not weight studies based on method or time frame, and include ranges around our means where possible (Conklin-Brittain *et al.* 2001). Despite these inherent difficulties in compiling an accurate quantitative comparison of FBF use between ape taxa, the published data are nevertheless sufficient to draw preliminary conclusions. Future comparative research on this topic would be best conducted as a collaboration

between researchers on the different ape species, whereby raw data could be compiled and analyzed in standard fashion instead of through comparisons of published data.

It is now widely recognized that in general fruit, and particularly ripe fruit, is the preferred food of all apes (Conklin-Brittain *et al.* 2001; Doran-Sheehy *et al.* 2009; Knott 2005; Marshall and Wrangham 2007; Tutin *et al.* 1997; Vogel *et al.* 2008, 2009; Yamagiwa 2004), though some exceptions to this are outlined below.

Chimpanzees (*Pan troglodytes*)

Chimpanzees feed on leaves, bark, stems, and piths, including terrestrial herbaceous vegetation (THV) when fruit is scarce (Basabose 2002; Hladik 1973; Knott 2005; Pruetz 2006; Wrangham *et al.* 1998). Chimpanzee feeding behavior is not identical across the species' range, and important differences in feeding ecology, including types of FBF resources, have been identified among subspecies: *Pan troglodytes verus* in West Africa, *P. t. troglodytes* in Central Africa, and *P. t. schweinfurthii* in East Africa (Doran and Greer 2002; Wrangham *et al.* 1994). Broadly speaking, western chimpanzees, which live in less seasonal rain forest habitats, consume more fruit, and, hence, presumably fewer FBFs, than their eastern relatives in Gombe and Mahale, Tanzania, though these differences are insufficient to distinguish taxa and leaf consumption appears very similar between east and western chimpanzees (Doran *et al.* 2002a).

Figs appear to be important foods for chimpanzees across their range (Table 1). For *Pan troglodytes schweinfurthii*, fig seeds were found in 99% of fecal samples collected and the proportion of fecal matter comprising figs varied from 78% to 100% in Budongo, Uganda (Tweheyo and Lye 2003); similar proportions have been reported in Kahuzi-Biega National Park, Congo (Basabose 2002; Yamagiwa and Basabose 2009); and in Kibale National Park, Uganda, fig seeds were present in high quantities in fecal samples in each of 29 study months (Wrangham *et al.* 1993). Based on direct observations, fig consumption accounts for, on average, 37–41% of feeding time in Budongo, expressed over a 17- and 15-mo study period, respectively (Newton-Fisher 1999; Tweheyo *et al.* 2004), and 37% of monthly feeding time in Kibale, where maximum monthly consumption can exceed 90% (Emery Thompson and Wrangham 2008). For *Pan troglodytes verus*, fecal analysis indicates that figs are one of the most important foods and are eaten for 11 mo of the year in Fongoli, Senegal (Pruetz 2006); direct observations from Bossou, Guinea (Yamakoshi 1998), and a combination of fecal and direct observations from Lopé, Gabon (Tutin *et al.* 1997), also indicate that figs are one of the most important dietary items. Preliminary information from fecal analysis of *Pan troglodytes vellerosus* in Gashaka Gumti National Park, Nigeria indicate figs may be less important, appearing in >50% of the fecal samples collected in only 3 out of 12 mo studied (Hohmann *et al.* 2006).

Although fig consumption can clearly be very high and figs are often referred to as a staple or keystone food instead of an FBF, it must be remembered that these terms are not mutually exclusive (Marshall and Wrangham 2007). Further, their consumption by both *Pan troglodytes verus* and *P. t. troglodytes* at many sites mirrors that of an FBF as defined by Marshall and Wrangham (2007) (Kibale: Wrangham *et al.* 1991, 1993, 1996; Budongo: Tweheyo and Lye 2003; Lopé,

Table 1 Consumption of potential FBF types and total FBF use by apes^{a,b}

Apes	Leaves	THV/pith	Bark	Figs	Mean total FBF	Mean total FBF exc. figs
Chimpanzee	<i>16 (0–56)</i>	<i>7 (0–59)^c</i>	<i>4 (0–41)^d</i>	<i>37–41 (?–91)</i>	66	27
Bonobo	14 (0–28)	25 (0–100)	2 (0–11)	Generally low	0–≥39	0–39
Lowland gorilla	31 (6–51)	<i>18 (7–43)</i>	<i>11 (0–32)^e</i>	Low	29	29
Mountain gorilla	Low	<i>91 (85–96)</i>	<i>3 (0–6)^e</i>	0	94	94
Sumatran orang-utan	<i>16 (11–20)</i>	Low	<i>2 (2–3)</i>	<i>36 (ca. 23–50)^f</i>	54	18
Bornean orang-utan	<i>17 (0–56)</i>	Low	<i>7 (0–67)</i>	Low	24	24
Gibbons ^g	<i>26 (2–72)</i>	0	0	<i>24 (17–45)</i>	50	26
Siamang ^g	<i>33 (17–48)</i>	0	0	<i>29 (22–43)</i>	62	29

^a Cells indicate the mean and range of the proportion of the diet comprising distinct food types. Italics denote cases where a particular food item can be unambiguously identified as an FBF for a particular ape; regular font denotes cases in which we do not consider a particular item to be a FBF for a particular ape taxon.

^b Information derived from summaries in Conklin-Brittain *et al.* (2001) for African apes, Morrogh-Bernard *et al.* (2009) for orang-utans and Elder (2009) for gibbons and siamangs. Note that the exact methods used, study durations, and meaning of figures vary among the studies cited in these summary papers and are not always given. Thus, these values are not perfectly comparable. Nevertheless, we consider that they provide reasonable quantitative estimates for the purposes of broad comparisons.

^c Maximum value from 11 yr of study (Emery Thompson and Wrangham 2008).

^d Also includes other miscellaneous and minor food types.

^e Also includes roots.

^f Mean for Ketambe taken from all individuals in Table 1 and ranges from Figure 1 in Wich *et al.* (2006).

^g Means are calculated from the means of all species, and ranges represent the ranges of mean values, presented by the most recent and complete source we could find (Elder 2009).

Gabon: Tutin *et al.* 1997; Ndoki Forest, Congo: Kuroda *et al.* 1996). However, this is clearly not the case at all sites (Pruetz 2006; Yamakoshi 1998), particularly those at higher altitude, such as Kahuzi-Biega National Park, Congo (Basabose 2002), where lower overall fruit availability and quality may result in figs being relatively more preferred than in lowland sites. Nevertheless, despite the continuing debate on this topic (Yamagiwa and Basabose 2009), we consider the bulk of the evidence to be in support of classifying figs as a primary FBF for chimpanzees.

In summary, it seems that, broadly speaking, figs can be classified as the major FBF and leaves, stems, pith, and bark as filler FBFs for the 2 chimpanzee subspecies on which researchers have conducted long-term studies. Some species of fibrous nonfig fruits are also used as filler FBFs in at least some sites (Doran 1997; Yamakoshi 1998).

Bonobos (*Pan paniscus*)

Like chimpanzees, bonobos are primarily frugivorous, but also consume a wide variety of other foodstuffs, including leaves, flowers, bark, pith, roots, invertebrates, and even an occasional vertebrate prey (Conklin-Brittain *et al.* 2001; Kano 1992). Indeed, analysis of differences between 4 chimpanzee and 2 bonobo populations'

diet composition based on Euclidean (average taxonomic) distances showed no ability to distinguish species via dietary differences and a similar level of reliance on THV between the 2 species, though bonobos and Tai chimpanzees do have a tendency toward higher fruit consumption, and Lomako bonobos are characterized by increased herbivory (Doran *et al.* 2002a). In Wamba, Democratic Republic of Congo, 10–20% of the diet is composed of leaves and other fibrous foods, as determined through a combination of direct observations and fecal analysis, and fibrous foods are reported as being more prominent in the diet during dips between fruiting seasons (Kano 1992). The most important fibrous food (Marantaceae herbs) is described as aseasonal, frequently consumed, uniformly distributed, and of very high quality, even for human consumption (Kano 1992). Seasonal patterns in consumption of nonfig fruits, figs, THV, and leaves were not evident in Lomako, Democratic Republic of Congo (White 1998). The abundance, protein content, and consumption of THV is higher for bonobos at Lomako than for chimpanzees in Kibale (Malenky *et al.* 1994; Malenky and Wrangham 1994), and the pith of 7 THV species constituted the second most frequently consumed food type at this site, after fruit (Badrian and Malenky 1984).

Comparison of the results from 6 studies at 2 sites (Conklin-Brittain *et al.* 2001; Table 1) presents a somewhat confusing picture: on the one hand, consumption of leaves and especially THV can be high, but on the other, evidence that either of these food types are FBFs for bonobos is ambiguous, particularly considering the high quality of THV consumed by bonobos (Marshall *et al.* 2009b). Similarly, though fig consumption has been reported as high in Lomako (Badrian and Malenky 1984) and fig seeds were also most common in feces in the 3 mo reported as having the lowest overall fruit availability in Salonga, Democratic Republic of Congo (Hohmann *et al.* 2006), it is unclear whether figs are a FBF for bonobos or not. Consequently, it could be argued that bonobo FBF consumption is either very high or very low, and detailed comparisons of potential FBF use vs. availability of preferred foods are needed before we can state confidently which of these scenarios is correct.

Gorillas (*Gorilla* spp.)

There is great interspecific variation in the proportion of fruit and THV in the diet among gorillas, with lowland gorillas being more frugivorous and less folivorous than mountain gorillas (mountain gorillas, *Gorilla beringei beringei*: Fossey 1977; Ganas *et al.* 2004; Goodall 1977; Robbins and McNeillage 2003; eastern lowland gorillas, *G. b. graueri*: Yamagiwa *et al.* 1994, 1996; western lowland gorillas, *G. gorilla gorilla*: Doran and Greer 2002; Doran and McNeillage 1999; Kuroda *et al.* 1996; Remis 1997a; Remis *et al.* 2001; Tutin *et al.* 1991). This is thought to be due to lower fruit availability in the mountain gorilla's generally montane habitats, rather than a preference for THV over fruit, as studies of mountain gorillas at lower elevations with more abundant fruit supplies have revealed higher levels of frugivory than at more elevated sites (Ganas *et al.* 2004; Harcourt and Stewart 2007; Robbins and McNeillage 2003). Fruit feeding can reach 70% of total feeding time in some lowland gorilla populations (Doran-Sheehy *et al.* 2009). The amount of fruit consumed correlates positively with fruit availability, whereas the degree of folivory

and bark eating decreases when fruit is abundant, to the point that bark may not be fed on for many months when fruit is available (Doran *et al.* 2002b; Doran-Sheehy *et al.* 2009; Nishihara 1995; Tutin *et al.* 1997; Yamagiwa *et al.* 1994; Yamagiwa and Basabose 2009; *cf.* Ganas *et al.* 2008). Like chimpanzees, western lowland gorillas use some species of highly fibrous fruit as FBFs (Doran *et al.* 2002b; Remis 2003). Thus, it seems reasonable to conclude that THV is a staple FBF for gorillas—as it is not preferred, but can constitute 100% of the diet, especially in mountainous areas where preferred fruit is scarce—and leaves, bark, and some fibrous fruits are filler FBFs.

Orang-utans (*Pongo* spp.)

Dietary variations also exist between Sumatran (*Pongo abelii*) and Bornean (*P. pygmaeus*) orang-utans: based on focal-animal follow methods, Bornean orang-utans generally eat less fruit and fewer insects, and more bark and leaves, than their Sumatran counterparts (Fox *et al.* 2004; Morrogh-Bernard *et al.* 2009; Wich *et al.* 2006). This is thought to be due to higher average fruit, and especially fig, availability in Sumatra than Borneo (Marshall *et al.* 2009a; Mather 1992), with the result that Sumatran orang-utans have less need to fall back on bark and leaves than orang-utans in Borneo (Knott 1998; Wich *et al.* 2006). Figs in Ketambe, Sumatra are eaten in large amounts throughout much of the year, but orang-utans switch to more preferred fruits when they are available (Wich *et al.* 2006), indicating that figs are the main FBF for orang-utans in at least some sites. However, Ketambe is well known for its high density of large strangler figs (Wich *et al.* 2004a, 2006), and it is unclear how prevalent this pattern is in other areas of Sumatra, where figs are often rarer (van Schaik 1999; Wich *et al.* 2004a). Using the largest sample size to date, Marshall *et al.* (2009) found no significant difference in fig stem density between islands, though this comparison was hindered by differences in data collection measures, which may mask a true inter-island difference.

Although bark may not be eaten for months at a time when fruit is available, bark consumption can reach 23–67% of time spent feeding during low fruit periods (Galdikas 1988; Harrison 2009; Knott 1998; Morrogh-Bernard *et al.* 2009; Vogel *et al.* 2008; Wich *et al.* 2006). Leaf consumption is typically higher, constituting *ca.* 16.7% of time spent feeding, on average, and $\geq 40\%$ in some months, and is less strongly related to fruit availability (Galdikas 1988; Harrison 2009; Morrogh-Bernard *et al.* 2009; Vogel *et al.* 2008; Wich *et al.* 2006). The available evidence points toward seeds not being an FBF for orang-utans: some seeds are very energy rich and are among the most preferred food items in both Sabangau and Gunung Palung, Borneo (Harrison 2009; Knott 1999). Thus, orang-utans typically consume bark and, to a lesser extent, leaves as filler FBFs in Borneo, with greater importance of figs in at least some Sumatran sites (Harrison 2009; Knott 1998; Leighton 1993; Vogel *et al.* 2008; Wich *et al.* 2006).

Gibbons (Hylobatidae, excluding *Symphalangus syndactylus*)

Broadly speaking, gibbon diets are similar to orang-utans, except that gibbons do not feed on bark or piths (Cheyne 2010; Chivers 2001; MacKinnon 1977; Vogel *et al.* 2009). Gibbons specialize on ripe, nonfig fruit and fall back on figs, flowers, and young leaves when preferred foods are unavailable (Chivers 2001; Elder 2009;

Leighton 1987; Marshall 2004). Leaf consumption varies between sites, and has been recorded as 3% in Gunung Palung, Borneo (Marshall 2004), 4% in Ketambe, Sumatra (Palombit 1997), 6% in Bangladesh (Islam and Feeroz 1992), 25% in Sabangau (Cheyne 2010), and up to 39% in Peninsular Malaysia (Gittins 1979). These studies were all conducted using focal-animal methods, with the exception of the former, which used independent observations along line transects.

Figs are generally more commonly eaten (Chivers 2001), comprising, e.g., 13% of the diet in Sabangau, Borneo (Cheyne *et al.*, in prep), 23% in Gunung Palung (Marshall 2004), and 45% in Ketambe (Palombit 1997; Ungar 1995). As in orang-utans, the higher incidence of fig consumption in Sumatra may be related to differences in fig abundance between the islands. In Gunung Palung, studies across forest-type gradients indicate that gibbon population density is limited by the abundance of figs, their most important FBF (Marshall 2004; Marshall and Leighton 2006). Compared to data collected concurrently on sympatric orang-utans in Ketambe, gibbons spent a greater proportion of feeding time eating fruit/figs and a lower proportion eating unripe fruits (Ungar 1995). Consumption of preferred foods (nonfig fruit) and FBFs (figs, liana products) by orang-utans and gibbons during a fallback episode in Tuanan, Borneo did not differ (Vogel *et al.* 2009), indicating similar patterns of FBF reliance between the species. In summary, therefore, gibbons appear to use both figs and leaves as filler FBFs.

Siamangs (*Symphalangus syndactylus*)

Siamang diet and food preferences are broadly similar to those of gibbons, with fruit the preferred food type (Chivers 2001; Elder 2009; MacKinnon and MacKinnon 1980; Palombit 1997; Raemaekers 1977). These studies also suggest that fruit consumption is generally lower and leaf consumption higher in siamangs, though these differences are not always statistically significant. Indeed, studies of sympatric siamangs and gibbons in Ketambe (Palombit 1997) and Kuala Lompat (MacKinnon and MacKinnon 1980; Raemaekers 1977) indicate similar levels of fig consumption, but higher leaf consumption by siamangs. Siamangs have been reported as spending 43% of time feeding eating figs in Ketambe, Sumatra (Palombit 1997), 58% eating leaves in Kuala Lompat, Malaysia (Chivers 1974), and a combined total of 91% eating figs and young leaves in Ulu Sempam, Peninsular Malaysia (Chivers 1974). Thus, siamangs appear to rely primarily on leaves and, to a lesser extent, figs as their major filler FBFs.

Summary

In summary, although there are similarities in the use of FBFs between apes, particularly in the use of THV by gorillas and chimpanzees and the use of figs by chimpanzees, Sumatran orang-utans, gibbons, and siamangs, each ape relies on different FBFs to different degrees and total combined FBF use varies among taxa (Table I). Although the same conclusion has been reached previously (Conklin-Brittain *et al.* 2001; Knott 2005), the FBFs named in this study differ somewhat because of the definition of FBFs used here (Marshall and Wrangham 2007). Marshall and Wrangham propose 2 types of FBF—staple and filler—but, rather than using mutually exclusive categories, it may be useful to envisage a “FBF Importance Continuum,” along which species can

be placed in reflection of the importance of (staple) FBFs vs. preferred foods in the diet (Marshall *et al.* 2009b). Such a continuum differs slightly from that described by Lambert (2007), as it is based on dietary importance of FBFs consumed, rather than their abundance and quality, though these 2 continuums are highly compatible (Marshall *et al.* 2009b). This basis is necessary in order to test predictions on the evolutionary implications of the dietary importance of FBFs on harvesting and processing adaptations (Marshall and Wrangham 2007).

Based on the total mean proportion of the diet composed of FBFs, mountain gorillas would lie very close to the stable end of this continuum, followed by chimpanzees, siamangs, Sumatran orang-utans, and gibbons in the mid-staple region, and lowland gorillas and Bornean orang-utans closest to the filler end of the spectrum (Table I). Excluding fig consumption, this ranking changes: mountain gorillas remain at the most extreme staple point on the continuum, followed by lowland gorillas and siamangs, chimpanzees, gibbons, and orang-utans, all of which lie closer to the filler end of the spectrum. Depending on whether THV, leaves, or figs are considered FBFs for bonobos or not, their position on the spectrum varies between intermediate, and most similar to gibbons and Sumatran orang-utans, to an extreme preferred food specialist with no FBF consumption.

Though this comparison is based on taxa-specific averages, it should be remembered that substantial intraspecific variation in diet exists in each ape taxon (Marshall *et al.* 2009b). There will therefore be substantial overlap between the extremes for different taxa. For example, the maximum reported time feeding on FBFs in siamangs (91% on figs plus leaves, Ulu Sempam, Chivers 1974) exceeds that in some gorilla populations, e.g., WLG in Bai Hokou, where nonfruit consumption—likely to represent mostly FBFs—can drop to 30% of total diet (Masi *et al.* 2009). Nevertheless, we suggest that this continuum represents a useful general framework for comparison of traits among different ape species.

Assessing Adaptations for Preferred and Fallback Food Consumption

Following the logic that high dietary importance of FBFs should drive adaptations towards processing abilities, whereas high dietary importance of preferred foods should drive adaptations towards harvesting abilities (Marshall and Wrangham 2007), we assess 20 traits pertaining to likely adaptations/repercussions of reliance on FBFs for each ape taxon (Table II). These comparisons are designed to assess the relative degree of specialization for exploitation of (staple) FBFs vs. preferred foods, based on Marshall and Wrangham's (2007) predictions, rather than the importance of these foods in the diet, with the expectation that these should match each other closely. We group these traits into:

- Harvesting adaptations, i.e., traits that facilitate travel to/detection of patchily distributed resources, such as fruits. Examples include high travel efficiency and large day range. These are expected to be shown in species that are relatively more reliant on preferred foods.
- Processing adaptations, i.e., traits that facilitate the exploitation of (fallback) foods that are difficult to process, such as leaves and bark. Examples include

robust jaws for processing physically challenging foods, and large gut volume for digesting foods with high fiber content. These are expected to be expressed more strongly by species that are relatively more reliant on FBFs.

- Repercussions, which represent traits that may emerge from a species' reliance on preferred or FBFs; e.g., high dietary importance of FBFs would be expected to lead to high amounts of fiber in the diet, high group stability, fast life history, etc. (*cf.* Marshall and Wrangham 2007).

We do not test some of the predictions for species reliant on preferred foods put forth by Marshall and Wrangham (2007): limited tool use, high visual acuity, high general cognitive abilities, good olfactory senses, and spatial navigation abilities. This is because these adaptations are difficult to define operationally and assess in an accurate, objective manner (general cognitive and spatial navigation abilities), are likely to be very similar across ape species (vision and olfaction), or are a highly debated topic deserved of much more attention than we can grant herein (tool use). Though this leads to bias in our analysis toward processing adaptations, species dependent mostly on preferred foods should show fewer specialized adaptations to this end and, thus, this approach should not create substantial bias in assessment. As some of these traits correlate with body size, which may also be influenced by factors other than diet, we attempt to control for body mass where relevant.

Although it is recognized that life history may be influenced by reproductive strategies of males and females (Galdikas and Wood 1990; Tutin 1994), that data are incomplete for the apes (Knott 2001), and that differences exist between the wild and captivity (De Lathouwers and Van Elsacker 2005; Knott 2001; Kuze *et al.* 2008; Wich *et al.* 2009b), we have not excluded life history from our analysis of traits. First, though an influence of reproductive strategies cannot be discounted, it has been suggested that food availability and energetics play a central role in determining ape reproductive strategies (Harrison and Chivers 2007; Knott 2001; Wich *et al.* 2009a). Second, it has been demonstrated convincingly that different life history characteristics are allometrically scaled and correlate highly (Harvey and Clutton-Brock 1985; Stearns 1983; Western 1979; Western and Ssemakula 1982), and, consequently, performing our analysis on only a subset of the full suite of life history characteristics should not influence the results. On these grounds, we consider the available data to be sufficient for broad comparative purposes. Third, we restrict our analysis to data from studies on wild individuals only, to avoid any potentially confounding influence of captivity. Finally, although preliminary, we consider inclusion of life history analysis to be useful for generating hypotheses for further testing when more data become available. Similar arguments could be made regarding grouping behavior, although we believe the evidence implicating an important role of food availability and energetics in ape grouping (Harrison and Chivers 2007; Hashimoto *et al.* 2003; Knott 1999, 2005; White 1998) is sufficient to justify inclusion in our analysis.

We base our predictions on the following key assumptions (Marshall and Wrangham, 2007):

1. FBFs are more common and evenly distributed in space and time than preferred foods and, hence, require less search effort. Heavy reliance on preferred foods will therefore be reflected through improved harvesting adaptations.

2. High reliance on FBFs should lead to reduced intraspecific competition, more stable social groups and faster life history, as food supply is more stable.
3. FBFs are more challenging to process than preferred foods, owing to mechanical properties, high fiber contents, or chemical defenses. This will be reflected in more specialized adaptations of the teeth/jaw and digestive system.

Adaptations Shown for the Exploitation of Preferred and Fallback Foods

We compared each of the traits listed in Table II across the apes and subjectively categorized each trait in each ape as indicative of high importance of staple FBFs or filler FBF/preferred foods, relative to the other apes listed (Table III). For example, body

Table II Traits used to assess reliance on FBFs^a

Trait	Heavy reliance on (staple) FBF indicated by...	Heavy reliance on preferred foods indicated by...
Harvesting		
Day range	Short	Long
Travel efficiency	Low	High
Travel speed	Slow	High
Processing		
Molar morphology	Specialized ^b	Nonspecialized
Incisor morphology	Lower curvature (for folivory) or very high curvature (for hard objects) ¹	High curvature (for frugivory) or intermediate (i.e., unspecialized) ¹
Mandibular morphology	Improved resistance to mandibular loads ²	Lower resistance to mandibular loads
Female body mass ^c	Large	Small
Colon surface area ^d	Large	Small
Colon surface area controlled for body mass ^c	High	Low
Coefficient of gut differentiation ^f	High	Low
Mean retention time of food in gut	Slow ^g	Fast
Mean retention time controlled for body mass ^h	High or very low ^g	Intermediate
Fiber digestion coefficient	High	Low
Repercussions/other		
Percentage fiber in wild diet ⁱ	High	Low
Food hard/toughness	High	Low
Fluctuations in resource availability	Low	High

Table II (continued)

Trait	Heavy reliance on (staple) FBF indicated by...	Heavy reliance on preferred foods indicated by...
Feeding competition ^j	Low	High
Group stability	High	Low
Life history ^k	Fast	Slow
Life history controlled for body size ^k	Fast	Slow

^a All comparisons are relative to the other ape taxa; e.g., a trait is classified as high or low in one ape relative to the remaining taxa.

^b Specialized adaptations of the molars for FBF exploitation include very thick molar enamel for consumption of hard FBFs and/or crenulated occlusal surfaces/well-developed shearing crests for folivory, which may be accompanied by thin enamel (Kay 1984; Ungar 2007; Vogel *et al.* 2008). Correspondingly, species more dependent on preferred foods are predicted to have nonspecialized molars, as indicated by intermediate thickness enamel or thin enamel without highly developed shearing crests.

^c Female body size is preferred here, as variations in male body size are likely to also be influenced by sexual selection and other pressures (Plavcan 2001), in addition to feeding-related selection pressures.

^d Ideally, colon surface area would be expressed here for females only to make the data more comparable with that on body masses. Unfortunately, data for females are not provided for all species listed in Chivers and Hladik (1980); hence, averages across the sexes, or male measurements for some species, were used where data on females were not available.

^e Ideally also expressed for females, but, as female gut measurements were not always available, values for male gut measurements were used in some cases.

^f The ratio of the surface area of the stomach, cecum, and colon, to the SA of the small intestine (Chivers and Hladik 1980).

^g Either high or very low mean retention time may represent adaptation toward the processing of large amounts of fibrous FBFs (Demment and van Soest 1985; Foley and Cork 1992; Parra 1978). Both strategies can be thought of as maximizing energy intake rate: in the former, fibrous foods are retained in the gut for longer periods, allowing more thorough fermentation and energy extraction from the food; in the latter, expected in smaller herbivores, food is digested less thoroughly, but at a faster rate. Intermediate passage rates would indicate relative unspecialization and, consequently, relatively low importance of fibrous FBFs.

^h Ideally expressed for females, but, as female gut measurements were not always available, values for male gut measurements were used in some cases.

ⁱ Percentage dry weight of organic matter composed of neutral-detergent fiber (the digestible fiber fraction). Unless stated otherwise, all figures for neutral-detergent fiber quoted in this article refer to percentage organic matter. Note that, for an equivalent percentage, the amount of fiber in organic matter will be less than that in dry matter, as the latter also includes inorganic elements; i.e., ash (Conklin-Brittain *et al.* 2006).

^j Derived from Plavcan and van Schaik's (1992) assessment of male–male competition levels. Though this may not reflect perfectly competition levels over food (which can include competition between other age–sex classes and scramble competition), this is taken as the best available assessment that covers all the ape taxa.

^k Increased importance of staple FBFs is hypothesized to lead to faster life history by Marshall and Wrangham (2007), because food supply is more constant, enabling increased investment in reproduction and, hence, higher reproductive rates. This is similar to Knott's (2001) Ecological Energetics hypothesis. An alternative, Ecological Life History hypothesis, has also been proposed for orang-utans (Wich *et al.* 2004b, 2009a), in which greater seasonal dependence on bark results in faster life history profiles, owing to increased mortality in these populations. Some have argued that these seemingly conflicting hypotheses probably represent short- and long-term strategies for energy allocation (Knott *et al.* 2009). In essence, this could also be thought of as representing differences between evolutionary and ecological time scales. Considering this, and being as the aim in this article is to test Marshall and Wrangham's (2007) predictions in apes, we have judged a faster life history as being more representative of higher importance of staple FBFs in the diet.

References: 1. Deane (2009); 2. Taylor *et al.* (2008).

mass in the great apes (>33 kg) is much higher than in hylobatids (<11 kg), and colon surface area in orang-utans and gorillas (>4100 cm²) is markedly greater than in the other apes (<3000 cm²). Thus, in both of these cases, the former groups were categorized as showing traits for staple FBF consumption, whereas the latter were categorized as showing traits for filler FBF/preferred food consumption. The grouping of filler FBFs and preferred foods here may seem counter intuitive, but, by definition, filler FBFs form only a relatively small part of the diet. Thus, the remaining majority of the diet must comprise of either preferred foods, foods that are neither preferred nor FBFs, i.e., are eaten in direct proportion to their abundance, or a combination of many filler FBFs. Consequently, adaptations for the exploitation of preferred foods and filler FBFs should generally be seen in tandem, with the relative balance in importance between the 2 food types influencing the expression of harvesting vs. processing traits, respectively.

As can be seen from Table III, there is much variation in the different apes' adaptations for exploiting staple FBFs vs. preferred foods/filler FBFs. Overall, mountain gorillas gain more staple FBF ratings than any other species (17), followed by eastern/western lowland gorillas (15), orang-utans (14), siamangs (7), and chimpanzees and gibbons (5). Bonobos gain very few staple ratings overall (3), but data are unavailable or insufficient to compare 7 of the traits tested. When looking at harvesting traits alone, orang-utans (3) > gorillas (2) > siamangs and gibbons (1) > chimpanzees and bonobos (0). Considering just processing traits, orang-utans (9) > mountain gorillas (8) > eastern/western lowland gorillas (7) > chimpanzees and siamangs (2) > gibbons (1) and, considering just the expected repercussions, gorillas (6) > siamangs (4) > gibbons (3) > chimpanzees and orang-utans (2). Bonobos receive relatively few staple FBF ratings for both processing adaptations (1) and expected repercussions (2), but data were unavailable for 6 and 1 of the traits compared in these categories, respectively. However, merely summing up the ratings in this manner is inappropriate, as many of the traits listed are clearly not independent of one another, e.g., colon surface area, mean retention time of digesta, and fiber digestion coefficient. Thus, a more considered discussion is necessary.

Harvesting Traits

As noted in the preceding text, many of the expected harvesting adaptations—general cognitive ability, visual acuity, olfaction, and spatial navigation abilities—could not be compared reliably and, hence, this comparison of relative harvesting abilities is restricted to observations on travel. As expected, gibbon and chimpanzee travel efficiency and travel speed, and chimpanzee day range, are all relatively high, in accordance with the high importance of fruit in their diet. The expression of harvesting traits in bonobos and chimpanzees appears very similar, although chimpanzee day range seems longer than that of bonobos. Siamangs and gibbons are similar in the expression of the majority of harvesting traits, but, though not entirely conclusive, the available evidence all points toward gibbons expressing harvesting traits more strongly than do siamangs (larger day range, presumably higher travel efficiency, and higher travel speed). Gorillas have a relatively short day range and travel relatively slowly, though the more frugivorous WLG travels relatively further each day, in line with expectations. Travel efficiency is comparable to, but slightly less than, chimpanzees, as may be expected from their similar modes

Table III Characteristics exhibited by apes indicative of high importance of staple FBFs vs. filler FBFs/preferred foods^{a,b} in the diet

Trait	Chimpanzee	Bonobo	Gorilla	Orang-utan	Gibbon	Siamang
Harvesting						
Day range	Eastern: 3.5 km/d (2.2–4.8); western: 1.7 km/d (1.0–2.4). ^{1–2}	2.4 km/d (0.4–6.0). ³	W. lowland: 1.9 km/d (1.2–2.6) ^{4,7} ; E. lowland: 1.5 km/d (0.8–2.1) km/d ^{8–9} ; mountain: 0.8 km/d (0.5–1.3). ^{10–11}	Females, Borneo: 0.6 km/d (0.2–1.0); Sumatra: 0.9 km/d (0.7–1.1). ¹²	Mean all species in ref. 13: 1.0 (0.8–1.8).	0.8 km/d (0.6–0.9). ¹³
Travel efficiency (kcal/m)	FILLER/PREF. Males expend 0.09 and females 0.08 kcal/m walked. ²	FILLER/PREF. Unknown. Likely similar to that of chimpanzees, based on similarities in travel modes and body mass.	Lowland: FILLER/PREF. Mountain: STAPLE W. lowland silverback males expend 0.58 and adult females 0.33 kcal/m walked. ¹⁴	STAPLE Bornean flanged males expend 0.43–0.47 and adult females 0.23–0.26 kcal/m traveled. ¹⁵	STAPLE Unknown, but 80% of travel is via brachiation, ¹⁶ a very efficient mode of travel. ^{17–20}	STAPLE Unknown, but typically travel via brachiation ²¹ and costs therefore likely to be similar to/slightly greater than gibbons.
Travel speed	FILLER/PREF. Walking speed 0.78–0.88 m/s. ²²	FILLER/PREF. Walking speed unknown. Average mean ranging rate 274 m/h. ²³	STAPLE W. lowland walking speed 0.65–0.75 m/s. ¹⁴	STAPLE Distance traveled/h up to 10 times lower than chimpanzees. ^{24–25}	FILLER/PREF. ≥ 2.6 m/s. ¹⁸	FILLER/PREF. Fast, but slightly slower than gibbons. ²⁶
Processing	INTERMEDIATE	INTERMEDIATE	INTERMEDIATE	STAPLE	FILLER/PREF.	FILLER/PREF.
Molar morphology	Enamel thickness intermediate (relative thickness on second lower molar 3.1%) ²⁷ Relative enamel thickness indistinguishable from that of gorillas. ²⁸ Least developed shearing crest of all apes and flat occlusal relief. ^{27,29–30}	Relative enamel thickness within chimpanzee range. ²⁸	Thin enamel (–23.4%) and most highly developed molar shearing crest of all apes. ²⁷ Relative enamel thickness indistinguishable from chimpanzees. ²⁸ High dental capacity for processing hard/tough foods. ^{29,31}	Very thick enamel (33.8%, thickest of all extant primates), indicating adaptation for consuming hard foods. ^{27,30,32} Relative enamel thickness greater than in gorillas and chimpanzees. ²⁸ Shearing crests not reduced. ^{27,30,33} Molar-cusp slope steepness and average	Intermediate enamel (3.02%, ranging: 1.63–7.8%). ²⁷ Shearing crest development less than in orang-utans and gorillas. ²⁷ Molar shearing planes flatter than in true folivores. ³⁵	Thin enamel (–19.2%) and highly-developed molar shearing crest ²⁷ .

surface slope height in between chimpanzees and gorillas;²⁹ Crenate occlusal surfaces on molars to reduce risk of tooth shatter.³⁴

Incisor morphology	<p>FILLER/PREF. Pronounced mesiodistal and cervico-incisal crown curvatures, and wide incisors, indicating soft-fruit consumption.³⁶ Enlarged spatuliform lower incisors with permanently sharp cutting edges, possibly for meat eating.³⁷</p>	<p>FILLER/PREF. Incisor crown morphology intermediate between that of chimpanzees and gorillas, but overwhelmingly frugivorous, closely resembling that of chimpanzees.³⁶</p>	<p>STAPLE Mountain least curved incisors, indicating dedicated folivory. Lowland intermediate curvature, indicating mixed frugivory/folivory.³⁶ Lowland: FILLER/PREF Mountain:</p>	<p>STAPLE Greatest mesiodistal and cervico-incisal curvature of all apes, and wider incisors relative to more folivorous taxa, indicating hard food consumption.³⁶</p>	<p>FILLER/PREF. Intermediate mixed frugivory/folivory³⁶</p>	<p>STAPLE Slightly high mesiodistal and cervico-incisal crown curvatures, indicating frugivory, though phylogeny possibly also a significant influence.³⁶</p>
Mandibular morphology	<p>FILLER/PREF Jaw least robust of great apes;³⁸ decreasing robusticity from west to east.³⁹</p>	<p>FILLER/PREF. No consistent differences from chimpanzees.³⁹</p>	<p>STAPLE Jaw most robust of great apes;³⁸ greatest robusticity in mountain gorillas.³⁹</p>	<p>STAPLE Jaw robusticity intermediate between that of chimpanzees and gorillas;³⁸ higher load-resistance abilities in Borneo.⁴⁰</p>	<p>FILLER/PREF. Jaw relatively weak and mandibular body “gracile” compared to that of great apes.^{41–42}</p>	<p>FILLER/PREF. Jaw relatively weak and mandibular body “gracile,” compared to that of great apes.^{41–42}</p>
Female body mass	<p>FILLER/PREF. 40.4 kg (mean 3 species in ref. 43).</p>	<p>FILLER/PREF. 33.7 kg.⁴³</p>	<p>STAPLE 80 kg (mean 3 species in ref. 43)</p>	<p>STAPLE 35.7 kg (mean 2 species in ref. 43).</p>	<p>FILLER/PREF. 10.7 kg.⁴⁴</p>	<p>FILLER/PREF. 10.7 kg.⁴⁴</p>
Colon surface area	<p>STAPLE 1812–2925 cm.²⁴⁵</p>	<p>STAPLE Unknown</p>	<p>STAPLE 4,813 cm² (male).⁴⁵</p>	<p>STAPLE 4198–5774 cm²⁴⁵–46^c.</p>	<p>FILLER/PREF. 765.5 cm² (mean 2 species)⁴⁵</p>	<p>FILLER/PREF. 1557 cm²⁵</p>

Table III (continued)

Trait	Chimpanzee	Bonobo	Gorilla	Orang-utan	Gibbon	Siamang
Colon surface area mean both sexes: controlled for body mass ^a	Females: 1271.4, 1230.0. FILLER/PREF	Unknown	Mean both sexes: 32.5. FILLER/PREF.	Females: 3286.9; mean both sexes: 974.5. STAPLE	Females: 212.7; mean both sexes: 44.4. (mean 2 species) FILLER/PREF.	Females: 150.7. STAPLE
Coefficient of gut differentiation	1.16. ⁴⁵ FILLER/PREF.	Unknown	1.62. ⁴⁵ STAPLE	1.08. ^{45-46; c} FILLER/PREF.	2.05 (mean 2 species). ⁴⁵ STAPLE	0.92. ⁴⁵ FILLER/PREF.
Mean retention time	37.7 h in captivity on high-fiber diet. ⁴⁸	Unknown	50–58.2 h in captivity. ⁴⁹⁻⁵¹	73.7 h in captivity. ⁵²	11–27.8 h in wild. ⁵³⁻⁵⁴	Unknown. Likely to be intermediate between that of gibbons and chimpanzees, based on gut morphology. FILLER/PREF.
Mean retention time controlled for body mass ^e	FILLER/PREF. –6.5	Unknown	STAPLE –10.2	STAPLE 31.9	FILLER/PREF. –6.8 (mean 2 species)	Unknown. Based on gut measurements, possibly slightly higher than in gibbons and chimpanzees, and much lower than in orang-utans. FILLER/PREF.
Fiber digestion coefficient	FILLER/PREF. 54.3% on high-fiber diet in captivity. ⁴⁸	Unknown	FILLER/PREF. 57.5% on high-fiber diet in captivity. ⁵⁵	STAPLE 59.4% on high-fiber diet in captivity. ⁵⁶	FILLER/PREF. Unknown. Likely to be low, considering gut anatomy and passage time.	Unknown. Likely to be higher than in gibbons and lower than in the great apes, based on gut morphology. FILLER/PREF.
Repercussions/other	STAPLE	Unknown. Probably within range of chimpanzees, based on comparison of food fiber contents. ⁵⁸	STAPLE	STAPLE	FILLER/PREF.	FILLER/PREF.
Percentage of fiber in wild diet	Potentially 24.7% of metabolizable energy from fiber. ⁵⁷	Unknown. Probably within range of chimpanzees, based on comparison of food fiber contents. ⁵⁸	Potentially 57.3% of metabolizable energy from colonic fiber fermentation. ⁵⁹	Potentially 34–37% of metabolizable energy from fiber. ^{57, 60}	Unknown. Likely lower than great apes, based on diet composition.	Unknown. Likely to be higher than gibbons, similar to that of chimpanzees and lower than gorillas and orang-utans, based on diet composition.

Food hard/ toughness ^f	FILLER/PREF. Fig hardness very low; data unavailable for other FBFs. Max. toughness nonfruit highest, but most FBFs lowest, of all apes. ^{30, 38}	FILLER/PREF. Unknown. Hardness and toughness likely to be intermediate between chimpanzees and gorillas, based on diet composition.	STAPLE Hardness data unavailable. Max. mountain toughness second highest among apes. Mean toughness lower than orang-utans, but higher than chimpanzees. ^{30,38, 61}	STAPLE Max. hardness much greater other apes; max. toughness lower than African apes, but higher than gibbons. Mean hardness and toughness highest of apes. ^{30, 38, 60, 62-63}	FILLER/PREF. Data unavailable, but hardness and toughness of FBFs likely similar to gibbons.
Fluctuations in resource availability	FILLER/PREF. Relatively low fluctuations in fruit availability. ⁶⁴⁻⁶⁶ THV availability probably higher than Asia. ⁶⁵	STAPLE Relatively low fluctuations in fruit availability. ⁶⁴⁻⁶⁶ THV availability probably higher than Asia, ⁶⁵ especially in mountains.	STAPLE High fluctuations in fruit availability, particularly in dipterocarp forests and in Borneo. ^{64-66, 70}	FILLER/PREF. High fluctuations in fruit availability, particularly in dipterocarp forests. ^{66, 74}	FILLER/PREF. High fluctuations in fruit availability, particularly in dipterocarp forests. ^{66, 74}
Feeding competition	STAPLE Low intensity, high frequency. ⁷⁵	STAPLE High intensity, low frequency. ⁷⁵	FILLER/PREF. High intensity, low frequency. ⁷⁵	FILLER/PREF. Low intensity, low frequency. ⁷⁵	FILLER/PREF. Low intensity, low frequency. ⁷⁵
Group stability	STAPLE Stable over long term; over short term group cohesion declines with reduced fruit availability. ⁷⁶⁻⁸¹	FILLER/PREF. Stable. Occasional splitting of groups during lean periods in W. lowland, but less than chimpanzees. ⁶ Group split rates estimated at 5 every 63-200 group yr. ⁸⁴	FILLER/PREF. No group cohesion. Less social during periods of low fruit availability and in Borneo. ^{15, 85-86} but see also ref. 87.	STAPLE Very high; stable monogamous pairs. ⁸⁸⁻⁹³	STAPLE Very high; stable monogamous pairs. ⁹⁴⁻⁹⁶
Life history	FILLER/PREF. Age first reproduction 13.0-15.4 yo, inter-birth interval 5.1-6.2 yr. ⁹⁷	STAPLE Mountain age first reproduction 10.1 yo, interbirth interval 3.9 yr (Watts 1991a); W. lowland interbirth interval 5.9-6.6 yr. ⁸⁴ Other aspects W. lowland life history slower than	FILLER/PREF. Slowest of extant apes. Age first reproduction 15.4-15.7 yo, interbirth interval 7.0-9.3 yr. ⁹⁷	STAPLE Age first reproduction and interbirth interval 2.8 yr (mean of 3 species listed in ref. 102).	STAPLE Age first reproduction 6.0 yo; interbirth interval 3.0 yr. ¹⁰²

Table III (continued)

Trait	Chimpanzee	Bonobo	Gorilla mountain. ¹⁰⁰⁻¹⁰¹	Orang-utan	Gibbon	Siamang
Life history controlled for body size ^a	FILLER/PREF.	FILLER/PREF.	STAPLE	FILLER/PREF.	STAPLE	STAPLE
	Age first reproduction	Age first reproduction	Age first reproduction	Age first reproduction	Age first reproduction	Age at first reproduction:
	0.09, interbirth interval 0.17	0.13, interbirth interval 0.19	0.16, interbirth interval 0.17	0.10, interbirth interval 0.22	interbirth interval 0.22	0.08, interbirth interval 0.05.
	FILLER/PREF.	FILLER/PREF.	STAPLE	FILLER/PREF.	FILLER/PREF.	STAPLE

^a STAPLE=indicative of relatively greater importance of staple FBF exploitation, compared to other ape species; FILLER/PREF. = indicative of relatively greater importance of filler FBF/preferred food exploitation. Classifications are ours.

^b Where a value is followed by a range of values in parentheses, these values correspond to the mean and range, respectively.

^c Data used exclude orang-utan P42, which was a publisher's error and was actually a siamang (*Chivers pers. comm.*), and include an adult female not included in the original data set (*Chivers unpubl. data*). This second orang-utan was smaller than P42, but the relative sizes of the different gut compartments and the coefficient of gut differentiation were nearly identical.

^d Using data on body masses and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997) when body masses were unavailable for a species/sex from Chivers and Hladik. Values for females represent residuals from the polynomial power regression of colon surface area and body mass ($\beta=0.704$, $R^2=0.496$, $df=13$, $p=0.05$), which produced the only significant predictive model for females. This model did not include gorillas, as data were available only on male gorillas from Chivers and Hladik. Values representing means of males and females contained all ape taxa, and are derived from unstandardised residuals from the linear regression of colon surface area and body mass ($\beta=0.953$, $R^2=0.908$, $df=15$, $p<0.001$), which produced a model with very similar predictive power as that from any polynomial regression. Negative values indicate smaller than expected colon surface area for a given body size.

^e Unstandardised residuals from the linear regression of mean retention time against wild female body mass for 16 simple-stomached primate species ($\beta=0.525$, $R^2=0.276$, $df=15$, $p=0.037$). These included data on mean retention time for the species analyzed by Clauss *et al.* (2008), mean retention time data from sources listed in this study, plus *Hylobates hooleck* (Ahsan 1994) and *H. muelleri* × *albibarbis* (*agilis*) (McConkey 2000). Body mass data on wild females from Smith and Jungers (1997) were used in preference to data on captive body masses used by Clauss *et al.* (2008), as 1) the captive primates were heavier than their wild counterparts (mean body mass of the species listed by Clauss *et al.* was 3.6 kg higher than when using body mass estimates for the same species in the wild from Smith and Jungers), probably as a result of increased fat accumulation and growth, which may not be reflected in mean retention time; and 2) orang-utans and gibbons were not included in the study of Clauss *et al.*, but were important to include in this analysis. Alternative polynomial regressions did not produce better models than did linear regression. Negative values indicate faster than expected mean retention time for a given body size.

^f In studies of primate food physical properties to date, most authors have concentrated on either the mean and/or maximum values for foods consumed, which we also use in our comparisons. It should be noted, however, that, in addition to these parameters, the dietary importance of the food item, i.e., cumulative lifetime loading, is also likely to have a

strong influence on crano-dental form (cf. Taylor 2006a, b). This has particular relevance with respect to the distinction between staple and filler FBFs. Such a comparison has not been made herein as, to our knowledge, published data with which to make this assessment are not yet available for any ape species.

[§] Unstandardized residuals from the linear regression of interbirth interval ($\beta = 0.582$, $R^2 = 0.763$, $df = 27$, $p < 0.001$) and age at first reproduction ($\beta = 0.827$, $R^2 = 0.685$, $df = 28$, $p < 0.001$) against wild female body mass for 28 nonhuman primate species. The test for interbirth interval excluded *Microcebus murinus*, which was an outlier due to its small size (62 g). Data are from Barrickman *et al.* (2008), with the addition of life history data for bonobos from Takahata *et al.* (1996) and Fruth (*pers. comm.* in Knott 2001), and siamangs from Harcourt and Schwartz (2001), plus body mass data for these species from Smith and Jungers (1997). Alternative polynomial regressions did not produce better fitting models than did linear regression. Negative values indicate faster than expected life history variables for a given body size.

References: 1. Doran *et al.* (2002a); 2. Pontzer and Wrangham (2004); 3. Kano and Mulawwa (1984); 4. Doran-Sheehy *et al.* (2004); 5. Goldsmith (1999); 6. Remis (1997b); 7. Tutin (1996); 8. Yamagiwa and Mwanza (1994); 9. Yamagiwa *et al.* (1996); 10. Goldsmith *et al.* (1998); 11. Watts (1991b); 12. Singleton *et al.* (2009); 13. Chivers (2001); 14. Masi (2008); 15. Knott (1999); 16. Andrews and Groves (1976); 17. Bertram *et al.* (1999); 18. Bertram and Chang (2001); 19. Cannon and Leighton (1996); 20. Preuschoft and Demes (1984); 21. Fleagle (1976); 22. Hunt (1989); 23. Furuichi *et al.* (2008); 24. Rodman (1984); 25. Rodman and Mitani (1987); 26. McConkey (2005); 27. Kay (1981); 28. Smith *et al.* (2005); 29. Ungar (2007); 30. Vogel *et al.* (2008); 31. Ungar (2004); 32. Harrison and Chivers (2007); 33. Ungar and Kay (1995); 34. Maas (1991); 35. Maier (1984); 36. Deane (2009); 37. Pickford (2005); 38. Taylor *et al.* (2008); 39. Taylor (2006a); 40. Taylor (2006b); 41. Daegling (1990); 42. Delson and Andrews (1975); 43. Smith and Jungers (1997); 44. Orgeldinger (1994); 45. Chivers and Hladik (1980); 46. Chivers (*unpubl. data*); 48. Milton and Demment (1988); 49. Caton (1999); 50. Remis (2000); 51. Remis and Dierenfield (2004); 52. Caton *et al.* (1999); 53. Ahsan (1994); 54. McConkey (2000); 55. Remis (2002); 56. Schmidt *et al.* (2005); 57. Conklin-Brittain *et al.* (2006); 58. Hohmann *et al.* (2010); 59. Popovich *et al.* (1997); 60. Harrison (2009); 61. Elgart-Berry (2004); 62. Cheyne *et al.* (in prep); 63. Vogel *et al.* (2009); 64. Harrison *et al.* (2010); 65. Knott (2005); 66. van Schaik and Pfannes (2005); 67. Badrnan and Malenky (1984); 68. Hohmann *et al.* (2006); 69. White (1998); 70. Marshall *et al.* (2009a); 71. Cheyne (2010); 72. Marshall and Leighton (2006); 73. McConkey (1999); 74. Medway (1972); 75. Plavcan and van Schaik (1992); 76. Chapman *et al.* (1995); 77. Goodall (1986); 78. Hashimoto *et al.* (2003); 79. Itoh and Nishida (2007); 80. Matsumoto-Oda *et al.* (1998); 81. Wrangham (1977); 82. Fruth and Hohmann (1996); 83. Mulawwa *et al.* (2008); 84. Robbins *et al.* (2004); 85. Sugardjito (1986); 86. Utami *et al.* (1997); 87. van Schaik (1999); 88. Carpenter (1940); 89. Gittins (1980); 90. Islam and Feeroz (1992); 91. Leighton (1987); 92. Mitani (1990); 93. Tilson (1981); 94. Chivers (1974); 95. Chivers (1978); 96. Palombit (1996); 97. Wich *et al.* (2004b); 98. Takahata *et al.* (1996); 99. Fruth (*pers. comm.* in Knott, 2001); 100. Breuer *et al.* (2009); 101. Nowell and Fletcher (2007); 102. Harcourt and Schwartz (2001).

of terrestrial locomotion. However, contrary to expectations based on diet, the traveling traits of orang-utans indicate consumption of staple FBFs.

As the 4 ape genera differ greatly in body size and, consequently, energy requirements, an equal distance traveled or number of calories expended on traveling may not indicate equal costs between genera. The percentage of total energy expenditure allocated to travel may therefore be a more informative measure, as it is independent of body size. Data on gibbon and siamang energy expenditure to calculate this measure are not available, but it is estimated that chimpanzees spend 15.6% of their total energy on travel (Pontzer and Wrangham 2004); adult female and silverback male western lowland gorillas 36.0% and 28.8%, respectively (Masi 2008); and adult female and flanged male Bornean orang-utans 7.2–10.0% and 4.2–8.2%, respectively (Knott 1999). However, these figures are difficult to interpret, as it could be hypothesized that species for which preferred foods are more important should allocate a greater proportion of their total energy expenditure to travel, because they need to travel further, or a lesser proportion, because they have evolved a more energy-efficient mode of travel. In support of the latter hypothesis, of the species for which data are available, Bornean orang-utans typically consume the least FBFs and expend the lowest proportion of their total energy expenditure on travel, whereas gorillas consume the most FBFs and expend the highest proportion of their energy on travel. However, the travel of orang-utans appears much less energy efficient than that of chimpanzees and only slightly less efficient than that of gorillas (Table III), in contrast to this suggestion. In addition, the day range of orang-utans is also substantially shorter than that of chimpanzees, and day range has also been found to be related to lifetime reproductive output across mammals (Pontzer and Kamilar 2009; though the figures presented for apes do not conform perfectly to this prediction), further complicating matters. Thus, this dilemma cannot be resolved with the evidence currently available and, consequently, we do not consider this to be a useful measure for assessing harvesting adaptations for preferred foods in apes.

In summary, based on comparisons of traits expressed (Table III), gibbons, followed by siamangs, chimpanzees and bonobos, appear better adapted for harvesting preferred foods than orang-utans and gorillas, which seem better adapted for the exploitation of staple FBFs (Table IV).

Processing Traits

Many of the processing traits analyzed (Table III) are clearly related. In addition, their expression may also depend on the mechanical and chemical properties of the FBF exploited. Nevertheless, these traits may be grouped as representing either adaptations of the masticatory anatomy or digestive system, and instructive comparisons can be made when these traits are considered in relation to FBF properties.

Comparison of the combined adaptations of the teeth and jaw indicates that: chimpanzees and bonobos show relatively little specialization, indicating a diet composed mostly of soft fruits; gorilla jaws are robust and their dental adaptations are congruent with a high degree of folivory (more so in mountain than lowland gorillas); orang-utans are adapted for feeding on hard foods, with some folivory; gibbons are relatively unspecialized, indicating a primarily frugivorous diet, with some folivory; and siamangs are similar to gibbons, but with more developed molar

Table IV Comparisons of relative rankings on a FBF continuum, based on observed diet, compared to expected traits for species reliant on staple FBFs vs. preferred foods, supplemented with filler FBFs

Comparison	Chimpanzee	Bonobo	Mountain gorilla	Lowland gorilla	Orang-utan	Gibbon	Siamang
Dietary importance	3	2–5?	7	5	2	1	3
Harvesting traits	3	4	6	5	7	1	2
Processing traits	3	?	7	6	6	1	2
Repercussions	1	2?	7	7	1	4	5
Combined traits	2	?	7	6	5	1	3

Scores are from 1 (reflecting high importance of preferred foods) to 7 (reflecting high importance of staple FBFs), and are based on our assessment of the available data (see Table III and text). Equal scores indicate tied ranks and question marks indicate cases where data are insufficient for complete comparison. Rank differences do not necessarily reflect the extent of differences between species, i.e., a rank difference of 2 between 2 apes does not necessarily indicate twice as large a difference as a rank difference of 1.

shearing crests, in line with the greater importance of leaves in their diet. Thus, these adaptations suggest consumption of staple FBFs in gorillas and orang-utans, with decreasing importance of (filler) FBFs through siamangs, gibbons, and chimpanzees/bonobos.

A similar picture emerges when comparing the apes' digestive adaptations. Even when body size is accounted for, the chimpanzee digestive system appears relatively poorly adapted for FBF exploitation, though chimpanzees are apparently still able to achieve a fairly high level of fibre digestion. Data are unavailable for bonobos. The colons of gorillas and orang-utans are voluminous, and mean retention time of digesta is consequently high, enabling high levels of fiber digestion and indicating a high importance of FBFs in the diet. Surprisingly, gorilla colon surface area was not larger than expected for their body size; this may be because gorillas are so large that they do not need to maximize colon surface area relative to body size to ensure efficient fiber digestion. Even when their small body size is accounted for, the gibbon's digestive system does not appear particularly well adapted for high levels of fibrous FBF consumption, and it is likely that gibbons are substantially less efficient at fiber digestion than the great apes. This suggests greater importance of preferred foods in their diet, supplemented with filler FBFs, in line with observations on diet. Siamangs exhibit a relatively large colon surface area in relation to their body size. To our knowledge, data on mean retention time in siamangs are not available, and it may be that siamang mean retention time is also relatively long in relation to their body size, which we have conservatively assumed not to be the case. Nevertheless, siamangs are probably still less efficient at digesting fiber than hominoids, but more efficient than gibbons, owing to their larger colon surface area and more specialized molars, enabling them to masticate the leaves they consume more thoroughly. In neither of these smaller apes do their digestive adaptations indicate a strategy of maximizing energy acquisition through rapid passage and reduced digestion of foods, as in some small mammalian herbivores (Foley and Cork 1992). This is not surprising, as hylobatid body mass is still relatively large compared to that of the small herbivores for which this strategy may apply, e.g., herbivorous rodents. Again, this picture is somewhat at odds with that implied by dietary comparisons.

Taken together, this analysis of processing traits indicates adaptation toward exploitation of staple FBFs in gorillas and orang-utans, and decreasing importance of filler FBFs in chimpanzees and possibly bonobos, followed by siamangs and gibbons (Table IV). In particular, the substantial processing traits of orang-utans indicate consumption of relatively poor-quality FBFs, particularly considering their relatively low actual levels of FBF consumption, compared to chimpanzees and mountain gorillas. Further, in line with expectations based on the degree of observed folivory, processing adaptations appear more strongly expressed in siamangs than gibbons: siamang molar tooth morphology is better suited for leaf consumption; body mass and colon surface area, including once controlled for body mass, are larger; and mean retention rate and fiber digestion coefficient are likely to be higher, though data are currently unavailable for these last 2 variables.

Repercussions

In agreement with the preceding analysis of cranio-dental and digestive adaptations, gorilla and orang-utan diets appear higher in fiber than those of chimpanzees, siamangs, gibbons, and probably also bonobos. Comparative analysis of the mechanical properties of FBFs is complicated by the lack of published data on gorilla, chimpanzee, bonobo, and siamang FBFs, particularly for hardness. Nevertheless, the available data indicate a relatively hard and tough diet in orang-utans; a tough, and we suspect hard, though these data are currently unavailable, diet in gorillas; an occasionally tough, but generally relatively physically unchallenging, diet in chimpanzees; and a diet of intermediate hardness and low toughness in gibbons (Cheyne *et al.*, in prep; Elgart-Berry 2004; Vogel *et al.* 2008; Vogel *et al.* 2009). Data are currently unavailable for bonobos and siamangs, but it is likely that their diets are mechanically similar to, if not slightly more challenging than, that of chimpanzees and gibbons, respectively, based on observed dietary proportions.

African apes appear to experience lower fluctuations in resource availability than their Asian counterparts (van Schaik and Pfannes 2005; Table III); the importance of this is discussed in detail in the next section. With the exception of the relatively high intensity of gorilla male–male competition, the remaining traits in this section are all indicative of staple FBF exploitation in gorillas and lower importance of FBFs in orang-utans. The remaining siamang repercussions all suggest high importance of FBFs, those of gibbons are largely similar to siamangs, and those of chimpanzees and bonobos are more mixed. Expected repercussions for species feeding largely on staple FBFs, relative to the other apes, are seen in chimpanzees and bonobos for resource availability and feeding competition, and for gibbons in feeding competition and group stability. Chimpanzees, bonobos, and gibbons all exhibit relatively slow life history, once corrected for body size, which might be expected in species focusing on preferred food exploitation. Similarly, the more folivorous siamang has an accelerated life history compared to gibbons, once corrected for differences in body mass. As noted previously, these life history observations should be treated with some caution, owing to a possible influence of other nonfeeding related pressures on life history parameters. We summarize the FBF reliance continuum based on these expected repercussions in Table IV.

Combining these results for harvesting and processing traits, plus expected repercussions of importance of staple FBFs vs. filler FBFs/preferred foods in the diet, it appears that, overall, mountain gorillas are best adapted for staple FBF exploitation, followed closely by lowland gorillas and orang-utans, and with siamangs, chimpanzees, and gibbons relatively more adapted for exploitation of preferred foods, supplemented with filler FBFs (Table IV). It is impossible to draw accurate conclusions regarding the traits exhibited by bonobos for FBF exploitation, owing to a lack of comparable data in many cases.

Discussion

Unsurprisingly, gibbons and gorillas appear to possess traits that reflect reasonably faithfully the observed importance of preferred foods/filler FBFs and staple FBFs, respectively, in their diets. This is not to downplay the critical role of gibbon filler FBFs during “crunch” periods, but merely reflects the generally lower importance of FBFs in their diet. Chimpanzees and siamangs occupy similar positions on the diet and adaptation continua, in line with the broadly similar importance of staple FBFs vs. filler FBFs/preferred foods in their diets, although siamangs possess a greater number of repercussion traits expected from a staple FBF-reliant individual, due to their relatively fast life history. Owing to a paucity of data, it is impossible to undertake any real assessment of traits in bonobos and, hence, we provide no further detailed discussion of this species.

The most notable positional changes between the 2 continua concern 1) orang-utans, which express many more harvesting and processing traits indicating reliance on FBFs than would be expected based on their observed FBF reliance; and 2) the positional switch between the diet and repercussions spectrum for chimpanzees and gibbons/siamangs. We believe there are 2 main reasons for this: the nature of the FBFs typically consumed by each ape, and differences in the availability/quality of preferred fruits and FBFs between African and Asian ape habitats (*cf.* Lambert 2007; Marshall *et al.* 2009b).

Chimpanzees appear to rely on figs as their main FBF, and gibbons and siamangs also rely on figs to a large extent. Unlike the THV fallen back on by gorillas and the bark/leaves fallen back on by Bornean (and possibly some Sumatran) orang-utans, figs have many characteristics typical of a preferred food. Although, as expected for a FBF, figs provide relatively low energy returns (4.4 kcal/min for orang-utans in Sabangau vs. a mean of 6.1 kcal/min for all fruits; Harrison 2009), contain reasonable amounts of fiber (neutral-detergent fiber: >31% dry matter and >51% organic matter; Conklin and Wrangham 1994; Harrison 2009; Knott 1999), and produce fruit fairly consistently over time (Janzen 1979; Leighton 1993; Marshall 2004; Raemaekers 1978; Raemaekers *et al.* 1980; Tweheyo and Lye 2003; Wrangham *et al.* 1993), they occur at low density (mean 2.2 food stems/ha, vs. 15 for fruit, 10 for bark, and 26 for leaves in Sabangau; Harrison 2009), their large crop sizes are patchily distributed in clumps (Raemaekers 1978; Raemaekers *et al.* 1980) and have low toughness compared to other fruits, leaves, and bark (Taylor *et al.* 2008; Harrison 2009; Vogel *et al.* 2008, 2009). As a result, they are easily processed (Wrangham *et al.* 1993).

Thus, the relative ease of processing figs, and their patchy spatial distribution, appear to have resulted in a less extreme tradeoff in adaptations for FBF (processing traits) vs. preferred food (harvesting traits) consumption in chimpanzees compared to orang-utans. Further, the selective pressures experienced by chimpanzees in some other areas, where the primary FBF used is other fruit species (Doran 1997; Yamakoshi 1998), should be very similar to those experienced by populations reliant on figs as their main FBF. This conclusion resonates with Lambert's (2007) scheme highlighting the importance of FBF quality in distinguishing the FBF strategies employed by gorillas (low quality) vs. chimpanzees (high quality). In this context, the observation of high fig consumption in Sumatran orang-utans in Ketambe (Wich *et al.* 2006) is anomalous, but the importance of figs in other Sumatran populations, not to mention in extinct populations on mainland Southeast Asia, where the majority of orang-utan evolution post divergence from the last common ancestor with the African apes occurred, remains unclear. Gibbons and siamangs also rely on figs as their main FBF, supplemented with leaves, and show a similar lack of extreme adaptations of the teeth, jaw, and digestive system as in chimpanzees.

Relative to the other apes, orang-utan teeth, jaws and digestive system are all indicative of exploitation of staple FBFs, despite the lack of staple FBFs in their diet and the relatively low levels of FBF consumption, compared to African apes. As discussed previously, differences in the properties of chimpanzee and orang-utan FBFs probably explain these observations with respect to these 2 genera. Further, it seems that the neutral-detergent fiber content of leaves eaten by African apes (western lowland gorilla, Bai Hokou, Central African Republic: 63.93% dry matter, Remis *et al.* 2001; Campo, Cameroon: 46.1%, Calvert 1985; chimpanzees, Kibale: 41.5%, Wrangham *et al.* 1991) is less than that of leaves eaten by orang-utans (Gunung Palung: 67.5% organic matter, Knott 1998; Sabangau: 48.3%, Harrison 2009). This is especially true considering that these measurements for African apes are percentage dry matter, which contains ash, whereas those for orang-utans are percentage organic matter, which excludes ash and that, consequently, produces higher apparent estimates of fiber content. The neutral-detergent fiber content of piths commonly consumed as FBFs by gorillas (western lowland gorilla, Bai Hokou: 67.41% dry matter, Remis *et al.* 2001; Campo: 55.9%, Calvert 1985) and chimpanzees (Kibale: 50.5%, Wrangham *et al.* 1991) is also lower than orang-utan bark (Gunung Palung: 74.3% organic matter, Knott 1999; Sabangau: 61.3%, Harrison 2009). Further, gorillas possess more highly developed molar shearing crests than orang-utans (Kay 1981; Ungar and Kay 1995), enabling them to break their food down into smaller pieces and facilitating fiber digestion. Development of such high shearing crests in orang-utans may be prohibited by the hard nature of their FBFs (and certain fruits, such as *Mezzetia leptopoda/parviflora*) and consequent need for thick molar enamel (Cheyne *et al.*, in prep; Kay 1985; Vogel *et al.* 2008). There also appears to be less protein in orang-utan bark and leaves (Gunung Palung: 7.1% and 13.7% organic matter, respectively, Knott 1998; Sabangau: 10.0 and 11.9%, Harrison 2009) than in the piths and leaves eaten by gorillas (Bai Hokou: all vegetation 18.86% dry matter, Remis *et al.* 2001; Campo: leaves 16.6%, Calvert 1985) and chimpanzees (Kanyawara: pith 9.3% dry matter, leaf 24.1%, Wrangham *et al.* 1991). Similarly, mean toughness of nonfruit foods consumed by orang-utans is also higher than for African apes (Taylor *et al.* 2008).

Thus, orang-utan FBFs appear to be of lower quality and more mechanically challenging than those used by African apes and the hylobatids, which we suggest explains the orang-utan's position on the processing spectrum. This may be influenced further by the physically challenging nature of some of the more preferred foods eaten by orang-utans, such as seeds (Harrison 2009; Vogel *et al.* 2008, 2009).

Southeast Asian rain forests are thought to experience more frequent and longer periods of low fruit availability relative to African forests, owing to community-level mast fruiting, which is unique to the region (van Schaik and Pfannes 2005). Further, the availability of nutritious THV in Africa has been suggested to be higher than in Southeast Asia (Knott 2005). In light of this, it is not surprising that, though Bornean orang-utans have been observed to enter prolonged periods of energy shortfall (Harrison *et al.* 2010; Knott 1998, 1999), similar observations have yet to be reported in African apes (Conklin-Brittain *et al.* 2006; Knott 2005; Masi 2008; Rothman *et al.* 2008), or in Sumatran orang-utans in the highly productive forests of Ketambe (Wich *et al.* 2006). Thus, it is possible that greater energetic stress in orang-utans, particularly in Borneo, has led to the evolution of more specialized food-processing abilities, in order to obtain maximum energy from poor-quality FBFs and to take maximum advantage of brief periods where high-quality foods are abundant (*cf.* Knott 1998; Leighton 1993; Wheatley 1982, 1987). Such a premium on energy may not exist for African apes (Conklin-Brittain *et al.* 2006; Harrison *et al.* 2010; Knott 2005; Masi 2008; Rothman *et al.* 2008).

Our analysis of processing traits may also be complicated by the presence of “wadging” behavior in some ape species, in which fibrous foods are processed through mastication, sucking out the nutritious juices and spitting out the remaining fibrous wad. This behavior is commonly seen in chimpanzees (Lambert 1999; Wrangham *et al.* 1991; Yamagiwa and Basabose 2009), and occurs occasionally in both bonobos (Kano 1983) and orang-utans (Galdikas 1982; Vogel *et al.* 2008; M. E. Harrison and A. J. Marshall, *pers. obs.*), but is not seen in gorillas (Yamagiwa and Basabose 2009), or, to our knowledge, in gibbons or siamangs. Wadging is thought to allow consumption of FBFs without ingesting large amounts of fiber into the gut, allowing more efficient harvesting of fruit and leaf crops (Yamagiwa and Basabose 2009). We suggest 2 additional explanations, which are compatible both with Yamagiwa and Basabose's hypothesis and with each other. First, if the overall resources available to a consumer are of low quality, as seems to be the case for Asian apes, then consumers may need to ingest the more fibrous parts of foods, in order to extract the energy from the fiber to meet their energetic needs. Second, a high incidence of wadging likely indicates decreased fiber digestion ability, which might be expected in taxa that do not rely on fibrous FBFs for extensive periods. This suggestion receives preliminary support through the comparison of the fiber contents of wild diets in Table III.

The positional switch between chimpanzees and gibbons/siamangs in the repercussions spectrum may also be at least partially a consequence of differences in food availability between African and Southeast Asian ape habitats. Lower and more unpredictable fruit availability in Southeast Asia compared to Africa has been suggested to have led to an increase in the spatial separation of Asian ape females, causing males to adopt one of two strategies to maintain access to females that are

not seen in African apes: monogamy (hylobatids) and range expansion to incorporate the ranges of numerous females (orang-utans) (Harrison and Chivers 2007). A similar explanation has also been proposed to explain the less cohesive social structure of chimpanzees vs. bonobos (Lambert 2007; Malenky *et al.* 1994; White 1998). Such a change in gibbons and siamangs would have resulted in high group stability and, consequently, increased feeding competition, vs. chimpanzees and orang-utans. Coupled with their small body size, consequently fast life history, and increased folivory in siamangs, this explains the observed positional switches in the repercussions spectrum among chimpanzees, siamangs, and gibbons. In itself, the small body size of hylobatids argues in favor of greater importance of preferred foods and higher-quality FBFs, such as figs, as it is this that enables the employment of energy-efficient brachiation for improved harvesting of patchily distributed foods (Cannon and Leighton 1994; Cannon and Leighton 1996; Leighton 1993; Marshall *et al.* 2009c; Preuschoft and Demes 1984, 1985).

The analysis in this article presents an apparent paradox: The availability of preferred foods (fruits) appears lower in Southeast Asia than in Africa, yet the importance of FBFs appears higher in African apes than in their Asian counterparts. Presumably, this is related to 1) lower availability and quality of FBFs in Southeast Asia, as suggested previously by Knott (2005), and 2) greater energetic stress in Southeast Asia apes, as discussed previously. Based on simple optimal foraging theory (Stephens and Krebs 1986), reduced FBF quality would result in decreases in preference for FBFs and a consequent drop in their consumption. That is, as the gap in quality between preferred and FBFs increases, lower levels of preferred food availability may be required before FBFs form part of the optimal diet. This might be compounded by energetic stress, resulting in pressure to maximize dietary quality by consuming the best foods, instead of switching to less energy-rich, but more easily found, FBFs. Stated simply, African apes may begin consuming FBFs at higher levels of preferred food availability than Asian apes, owing to generally higher FBF quality in Africa, though intracontinental differences between taxa also appear apparent, and more formal comparisons are required to test this hypothesis. Thus, when viewed from the perspective of FBF instead of preferred food quality and availability, this apparent paradox disappears. Though this may be true, these are unlikely to be the only effects of reduced availability or quality of FBFs; declines in density are particularly likely, for example (Cant 1980; Marshall and Leighton 2006; Marshall *et al.* 2009b; Mather 1992; Wich *et al.* 2004a).

Comparison of differences in traits expressed by gibbons and siamangs are broadly in line with expectations based on the higher degree of folivory seen in siamangs. The most important underlying adaptations expressed by siamangs in response to this diet appear to be an increase in body and gut size, which probably have knock-on effects on travel speed, travel efficiency and day range, and increased development of molar shearing crests. These adaptations, and a shift to a less spatiotemporally variable diet, are also likely to be linked to the relatively faster life history profile seen in siamangs, particularly once controlled for body size.

In summary, the general hypotheses proposed by Marshall and Wrangham (2007)—that adaptations for exploiting FBFs tend to enhance processing, whereas adaptations for exploiting preferred foods tend to enhance harvesting—are supported by this analysis of apes. Further, relative positions on the diet and traits continua generally

concur, indicating that classification of FBFs as staple and filler, based on dietary importance, is a potentially useful distinction. However, some observations appear at odds with these hypotheses, especially for orang-utans, which can generally be explained by variations in the quality/availability of preferred/FBFs used. In particular, this includes differences in: 1) the importance of figs, THV, leaves, and bark as FBFs between ape taxa and 2) the availability of fruit between habitats, as a result of community-level mast-fruiting in Southeast Asia. Thus, as suggested previously (Marshall *et al.* 2009b), this analysis 1) supports the contention that both the importance of FBFs in the diet (Marshall and Wrangham 2007) and their quality (Lambert 2007) should be considered in tandem when attempting to understand the influence of FBFs use on ape ecology and 2) that these are key influences on ape ecology and, hence, are likely to have been of crucial importance in ape, and probably also human, evolution.

Acknowledgments We originally presented this article at the 2nd Congress of the European Federation for Primatology in Prague, September 2007. M. E. Harrison's attendance at this meeting was funded by an Avrith Travel Grant, from the Department of Physiology, Development and Neuroscience, University of Cambridge. The Howard Hyam Wingate Foundation and the Orang-utan Tropical Peatland Project provided partial funding for this project. We thank various delegates of the 2nd European Federation for Primatology Congress, Erin Vogel, David Chivers, and 2 anonymous reviewers for comments that improved the manuscript, and CIMTROP for supporting M. E. Harrison in his research in Indonesia.

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