Strategies for the Use of Fallback Foods in Apes

Mark E. Harrison • Andrew J. Marshall

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 hyllobatids, 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 hyllobatids, 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.
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
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 Hyllobatidae, 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-Sheehey 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 I). 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,
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).

**Table I** Consumption of potential FBF types and total FBF use by apes

| Ape            | Leaves   | THV/pith | Bark   | Figs        | Mean total FBF | Mean total FBF exc. figs |
|----------------|----------|----------|--------|-------------|----------------|--------------------------|
| Chimpanzee     | 16 (0–56)| 7 (0–59) | 4 (0–41) | 37–41 (?–91) | 66             | 27                       |
| Bonobo         | 14 (0–28)| 25 (0–100)| 2 (0–11) | Generally low | 0–39          | 0–39                     |
| Lowland gorilla| 31 (6–51)| 18 (7–43)| 11 (0–32) | Low         | 29             | 29                       |
| Mountain gorilla| Low      | 91 (85–96)| 3 (0–6)  | 0           | 94             | 94                       |
| Sumatran orang-utan | 16 (11–20) | Low     | 2 (2–3)  | 36 (ca. 23–50) | 54             | 18                       |
| Bornean orang-utan | 17 (0–56)| Low     | 7 (0–67) | Low         | 24             | 24                       |
| Gibbons⁸       | 26 (2–72)| 0        | 0       | 24 (17–45)  | 50             | 26                       |
| Siamang⁹       | 33 (17–48)| 0       | 0       | 29 (22–43)  | 62             | 29                       |

⁸ Also includes other miscellaneous and minor food types.
⁹ Also includes roots.

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 McNeilage 2003; eastern lowland gorillas, G. b. graueri: Yamagiwa et al. 1994, 1996; western lowland gorillas, G. gorilla gorilla: Doran and Greer 2002; Doran and McNeilage 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 McNeilage 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 ≥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 1). 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 FBFsa

| 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           | Specializedb                                 | 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 loads2      | Lower resistance to mandibular loads          |
| Female body massc          | Large                                         | Small                                         |
| Colon surface aread        | Large                                         | Small                                         |
| Colon surface area controlled for body masse | High                                      | Low                                           |
| Coefficient of gut differentiationf | High                                    | Low                                           |
| Mean retention time of food in gut | Slowg                                   | Fast                                          |
| Mean retention time controlled for body massh | High or very lowg | Intermediate                                |
| Fiber digestion coefficient | High                                         | Low                                           |
| Repercussions/other        |                                               |                                               |
| Percentage fiber in wild dietl | High                                    | Low                                           |
| Food hard/toughness        | High                                          | Low                                           |
| Fluctuations in resource availability | Low                                      | High                                           |
| Trait | Heavy reliance on (staple) FBF indicated by... | Heavy reliance on preferred foods indicated by... |
|-------|---------------------------------------------|---------------------------------------------|
| Feeding competition | Low | High |
| Group stability | High | Low |
| Life history | Fast | Slow |
| Life history controlled for body size | 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
| Trait | Chimpanzee | Bonobo | Gorilla | Orang-utan | Gibbon | Siamang |
|-------|------------|--------|---------|------------|--------|---------|
| Harvesting | | | | | | |
| Day range | Eastern: 3.5 km/d | 2.4 km/d (0.4–6.0) | W. lowland: 1.9 km/d (1.2–2.6) | Females, Borneo: 0.6 km/d (0.2–1.0); Sumatra: 0.9 km/d (0.7–1.1) | Mean all species in ref. 13: 1.0 (0.8–1.8). | 0.8 km/d (0.6–0.9) |
| | (2.2–4.8); western: 1.7 km/d (1.0–2.4) | | E. lowland: 1.5 km/d (0.8–2.1) | | | |
| | | | mountain: 0.8 km/d (0.5–1.3) | | | |
| | | | | | | |
| FILLER/PREF. | | | | | | |
| Travel efficiency (kcal/m) | | | | | | |
| Males | Males expend 0.09 | Unknown. Likely similar to that of chimpanzees, based on similarities in travel modes and body mass. | W. lowland silverback males expend 0.58 and adult females 0.33 kcal/m walked. | Bornean flanged males expend 0.43–0.47 and adult females 0.23–0.26 kcal/m traveled. | Unknown, but 80% of travel is via brachiation, a very efficient mode of travel. | |
| Females | 0.08 kcal/m walked. | | | | Unknown, but typically travel via brachiation and costs therefore likely to be similar to/slightly greater than gibbons. | |
| | | | | | | |
| FILLER/PREF. | | | | | | |
| Travel speed (m/s) | Walking speed 0.78–0.88 | Walking speed unknown. Average mean ranging rate 274 m/h. | W. lowland walking speed 0.65–0.75 m/s. | Distance traveled/h up to 10 times lower than chimpanzees. | ≥26 m/s. | Fast, but slightly slower than gibbons. |
| | | | | | | |
| INTERMEDIATE | | | | | | |
| Processing | | | | | | |
| Molar morphology | Enamel thickness intermediate (relative thickness on second lower molar 3.1%). | Relative enamel thickness within chimpanzee range. | Thin enamel (~23.4%) and most highly developed molar shearing crest of all apes. | Very thick enamel (33.8%, thickest of all extant primates), indicating adaptation for consuming hard foods. | Intermediate enamel (3.02%, range: 16.3–7.8%). | Thin enamel (~19.2%) and highly-developed molar shearing crest. |
| | | | and most highly developed molar shearing crest of all apes. | | | |
| | | | indicating adaptation for consuming hard foods. | | | |
| | | | >25, 26, 27, 28 | | | |
| | | | Relative enamel thickness indistinguishable from that of gorillas. | | | |
| | | | Least developed shearing crest of all apes and flat occlusal relief. | | | |
| | | | | | | |
| | | | | | | |
| | | | | | | |
| Trait                      | Chimpanzee | Bonobo | Gorilla | Orang-utan | Gibbon | Siamang |
|---------------------------|------------|--------|---------|------------|--------|---------|
| Surface slope height      |            |        |         |            |        |         |
| In between chimpanzees and gorillas. |            |        |         |            |        |         |
| Crenate occlusal surfaces on molars to reduce risk of tooth shatter. |            |        |         |            |        |         |

| Incisor morphology        |            |        |         |            |        |         |
| Pronounced mesiodistal and cervico-incisal crown curvatures, and wide incisors, indicating soft-fruit consumption. |            |        |         |            |        |         |
| Enlarged spatuliform lower incisors with permanently sharp cutting edges, possibly for meat eating. |            |        |         |            |        |         |

| Mandibular morphology     |            |        |         |            |        |         |
| Jaw least robust of great apes; decreasing robusticity from west to east. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 40.4 kg (mean 3 species in ref. 43). |            |        |         |            |        |         |

| Colon surface area        |            |        |         |            |        |         |
| 1812–2925 cm² |            |        |         |            |        |         |

| Incisor crown morphology  |            |        |         |            |        |         |
| Incisor crown morphology intermediate between that of chimpanzees and gorillas, but overwhelmingly frugivorous, closely resembling that of chimpanzees. |            |        |         |            |        |         |

| Mandibular morphology     |            |        |         |            |        |         |
| No consistent differences from chimpanzees. |            |        |         |            |        |         |

| Jaw most robust of great apes; greatest robusticity in mountain gorillas. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 33.7 kg. |            |        |         |            |        |         |

| Colon surface area        |            |        |         |            |        |         |
| Unknown |            |        |         |            |        |         |

| Jaw robusticity intermediate between that of chimpanzees and gorillas; higher load-resistance abilities in Borneo. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 80 kg (mean 3 species in ref. 43) |            |        |         |            |        |         |

| Jaw relatively weak and mandibular body “gracile” compared to great apes. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 35.7 kg (mean 2 species in ref. 43). |            |        |         |            |        |         |

| Jaw relatively weak and mandibular body “gracile” compared to that of great apes. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 4,813 cm² (male). |            |        |         |            |        |         |

| Jaw relatively weak and mandibular body “gracile” compared to that of great apes. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 10.7 kg. |            |        |         |            |        |         |

| Jaw relatively weak and mandibular body “gracile”. |            |        |         |            |        |         |

| Female body mass          |            |        |         |            |        |         |
| 1557 cm² |            |        |         |            |        |         |

| Jaw relatively weak and mandibular body “gracile”. |            |        |         |            |        |         |
| Trait                                      | Chimpanzee                          | Bonobo | Gorilla                      | Orang-utan                         | Gibbon                              | Siamang                             |
|-------------------------------------------|-------------------------------------|--------|------------------------------|------------------------------------|-------------------------------------|-------------------------------------|
| Colon surface area controlled for body    | Females: 1271.4; mean both sexes:   | Unknown| Mean both sexes: 32.5        | Females: 3286.9; mean both sexes: 974.5 | Females: 212.7; mean both sexes: 44.4 (mean 2 species) | Females: 150.7                      |
| mass³                                      | 1250.0                              |        |                              |                                    |                                     |                                     |
| Coefficient of gut differentiation        | 1.16;⁴⁵                            | Unknown| 1.62;⁴⁵                      | 1.08;⁴⁵–⁴⁶;⁵⁶                      | 2.05 (mean 2 species);⁴⁵             | 0.92;⁴⁵                            |
| Mean retention time                       | 37.7 h in captivity on high-fiber   | Unknown| 50–58.2 h in captivity⁶⁰–⁶¹ | 73.7 h in captivity⁵²              | 11–27.8 h in wild⁵³–⁵⁴            | Unknown. Likely to be intermediate between that of gibbons and chimpanzees, based on gut morphology. |
|                                          |                                    |        |                              |                                    |                                     |                                     |
| Mean retention time controlled for body   | –6.5                                | Unknown| –10.2                        | 31.9                               | –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. |
| mass⁶                                      |                                    |        |                              |                                    |                                     |                                     |
| Fiber digestion coefficient               | 54.3% on high-fiber diet in captivity⁴⁸ | Unknown| 57.5% on high-fiber diet in captivity⁵³ | 59.4% on high-fiber diet in captivity⁵⁰ | 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. |
| Repercussions/other                       | STAPLE                              | STAPLE | STAPLE                       | FILLER/PREF                        | 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 contents⁵⁸ | Potentially 57.3% of metabolizable energy from colonic fiber fermentation;⁵⁹ | Potentially 34–37% of metabolizable energy from fiber⁷⁵, ⁹⁰ | 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. |
| Trait | Chimpanzee | Bonobo | Gorilla | Orang-utan | Gibbon | Siamang |
|-------|------------|--------|---------|------------|--------|---------|
| Food hardness & toughness | Filler/Pref. | Filler/Pref. | Staple | Staple | Filler/Pref. | Filler/Pref. |
| Fig hardness | Very low; data unavailable for other FBFs. Max. toughness non-fruit highest, but most FBFs lowest of all apes. | 30, 38 | | | | |
| Max. toughness | | | | | | |
| | | | | | | |
| Fluctuations in resource availability | Relatively low fluctuations in fruit, THV and leaf availability. | Low fluctuations in fruit, THV and leaf availability. | Relatively low fluctuations in fruit availability. | High fluctuations in fruit, THV and leaf availability. | Low intensity, high frequency. | Low intensity, high frequency. |
| THV availability | Probably higher than Asia. | | Probably higher than Asia. | | | |
| Feeding competition | Low intensity, high frequency. | Low intensity, high frequency. | High intensity, low frequency. | High intensity, low frequency. | Low intensity, low frequency. | Low intensity, low frequency. |
| Group stability | Stable over long term; over short term group cohesion declines with reduced fruit availability. | Stable over long term; over short term group cohesion generally declines with reduced fruit availability. | Stable. Occasional splitting of groups during lean periods in W. lowland, but less than chimpanzees. | No group cohesion. | Very high; stable monogamous pairs. | Very high; stable monogamous pairs. |
| Life history | Age first reproduction 13.0-15.4 yo, inter-birth interval 5.1-6.2 yr. | Age first reproduction 13-15 yo (Kuroda 1989), interbirth interval 6.25 yo (4.5–8.0). | Mountain age first reproduction 10.1 yo, interbirth interval 3.9 yr (Watts 1991a); W. lowland interbirth interval 5.9–6.6 yr. | Other aspects W. lowland life history slower than | Slowest of extant apes. | Age first reproduction 6.0 yo; interbirth interval 3.0 yr. |
| | | | | | | |
| | | | | | | |
| Trait          | Chimpanzee | Bonobo | Orang-utan | Gibbon | Siamang |
|---------------|------------|--------|------------|--------|---------|
| Life history  | FILLER/PREF. | FILLER/PREF. | STAPLE | FILLER/PREF. | STAPLE |
| Age first reproduction | 0.10, interbirth interval 0.17 | 0.10, interbirth interval 0.17 | 0.16, interbirth interval 0.17 | 0.12, interbirth interval 0.17 | 0.17, interbirth interval 0.17 |
| Interbirth interval | 0.17 | 0.17 | 0.17 | 0.17 | 0.17 |

- **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.

- *a* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values 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.

- *b* 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.

- *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 mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values 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.

- *e* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values 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 (Chiers *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.

- *f* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values exclude orang-utan P42, which was a publisher’s error and was actually a siamang (Chiers *pers. comm.*), and include an adult female not included in the original data set (Chiers *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.

- *g* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values exclude orang-utan P42, which was a publisher’s error and was actually a siamang (Chiers *pers. comm.*), and include an adult female not included in the original data set (Chiers *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.

- *h* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values exclude orang-utan P42, which was a publisher’s error and was actually a siamang (Chiers *pers. comm.*), and include an adult female not included in the original data set (Chiers *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.

- *i* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values exclude orang-utan P42, which was a publisher’s error and was actually a siamang (Chiers *pers. comm.*), and include an adult female not included in the original data set (Chiers *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.

- *j* Using data on body mass and gut dimensions of simple-stomached Old World primates from Chivers and Hladik (1980), supplemented with data from Smith and Jungers (1997). Values exclude orang-utan P42, which was a publisher’s error and was actually a siamang (Chiers *pers. comm.*), and include an adult female not included in the original data set (Chiers *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.
strong influence on cranio-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 \( (\beta = 0.763, R^2 = 0.582, df = 27, p < 0.001) \) 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 Mulavwa (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. Preusschoft 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 Dierenfeld (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. Bradan 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. Plavecan 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. Mulavwa 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. Tison (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
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.

| 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.
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 orangutan’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 wadge. 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/FFBs 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.

Open Access This article is distributed under the terms of the Creative Commons Attribution Noncommercial License which permits any noncommercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

References

Ahsan, M. D. F. (1994). Behavioural ecology of the hoolock gibbon (Hylobates hoolock) in Bangladesh. Ph.D. thesis, University of Cambridge, Cambridge.
Andrews, P., & Groves, C. P. (1976). Gibbons and brachiation. In D. M. Rumbaugh (Ed.), Gibbon and siamang, vol. 4 (pp. 167–218). Basel: Karger.
Badrian, N., & Malenky, R. K. (1984). Feeding ecology of Pan paniscus in the Lomako forest, Zaïre. In R. L. Susman (Ed.), The pygmy chimpanzee: Evolutionary biology and behavior (pp. 275–299). New York: Plenum Press.
Barrickman, N. L., Bastian, M. L., Isler, K., & van Schaik, C. P. (2008). Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild. Journal of Human Evolution, 54, 568–590.
Basabose, A. K. (2002). Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American Journal of Primatology, 58, 1–21.
Bertram, J. E. A., & Chang, Y. H. (2001). Mechanical energy oscillations of two brachiation gaits: measurement and simulation. American Journal of Physical Anthropology, 115, 319–326.
Bertram, J. E. A., Ruina, A., Cannon, C. E., Chang, Y. H., & Coleman, M. J. (1999). A point-mass model of gibbon locomotion. Journal of Experimental Biology, 202, 2609–2617.
Breuer, T., Hockenba, M. B.-N., Olejniczak, C., Parnell, R. J., & Stokes, E. J. (2009). Physical maturation, life-history classes and age estimates of free-ranging western gorillas—Insights from Mbili Bai, Republic of Congo. American Journal of Primatology, 71, 106–119.
Calvert, J. J. (1985). Food selection by western gorillas (G. g. gorilla) in relation to food chemistry. Oecologia, 65, 236–246.
Cannon, C. H., & Leighton, M. (1994). Comparative locomotor ecology of gibbons and macaques: selection of canopy elements for crossing gaps. American Journal of Physical Anthropology, 93, 505–524.
Cannon, C. H., & Leighton, M. (1996). Comparative locomotor ecology of gibbons and macaques: does brachiation minimize travel costs? Tropical Biodiversity, 3, 261–267.
Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and
Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2001). The feeding ecology of apes. In
Daegling, D. J. (1990).

Conklin, N. L., & Wrangham, R. W. (1994). The value of figs to a hind-gut fermenting frugivore: a
De Lathouwers, M., & Van Elsacker, L. (2005). Reproductive parameters of female
Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: comparisons
Chivers, D. J. (1974).

Chivers, D. J. (2001). The swinging singing apes: Fighting for food and family in Far-East forests. In
Chivers, D. J. (1978). Sexual behaviour of wild siamang. In D. J. Chivers & J. Herbert (Eds.),
Cheyne, S. M. (2010). Behavioural ecology of gibbons (Hylobates albibarbis) in a degraded peat-swamp
Doran, D. M., Jungers, W. J., Sugiyama, Y., Fleagle, J. G., & Heesy, C. P. (2002). Multivariate and
Doran, D., & Greer, D. (2002). The influences of swamp use and fruit consumption on western gorilla
Doran-Sheehy, D. M., Greer, D., Mongo, P., & Schwindt, D. (2004). Impact of ecological and social

Cantor, J. G. H. (1980). What limits primates? Primates, 21, 538–544.
Carpenter, C. R. (1940). A field study in Siam of the behaviour and social relations of the gibbon

Hylobates lar. Comparative Psychological Monographs, 16.

Caton, J. M. (1999). A preliminary report on the digestive strategy of the western lowland gorilla.
Australian Primatologist, 13, 2–7.

Caton, J. M., Hume, I. D., Hill, D. M., & Harper, P. (1999). Digesta retention in the gastro-intestinal tract
of the orangutan (Pongo pygmaeus). Primates, 40, 551–558.

Chapman, C. A., & Chapman, L. J. (1990). Dietary variability in primate populations. Primates, 31, 121–128.

Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: an analysis
of spider monkey and chimpanzee subgroups. Behavioral Ecology and Sociobiology, 36, 59–70.

Cheyne, S. M. (2010). Behavioural ecology of gibbons (Hylobates albibarbis) in a degraded peat-swamp
forest. In J. Supriatna & S. L. Gursky (Eds.), Indonesian primates (pp. 121–156). New York: Springer.

Chivers, D. J. (1974). The siamang in Malaya: A field study of a primate in tropical rainforest. Basel:
Karger.

Chivers, D. J. (1978). Sexual behaviour of wild siamang. In D. J. Chivers & J. Herbert (Eds.), Recent
advances in primatology (pp. 609–610). London: Academic Press.

Chivers, D. J. (2001). The swinging singing apes: Fighting for food and family in Far-East forests. In The
apes: Challenges for the 21st century (pp. 1–28). Brookfield, IL: Chicago Zoological Society.

Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: comparisons
with other mammals in relation to diet. Journal of Morphology, 166, 337–386.

Clauss, M., Streich, W. J., Nunn, C. L., Ortmann, S., Hohmann, G., Schwarm, A., et al. (2008). The
influence of natural diet composition, food intake level, and body size on ingesta passage in primates.
Comparative Biochemistry and Physiology A, 150, 274–281.

Conklin, N. L., & Wrangham, R. W. (1994). The value of figs to a hind-gut fermenting frugivore: a
nutritional analysis. Biochemical Systematics and Ecology, 22, 137–151.

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2001). The feeding ecology of apes. In The
apes: Challenges for the 21st century (pp. 167–174). Brookfield, IL: Chicago Zoological Society.

Conklin-Brittain, N. L., Knott, C. D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and
orangutans: Methodological considerations and a preliminary comparison. In G. Hohmann, M. M.
Robbins, & C. Boesch (Eds.), Feeding ecology in apes and other primates. Ecological, physical and
behavioral aspects (pp. 445–471). Cambridge: Cambridge University Press.

Daegling, D. J. (1990). Geometry and biomechanics of hominoid mandibles. Ph.D. thesis, State University
of New York at Stony Brook, New York.

De Lathouwers, M., & Van Elsacker, L. (2005). Reproductive parameters of female Pan paniscus and P.
troglodytes: quality versus quantity. International Journal of Primatology, 26, 55–71.

Deane, A. (2009). First contact: understanding the relationship between hominoid incisor curvature and
diet. Journal of Human Evolution, 56, 263–274.

Dolson, E., & Andrews, P. (1975). Evolution and interrelationships of the catarrhine primates. In W. P.

Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant
and nonruminant herbivores. The American Naturalist, 125, 641–672.

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping
patterns in Tai chimpanzees. International Journal of Primatology, 18, 183–206.

Doran, D., & Greer, D. (2002). The influences of swamp use and fruit consumption on western gorilla
(Gorilla gorilla gorilla) ranging behavior at Mondika Research Center. American Journal of Physical
Anthropology (Supplement), 34, 64–65.

Doran, D., & McNeilage, A. (1999). Diet of western lowland gorillas in south-west Central African
Republic: implications for subspecific variation in gorilla grouping and ranging patterns. American
Journal of Physical Anthropology (Supplement), 28, 121.

Doran, D. M., Jungers, W. J., Sugiyama, Y., Fleagle, J. G., & Heesy, C. P. (2002). Multivariate and
phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In C. Boesch,
G. Hohmann, & L. F. Marchant (Eds.), Behavioural diversity in chimpanzees and bonobos (pp. 14–34).
Cambridge: Cambridge University Press.

Doran, D. M., McNeilage, A., Greer, D., Bocian, C., Mehlman, P., & Shah, N. (2002). Western lowland
gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect
sampling methods. American Journal of Primatology, 58, 91–116.

Doran-Sheehy, D. M., Greer, D., Mongo, P., & Schwindt, D. (2004). Impact of ecological and social
factors on ranging in western gorillas. American Journal of Primatology, 64, 207–222.
Doran-Sheehy, D., Mongo, P., Lodwick, J., & Conklin-Brittain, N. L. (2009). Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus Old World monkey foraging strategies. *American Journal of Physical Anthropology, 140*, 727–738.

Elder, A. A. (2009). Hylobatid diets revisited: The importance of body mass, fruit availability, and interspecific competition. In S. Lappan & D. J. Whittaker (Eds.), *The gibbons: New perspectives on small ape socioecology and population biology* (pp. 133–159). New York: Springer.

Elgart-Berry, A. (2004). Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. *American Journal of Primatology, 62*, 275–285.

Emery Thompson, M., & Wrangham, R. W. (2008). Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *American Journal of Physical Anthropology, 135*, 171–181.

Fleagle, J. G. (1976). Locomotion and posture of the Malayan siamang and implications for hominid evolution. *Folia Primatologica, 26*, 245–269.

Foley, W. J., & Cork, S. J. (1992). Use of fibrous diets by small herbivores: how far can the rules be 'bent'? *Trends in Ecology and Evolution, 7*, 159–162.

Fossey, D. (1977). Feeding ecology of free ranging mountain gorillas (*Gorilla gorilla beringei*). In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes* (pp. 539–556). London: Academic Press.

Fox, E. A., van Schaik, C. P., Sitompul, A., & Wright, D. N. (2004). Intra- and inter-population differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology, 125*, 162–174.

Fruth, B., & Hohmann, G. (1996). Nest building behavior in the great apes: The great leap forward? In W. C. McGrew, L. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 224–240). Cambridge: Cambridge University Press.

Furuichi, T., Mulavwa, M., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., et al. (2008). Relationships among fruit abundance, ranging rate, and party size and composition of bonobos at Wamba. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology, and conservation* (pp. 135–149). New York: Springer.

Galdikas, B. M. F. (1982). Orangutans as seed dispersers at Tanjung Puting, Central Kalimantan: Implications for conservation. In L. E. M. de Boer (Ed.), *The orangutan: Its biology and conservation* (pp. 285–298). The Hague: Dr W. Junk Publishers.

Galdikas, B. M. F. (1988). Orangutan diet, range and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology, 9*, 1–35.

Galdikas, B. M. F., & Wood, J. W. (1990). Birth spacing patterns in humans and apes. *American Journal of Physical Anthropology, 83*, 185–191.

Ganas, J., Ortmann, S., & Robbins, M. M. (2008). Food choice strategies of mountain gorilla groups in Bwindi Impenetrable National Park, Uganda. *Folia Primatologica, 79*, 331.

Ganas, J., Robbins, M. M., Nkurunungi, J. B., Kaplin, B. A., & McNeilage, A. (2004). Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology, 25*, 1043–1072.

Ghiglieri, M. P. (1987). Sociobiology of the great apes and the hominin ancestor. *Journal of Human Evolution, 16*, 319–357.

Gittins, S. P. (1979). *The behaviour and ecology of the agile gibbon* (Hylobates agilis). Ph.D. thesis, University of Cambridge, Cambridge.

Gittins, S. P. (1980). Territorial behaviour in the agile gibbon. *International Journal of Primatology, 1*, 381–399.

Goldsmith, M. L. (1999). Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatology, 20*, 1–23.

Goldsmith, M. L., Hanke, A. E., Nkurunungi, J. B., & Stanford, C. B. (1998). Comparative behavioral ecology of sympatric Bwindi gorillas and chimpanzees, Uganda: preliminary results. *American Journal of Physical Anthropology (Supplement), 26*, 101.

Goodall, A. (1977). Feeding and ranging behaviour of a mountain gorilla group (*Gorilla gorilla beringei*) in the Tshibinda-Kahuzi region (Zaire). In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes* (pp. 449–479). Chicago: University of Chicago Press.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
Harcourt, A. H., & Schwartz, M. W. (2001). Primate evolution: a biology of Holocene extinction and survival on the Southeast Asian Sunda Shelf islands. American Journal of Physical Anthropology, 114, 4–17.

Harcourt, A. H., & Stewart, K. J. (2007). Gorilla society. Chicago: University of Chicago Press.

Harrison, M. E. (2009). Orang-utan feeding behaviour in Sabangau, Central Kalimantan. Ph.D. thesis, University of Cambridge, Cambridge.

Harrison, M. E., & Chivers, D. J. (2007). The orang-utan mating system and the unflanged male: a product of declining food availability during the late Miocene and Pliocene? Journal of Human Evolution, 52, 275–293.

Harrison, M. E., Morrogh-Bernard, H. C., & Chivers, D. J. (2010). Orangutan energy intake and the influence of fruit availability in the non-masting peat-swamp forest of Sabangau, Indonesian Borneo. International Journal of Primatology, 31, 585–607.

Harrison, M. E., Vogel, E. R., Morrogh-Bernard, H., & van Noordwijk, M. A. (2009). Methods for calculating activity budgets compared: a case study using orangutans. American Journal of Primatology, 71, 353–358.

Harrison, M. E., Morrogh-Bernard, H. C., & Chivers, D. J. (2010). Orangutan energy intake and the influence of fruit availability in the non-masting peat-swamp forest of Sabangau, Indonesian Borneo. International Journal of Primatology, 31, 585–607.

Harvey, P. H., & Clutton-Brock, T. H. (1985). Life history variation in primates. Evolution, 39, 559–581.

Hashimoto, C., Suzuki, S., Takenoshiba, Y., Yamagiwa, J., Basabose, A. K., & Furuichi, T. (2003). How fruit abundance affects the chimpanzee party size: a comparison between four study sites. Primates, 44, 77–81.

Hladik, C. M. (1973). Alimentation et activité d’un groupe de chimpanzés réintroduits en forêt Gabonaise. Terre Vie, 27, 343–413.

Hohmann, G., Fowler, A., Sommer, V., & Ortmann, S. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: The influence of abundance and nutritional quality of fruit. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), Feeding ecology in apes and other primates: Ecological, physical and behavioral aspects (pp. 123–159). Cambridge: Cambridge University Press.

Islam, M. A., & Feeroz, M. M. (1992). Ecology of hoolock gibbon of Bangladesh. Primates, 33, 451–464.

Itoh, N., & Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. Primates, 48, 87–96.

Janzen, D. H. (1979). How to be a fig. Annual Review of Ecology and Systematics, 10, 13–51.

Kano, T. (1983). An ecological study of the pygmy chimpanzees (Pan paniscus) of Yalosidi, Republic of Zaire. International Journal of Primatology, 4, 1–31.

Kano, T. (1992). The last ape: Pygmy chimpanzee behavior and ecology. Stanford, CA: Stanford University Press.

Kano, T., & Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzees (Pan paniscus) of Wamba. In R. L. Susman (Ed.), The pygmy chimpanzee: Evolutionary biology and behavior (pp. 233–274). New York: Plenum Press.

Kay, R. F. (1981). The nut-crackers—a new theory of the adaptations of the Ramapithecinae. American Journal of Physical Anthropology, 55, 141–151.

Kay, R. F. (1984). On the use of anatomical features to infer foraging behavior in extinct apes. In P. S. Rodman & J. G. H. Cant (Eds.), Adaptations for foraging in non-human primates: Contributions to an organismal biology of prosimians, monkeys and apes (pp. 21–53). New York: Columbia University Press.

Kay, R. F. (1985). Dental evidence for the diet of Australopithecus. Annual Review of Anthropology, 14, 315–341.

Knott, C. D. (1998). Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. International Journal of Primatology, 19, 1061–1079.

Knott, C. D. (1999). Reproductive, physiological and behavioural responses of orangutans in Borneo to fluctuations in food availability. Ph.D. thesis, Harvard University.

Knott, C. D. (2001). Female reproductive ecology of the apes: Implications for human evolution. In P. T. Ellison (Ed.), Reproductive ecology and human evolution (pp. 429–463). New York: Walter de Gruyter.

Knott, C. D. (2005). Energetic responses to food availability in the great apes: Implications for hominin evolution. In D. Brockman & C. P. van Schaik (Eds.), Primate seasonality: Implications for human evolution (pp. 351–378). Cambridge: Cambridge University Press.

Knott, C. D., Emery Thompson, M., & Wich, S. A. (2009). The ecology of female reproduction in wild orangutans. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.),
Malenky, R. K., & Wrangham, R. W. (1994). A quantitative comparison of terrestrial herbaceous food consumption by bonobos, chimpanzees, and gorillas. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), Chimpanzee cultures (pp. 59–75). Cambridge: Harvard University Press.

Malenky, R. K., & Wrangham, R. W. (1994). The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), Chimpanzee cultures (pp. 59–75). Cambridge: Harvard University Press.

Kuroda, S. (1989). Developmental retardation and behavioral characteristics in the pygmy chimpanzees. In P. G. Heltne & L. Marquardt (Eds.), Understanding chimpanzees (pp. 184–193). Cambridge, MA: Harvard University Press.

Kuroda, S., Nishihara, T., Suzuki, S., & Oko, R. A. (1996). Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), Great ape societies (pp. 71–81). Cambridge: Cambridge University Press.

Kuze, N., Sipangkui, S., Malim, T. P., Bernard, H., Ambu, L. N., & Kohshima, S. (2008). Reproductive parameters over a 37-year period of free-ranging female Borneo orangutans at Sepilok Orangutan Rehabilitation Centre. Primates, 49, 126–134.

Lambert, J. E. (1999). Seed handling in chimpanzees (Pan troglodytes) and redtail monkeys (Cercopithecus ascanius): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. American Journal of Physical Anthropology, 109, 365–386.

Lambert, J. E. (2007). Seasonality, fallback strategies, and natural selection: A chimpanzee and cercopithecoid model for interpreting the evolution of the hominin diet. In P. S. Ungar (Ed.), Evolution of the human diet: The known, the unknown, and the unknowable (pp. 324–343). Oxford: Oxford University Press.

Leighton, D. R. (1987). Gibbons: Territoriality and monogamy. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), Primate societies (pp. 135–145). Chicago: University of Chicago Press.

Leighton, M. (1993). Modelling dietary selectivity by Bornean orangutans: evidence of multiple criteria in fruit selection. International Journal of Primatology, 14, 257–313.

Maas, M. C. (1991). Enamel structure and microwear: an experimental study of the response of enamel to shearing force. American Journal of Physical Anthropology, 85, 31–50.

MacKinnon, J. R. (1977). A comparative ecology of Asian apes. Primates, 18, 747–772.

MacKinnon, J. R., & MacKinnon, K. S. (1980). Niche differentiation in a primate community. In D. J. Chivers (Ed.), Malayan forest primates: Ten years’ study in tropical rain forest (pp. 167–190). New York: Plenum Press.

Maier. (1984). The functional morphology of gibbon dentition. In H. Preuschoft, W. Y. Brockelman, D. J. Chivers, & N. Creel (Eds.), The lesser apes: Evolutionary and behavioural biology (pp. 180–191). Edinburgh: Edinburgh University Press.

Malenky, R. K., Kuroda, S., Vineberg, E. O., & Wrangham, R. W. (1994). The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans: Are Sumatran forests better orangutan habitat than Bornean forests? In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), Orangutans: Geographic variation in behavioral ecology and conservation (pp. 97–116). Oxford: Oxford University Press.

Marshall, A. J., Boyko, C. M., Feilen, K. L., Boyko, R. H., & Leighton, M. (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. American Journal of Physical Anthropology, 140, 603–614.

Marshall, A. J., Cannon, C. H., & Leighton, M. (2009). Competition and niche overlap between gibbons (Hylobates albibarbis) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In S. Lappan & D. J. Whittaker (Eds.), The gibbons: New perspectives on small ape socioecology and population biology (pp. 161–188). New York: Springer.

Marshall, A. J., & Leighton, M. (2006). How does food availability limit the population density of white-bearded gibbons? In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), Feeding ecology in apes and other primates: Ecological, physical and behavioral aspects (pp. 311–333). Cambridge: Cambridge University Press.
Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology, 28,* 1219–1235.

Masi, S. (2008). *Seasonal influence on foraging strategies, activity and energy budgets of western lowland gorillas* (Gorilla gorilla gorilla) *in Bai Hokou, Central African Republic.* Ph.D. thesis, University of Rome La Sapienza, Rome.

Masi, S., Cipolletta, C., & Robbins, M. M. (2009). Western lowland gorillas (Gorilla gorilla gorilla) change their activity patterns in response to frugivory. *American Journal of Primatology, 71,* 91–100.

Mather, R. (1992). *A field study of hybrid gibbons in Central Kalimantan, Indonesia.* Ph.D. thesis, University of Cambridge, Cambridge.

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale mountains. *International Journal of Primatology, 19,* 999–1011.

McConkey, K. R. (1999). *Gibbons as seed dispersers in the rainforests of Central Borneo.* Ph.D. dissertation, University of Cambridge, Cambridge.

McConkey, K. R. (2000). Primary seed shadow generated by gibbons in the rainforests of Barito Ulu, Central Borneo. *American Journal of Primatology, 52,* 13–29.

McConkey, K. R. (2005). Sumatran orangutan (Pongo abelii). In J. O. Caldecott & L. Miles (Eds.), *World atlas of great apes and their conservation* (pp. 185–204). United Nations Environment Programme, World Conservation Monitoring Centre.

Medway, L. (1972). Phenology of a tropical rain forest in Malaya. *Biological Journal of the Linnean Society,* 4, 117–146.

Milton, K., & Demment, M. W. (1988). Digestion and passage kinetics of chimpanzees fed high and low fibre diets and comparisons with human data. *Journal of Nutrition, 118,* 1082–1088.

Mitani, J. C. (1990). Demography of agile gibbons (Hylobates agilis). *International Journal of Primatology, 11,* 411–424.

Morrogh-Bernard, H. C., Husson, S. J., Knott, C. D., Wich, S. A., van Schaik, C. P., van Noordwijk, M. A., et al. (2009). Orangutan activity budgets and diet: A comparison between species, populations and habitats. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 119–133). Oxford: Oxford University Press.

Mulavwa, M., Furuichi, T., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G., et al. (2008). Seasonal changes in fruit production and party size of bonobos at Wamba. In T. Furuichi & J. Thompson (Eds.), *The bonobos: Behavior, ecology, and conservation* (pp. 121–134). New York: Springer.

Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology, 37,* 344–354.

Nishihara, T. (1995). Feeding ecology of western lowland gorillas in the Nouabalé-Ndoki National Park, Congo. *Primates, 36,* 151–168.

Nowell, A. A., & Fletcher, A. W. (2007). Development of independence from the mother in Gorilla gorilla gorilla. *International Journal of Primatology, 28,* 441–455.

Orgelnder, M. (1994). Monitoring body weight in captive primates, with special reference to siamangs. *International Zoo News, 41,* 17–26.

Palombit, R. A. (1996). Pair bonds in monogamous apes: a comparison of the siamang Hylobates syndactylus and the white-handed gibbon H. lar. *Behaviour, 133,* 321–356.

Palombit, R. A. (1997). Inter- and Intraspecific variation in the diets of sympatric siamang (Hylobates syndactylus) and lar gibbons (Hylobates lar). *Folia Primatologica, 68,* 321–337.

Parra, R. (1978). Comparison of foregut and hindgut fermentation in herbivores. In G. G. Montgomery (Ed.), *The ecology of arboreal folivores* (pp. 205–230). Washington: Smithsonian Institution Press.

Pickford, M. (2005). Incisor-molar relationships in chimpanzees and other hominoids: implications for diet and phylogeny. *Primates, 46,* 21–32.

Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology, 44,* 25–53.

Plavcan, J. M., & van Schaik, C. P. (1992). Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology, 87,* 461–477.

Pontzer, H., & Kamilar, J. M. (2009). Great ranging associated with greater reproductive investment in mammals. *Proceedings of the National Academy of Sciences USA, 106,* 192–196.

Pontzer, H., & Wrangham, R. W. (2004). Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *Journal of Human Evolution, 46,* 317–335.
Smith, T. M., Olejniczak, A. J., Martin, L. B., & Reid, D. J. (2005). Variation in hominoid molar enamel thickness. *Journal of Human Evolution, 48*, 575–592.

Stearns, S. C. (1983). The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos, 41*, 173–187.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton: Princeton University Press.

Sugardjito, J. (1986). Ecological constraints on the behavior of Sumatran orangutans in the Gunung Leuser National Park. Indonesia. Ph.D. dissertation: Utrecht University, Netherlands.

Takahata, Y., Ihobe, H., & Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: Do females exhibit proceptivity or receptivity? In W. C. McGrew, T. Nishida, & L. Marchant (Eds.), *Great ape societies* (pp. 146–155). Cambridge: Cambridge University Press.

Taylor, A. B. (2006a). Diet and mandibular morphology in African apes. *International Journal of Primatology, 27*, 181–201.

Taylor, A. B. (2006b). Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. *Journal of Human Evolution, 50*, 377–393.

Taylor, A. B., Vogel, E. R., & Dominy, N. J. (2008). Masticatory biomechanics and food mechanical properties in large-bodied hominoids. *Journal of Human Evolution, 55*, 604–616.

Tilson, R. L. (1981). Family formation strategies among Kloss gibbons. *Folia Primatologica, 35*, 259–287.

Tutin, C. E. G. (1994). Reproductive success story: Variability among chimpanzees and comparisons with gorillas. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 181–193). Cambridge, MA: Harvard University Press.

Tutin, C. E. G. (1996). Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 58–70). Cambridge: Cambridge University Press.

Tutin, C. E. G., Fernandez, M., Rogers, M. E., Williamson, E. A., & McGrew, W. C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society B-Biological Sciences, 334*, 179–185.

Tutin, C. E. G., Ham, R. M., White, L. J. T., & Harrison, M. J. S. (1997). The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology, 42*, 1–24.

Tweheyo, M., & Lye, K. A. (2003). Phenology of figs in Budongo forest Uganda and its importance for the chimpanzee diet. *African Journal of Ecology, 43*, 306–316.

Tweheyo, M., Lye, K. A., & Weladji, R. B. (2004). Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management, 188*, 267–278.

Ungar, P. S. (1995). Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. *International Journal of Primatology, 16*, 221–245.

Ungar, P. (2004). Dental topography and diets of *Australopithecus afarensis* and early Homo. *Journal of Human Evolution, 46*, 605–622.

Ungar, P. S. (2007). Dental functional morphology: The known, the unknown and the unknowable. In P. S. Ungar (Ed.), *Evolution of the human diet: The known, the unknown and the unknowable* (pp. 39–55). Oxford: Oxford University Press.

Ungar, P. S., & Kay, R. F. (1995). The dietary adaptations of European Miocene catarrhines. *Proceedings of the National Academy of Sciences of the USA, 92*, 5479–5481.

Utami, S. S., Wich, S. A., Sterck, E. H. M., & van Hooff, J. A. R. A. M. (1997). Food competition between wild orangutans in large fig trees. *International Journal of Primatology, 18*, 909–927.

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates, 40*, 69–86.

van Schaik, C. P., & Pfannes, K. R. (2005). Tropical climates and phenology: A primate perspective. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and nonhuman primates* (pp. 23–54). Cambridge: Cambridge University Press.

Vogel, E. R., Haag, L., Mitra-Setia, T., van Schaik, C. P., & Dominy, N. J. (2009). Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical Anthropology, 140*, 716–726.

Vogel, E. R., van Woerden, J. T., Lucas, P. W., Utami Atmoko, S. S., van Schaik, C. P., & Dominy, N. J. (2008). Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of Human Evolution, 55*, 60–74.

Watts, D. (1991a). Mountain gorilla reproduction and sexual behavior. *American Journal of Primatology, 24*, 211–226.

Watts, D. P. (1991b). Strategies of habitat use by mountain gorillas. *Folia Primatologica, 56*, 1–16.

Western, D. (1979). Size, life history and ecology in mammals. *African Journal of Ecology, 17*, 185–204.
Western, D., & Ssemakula, J. (1982). Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia*, 54, 281–290.

Wheatley, B. P. (1982). Energetics of foraging in *Macaca fascicularis* and *Pongo pygmaeus* and a selective advantage of large body size in the orangutan. *Primates*, 23, 348–363.

Wheatley, B. P. (1987). The evolution of large body size in orangutans: a model for hominoid divergence. *American Journal of Primatology*, 13, 313–324.

White, F. J. (1998). Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *International Journal of Primatology*, 19, 1013–1027.

Wich, S. A., Buij, R., & van Schaik, C. P. (2004). Determinants of orangutan density in the dryland forests of the Leuser Ecosystem. *Primates*, 45, 177–182.

Wich, S. A., de Vries, H., Ancrenza, M., Perkins, L., Shumaker, R. W., Suzuki, A., et al. (2009). Orangutan life history variation. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 65–75). Oxford: Oxford University Press.

Wich, S. A., Shumaker, R. W., Perkins, L., & de Vries, H. (2009). Captive and wild orangutan (*Pongo sp.*) survivorship: a comparison and the influence of management. *American Journal of Primatology*, 71, 680–686.

Wich, S. A., Utami-Atmoko, S. S., Mitra Setia, T., Djojosudharmo, S., & Geurts, M. L. (2006). Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. *International Journal of Primatology*, 17, 1535–1550.

Wich, S. A., Utami-Atmoko, S. S., Mitra Setia, T., Rijken, H. D., Schürmann, C. L., van Hooff, J. A. R. A. M., et al. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*). *Journal of Human Evolution*, 47, 385–398.

Wrangham, R. W. (1977). Feeding behavior of chimpanzees in Gombe National Park, Tanzania. In T. H. Clutton-Brook (Ed.), *Primate ecology: Studies of feeding behaviour in lemurs, mankeys and apes* (pp. 504–538). London: Academic Press.

Wrangham, R. W., Chapman, C. A., Clark Arcadi, A. P., & Isibirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of great ape groups. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45–57). Cambridge: Cambridge University Press.

Wrangham, R. W., Conklin, N. L., Chapman, C. A., & Hunt, K. D. (1991). The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society B–Biological Sciences*, 334, 171–178.

Wrangham, R. W., Conklin, N. L., Etot, G., Obua, J., Hunt, K. D., Hauser, M. D., et al. (1993). The value of figs to chimpanzees. *International Journal of Primatology*, 14, 243–256.

Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary responses of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, 19, 949–970.

Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., & Heltnne, P. G. (1994). *Chimpanzee cultures*. Cambridge: Harvard University Press.

Yamagiwa, J. (2004). Diet and foraging of the great apes: Ecological constraints on their social organizations and implications for their divergence. In A. E. Russon & D. R. Begun (Eds.), *The evolution of thought: Evolutionary origins of great ape intelligence* (pp. 210–233). Cambridge: Cambridge University Press.

Yamagiwa, J., & Basabose, A. K. (2009). Fallback foods and dietary partitioning among *Pan* and *Gorilla*. *American Journal of Physical Anthropology*, 140, 739–750.

Yamagiwa, J., Maruhashi, T., Yumoto, T., & Mwanza, N. (1996). Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 82–98). Cambridge: Cambridge University Press.

Yamagiwa, J., & Mwanza, N. (1994). Day-journey length and daily diet of solitary male gorillas in lowland and highland habitats. *International Journal of Primatology*, 15, 207–224.

Yamagiwa, J., Mwanza, N., Yumoto, T., & Maruhashi, T. (1994). Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates*, 35, 1–14.

Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, 106, 283–295.