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Initial Studies on the Contributions of Body Size and Gastrointestinal Passage Rates to Dietary Flexibility Among Gorillas

M.J. REMIS*
Department of Sociology and Anthropology, Purdue University,
West Lafayette, Indiana 47907-1365

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ABSTRACT Large body size has been traditionally seen as the primary dietary adaptation of gorillas, facilitating their consumption of fibrous foods (Schaller [1963] The Mountain Gorilla; Watts [1990] Int. J. Primatol. *11:*21–45). Nevertheless, recent research has emphasized frugivory among western lowland gorillas, as well as the influence of habitat and seasonality on gorilla diet and behavior across subspecies (Watts [1990] Int. J. Primatol. *11:*21–45; Tutin et al. [1991] Philos. R. Soc. Trans. Lond. Biol. *334:*179–186; Remis [1994] Ph.D. Thesis, [1997a] Am. J. Primatol. *43:*87–109, [1997b] Am. J. Primatol. *43:*111–133, [1998] Primate Locomotion: Recent Advances, p 95–¹108, [1999] Primates *40:*383–396; Nishihara [1995] Primates *36:*151–168; Goldsmith [1999a] Int. J. Primatol. *20:*1–23, [1999b] Nonhuman Primates, p 58–63). This study provides preliminary data to address the physiological underpinnings of dietary flexibility among gorillas, and their consumption of a broad range of fibrous and tannin-rich foods. To date, little is known about the digestive physiology of the African apes (but see Milton [1984] Adaptations for Foraging in Nonhuman Primates, p 249–279, Milton [1984][1999] Evol. Anthropol. *8:*11–20; Milton and Demment [1988] J. Nutr. *118:*1082–1088; Lambert [1997] Ph.D. Dissertation), although gastrointestinal morphology and proportions are roughly similar among species (Chivers and Hladik [1980] J. Morphol. *166:*337–386). This study provides additional experimental data on the gastrointestinal passage times of gorillas (*Gorilla gorilla gorilla*) fed a captive diet in a zoological park setting and discusses results in relation to field research on gorilla feeding ecology. In this study, 480 small plastic markers were fed to six captive gorillas. The mean gut retention time (MRT) of the adult gorillas in this study was 50 hr, longer than the 31 hr reported for chimpanzees fed a similar diet (Lambert [1997] Ph.D. Dissertation). These data suggest that gorillas may retain foods in their gastrointestinal tracts longer than smaller hominoids, and that the large body size likely forms the primary basis for consumption of fiber. This research provides additional data to contribute to our understanding of the relationships of body size and morphology to ecology, and the evolution of body size, foraging strategy and social organization among the African apes. Am J Phys Anthropol 112:171–180, 2000. © 2000 Wiley-Liss, Inc.

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*Correspondence to: M.J. Remis, Department of Sociology and Anthropology, Purdue University, West Lafayette, IN 47907-1365. E-mail: remis@sri.soc.purdue.edu
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Gorillas have traditionally been classified as herbivore-folivores (Schaller, 1963; Fossey and Harcourt, 1977; Watts, 1990, 1996), and this diet has been seen as fundamental to cohesive grouping patterns (Wrangham, 1979). Nevertheless, gorillas' consumption of fruit and corresponding ranging, grouping, and social behavior vary with resource availability, within and between sites and subspecies (Tutin and Fernandez, 1985; Watts, 1990; Tutin et al., 1991, 1997; Remis, 1994, 1997a,b, 1998, 1999; Goldsmith, 1996, 1999a,b; Yamagiwa et al., 1996; Doran and McNeilage, 1998). At many sites, gorillas are seasonal frugivores, but they are often described as less persistent in their fruit-eating than sympatric chimpanzees (Nishihara, 1995; Kuroda et al., 1996; Yamagiwa et al., 1996) or bonobos (Malenky, 1990), and this factor likely shapes species-specific social and grouping behavior.

Generalizations concerning the relationship of body size to diet lead us to infer that gorillas should be more folivorous than sympatric chimpanzees (Gaulin and Konner, 1977; Temerin et al., 1984; Demment and Van Soest, 1985; Salier et al., 1985; Chivers and Langer, 1994). Moreover, the limited available physiological evidence suggests that gorillas may be anatomically equipped to digest fiber (Chivers and Hladik, 1980; Collet et al., 1984; Milton, 1984). As herbivores, high-altitude Virunga mountain gorillas conform to these expectations, but they live in an environment where fruits are scarce (Schaller, 1963; Watts, 1996). Virunga and Bwindi mountain gorillas have a more diverse diet and consume more fruit at lower elevations (McNeilage, 1995; Goldsmith, 1999b). Observational data on sympatric African apes in lowland forests reveal broad similarity and overlap in diets (Remis, 1997a; Kuroda et al., 1996; Tutin et al., 1991, 1997), which makes it difficult to use a size-based model to predict their diets (Schoener, 1971; Jarman, 1974; cf. Perrin, 1994).

Despite their penchant for fruit, the large size of gorillas probably lends them greater dietary flexibility than chimpanzees (Demment, 1983). It may facilitate niche separation during the dry season, when gorillas exploit fallback foods relatively high in structural carbohydrates (fiber), condensed tannins, and phenols. On the other hand, during seasons of scarcity, chimpanzees rely on flexible grouping patterns to facilitate continued fruit consumption, although some of these fruits are fibrous or tannin-rich (Tutin and Fernandez, 1991, 1993; Wrangham and Waterman, 1983; Wrangham et al., 1991, 1993; Remis, 1997a, 1999; Remis, et al., unpublished findings; Reynolds et al., 1998).

DIETARY SELECTIVITY AND PLANT BIOCHEMISTRY

Variation in dietary selectivity among primates is presumed to reflect differences in digestive adaptations for metabolizing the nutrients and secondary compounds found in plants (Freeland and Janzen, 1974; Feeney, 1976; Rhodes and Cates, 1976; Glander, 1981; Waterman, 1984; Ganzhorn, 1989; Chivers and Langer, 1994; Milton, 1998). Folivorous primates often consume foods that are high in digestion inhibitors, such as lignin and secondary plant compounds (Oates et al., 1977; Freeland, 1991; Waterman and Kool, 1994), although many of these foods are also high in protein (Hladik, 1978; Milton, 1981; Mckey et al., 1981; Waterman et al., 1983; Davies and Oates, 1994).

While gorillas are commonly classified as folivores, they do not have the morphological specializations associated with forestomach fermentation that may allow colobines to detoxify alkaloids (Oates et al., 1977, 1980; Kay and Davies, 1994). Gorillas do, however, have a somewhat enlarged hindgut relative to chimpanzees and other frugivores, associated with high rates of colic-cecal fermentation (Eftman and Atkinson, 1950; Hosakawa and Kamiya, 1961; Bauchop, 1978; Parra, 1978; Chivers and Hladik, 1980; Clemmens and Philips, 1980; Milton and Demment, 1988). In addition, gorillas may use geophagia to facilitate consumption of secondary compounds (Watts, 1990; Remis, 1997a) and sometimes practice copraphagy under conditions of low food availability (Harcourt and Stewart, 1978; Hladik, 1978; Rogers et al., 1992).

Folivorous species generally have large populations of microbial gut flora and appear better able to digest high-fiber and tannin-rich foods than most frugivores (Milton, 1981; Milton and McBee, 1983; Watkins et al., 1985; Crissey et al., 1991; Dierenfeld et al., 1992). In fact, they might be committed to a digestive strategy (e.g., Nordin, 1981; Power and Oftedal, 1996) that requires them to consume leaves to meet their protein needs, even when fruit is abundant (Milton, 1981; Maisels, 1993; Tutin and Fernandez, 1994).

GORILLA BODY SIZE AND MORPHOLOGY: IMPLICATIONS FOR DIGESTIVE STRATEGIES AND DIET

Body size, in itself, has long been considered a mechanism for interspecific and intraspecific differences in diet (Bell, 1970; Jarman, 1974; Demment, 1983). Large body size facilitates digestion of high-fiber or chemically defended plant foods, and may allow gorillas to consume a folivorous diet without many of the gastrointestinal specializations of smaller-bodied folivores. The proportion of metabolic requirements to gut capacity decreases with body size. Larger animals can, therefore, retain foods longer in the gut and consume a lower-quality diet than smaller individuals with similar gut morphology (Demment and Van Soest, 1985; Feer, 1995; but see Lambert, 1997).

Gorillas are the largest and among the most sexually dimorphic of any primate species, with males typically twice the size of females (*G. g. gorilla* females approximately 72 kg, males 169 kg; Jungers and Susman, 1984; Zihlman, 1997). The evolution of differences in body size, muscle mass, and patterns of sexual dimorphism among the apes has been linked to species differences in socioecology, but these differences have yet to be fully evaluated (Leigh, 1994, 1995; Leigh and Shea, 1995; Janson and van Schaik, 1993; Martin et al., 1995; Zihlman and McFarland, unpublished findings).

In addition to body size, anatomical correlates of diet include craniodental and gastrointestinal specializations. All gorillas have a generalized craniodental morphology characteristic of the hominoids (Kay, 1975; Shea, 1983; Uchida, 1998; but see Hartman, 1988). Nevertheless, mountain gorillas have higher shearing crests and narrower central incisors than western lowland gorillas, correlating with their greater folivory (Groves, 1986; Uchida, 1996). While gorillas are similar to chimpanzees in the morphology and general proportions of the gut (Chivers and Hladik, 1980, 1984; Martin et al., 1985), they have relatively larger colons with more cellulose-digesting ciliates (File et al., 1976; Collet et al., 1984). Preliminary investigations have suggested that gorillas have slow gut transit times relative to those of chimpanzees (Milton, 1984; but see Milton, 1999).

Retention of food in the gastrointestinal tract is presumed to allow animals to maximize the amount of nutrients absorbed (see Lambert, 1999 for review). Nevertheless, absolute surface area of the gut is likely as important as retention time in facilitating microbial activity and nutrient absorption (Kay and Davies, 1994). Large gut volume and surface area allow for greater production of volatile fatty acids as well as absorption and assimilation of these end products among simple stomached catarrhines (Brourton and Perrin, 1991). These features may permit gorillas to tolerate high levels of fiber, total phenols, and condensed tannins in their foods (Rogers et al., 1990; Cork and Foley, 1991). Gorillas may consume high-fiber foods in order to meet their total energetic or protein needs, to maximize digestive efficiency, or to maintain colonies of ciliates in the gut (Milton, 1984; Rogers et al., 1992; Tutin and Fernandez, 1994; Popovich et al., 1997).

The primary aim of this research was to conduct experimental observational study of gut passage times among captive gorillas. These initial laboratory-based data assist our efforts to better understand the effects of body size and digestive physiology on dietary flexibility of gorillas in their natural habitats.

METHODS

Study subjects, housing conditions, and diet

This study was conducted on six western lowland gorillas (*Gorilla gorilla gorilla*) housed at the San Francisco Zoo, March 1999. Study subjects included: three adult females, one of whom was lactating and one

TABLE 1. Study subjects Gorilla gorilla gorilla *at the San Francisco Zoological Gardens*

Individual	Sex	Age	Birth date	Weight in kg (date recorded)	History/condition
Pogo	F	41	1958	109.8 (3/96)	Wild-caught, hand-reared, nulliparous
Bawang	F	18	7/13/80	87 (4/96)	Cin Zoo born, hand-reared, lactating mother to female, born 9/98
Zura	F	17	9/13/81	77 (11/93)	Col. Zoo born, hand-reared, nulliparous
Mkubwa	M	23	5/01/75	169.6 (3/96)	San Francisco Zoo born, parent-raised
Shango	M	10	3/11/89	Est. 150	San Francisco Zoo born, mother-reared
Barney	M	5	10/01/93	Est. 50	San Francisco Zoo born, mother-reared

TABLE 2. Diet of study subjects at the San Francisco Zoological Gardens, 1999[1]

Food	Male 4,900 kcal	Female 4,000 kcal
Banana	125 g	125 g
Apple	450 g	300 g
Orange	500 g	350 g
Yam	300 g	250 g
Carrot	900 g	675 g
Celery	3,000 g	1,500 g
Mixed greens (kale, collards, romaine)	500 g	500 g
Browse	200 g	200 g
High-Fiber Mazuri Leaf Eater Chow	800 g	400–700 g

[1] In addition to the above set diets, large quantities of browse (*Acacia longifolia* branches), as well as six supplemental domestic vegetables per individual per day and scratch feed (2 parts cracked corn, 1 part popcorn, 1 part sunflower seeds, with additional grapes and peanuts) are scattered in the grotto. Animals consume these foods ad libitum. Milk or yogurt (8 oz) is also given daily to the lactating female. One and a half tablespoons of Metamucil mixed in water are also occasionally administered to Zura to facilitate the gut passage of foreign objects consumed in the grotto.

of whom was wild-born, a silverback, a blackback, and a juvenile male (see Table 1). The gorillas are currently group-housed in a large off-exhibit indoor night-quarter facility and have access to an outdoor grotto (22,000 square feet), weather permitting, from 10:00–16:00 hr daily. Mean temperature in the outdoor grotto was 20°C (range, 18.9–22.8°C), and the mean temperature indoors was 20.5°C (range, 16.7–25.0°C).

During AM and PM meals, at 8:00 and 16:00 hr, animals are temporarily separated into individual enclosures in the night quarters and fed meals of high-fiber monkey chow and fruits and vegetables (see Table 2). In addition, the animals receive browse, vegetables, grapes, and peanuts scattered in their outdoor grotto at 10 AM daily. This diet provides the gorillas approximately 17.85% dry-matter neutral detergent fiber and 9.46% dry-matter acid detergent fiber (Dierenfeld, personal communication). It is high-quality, relative to many of the foods consumed by gorillas in the wild (gorilla foods at Bai Hokou eaten during fruit scarcity: mean neutral detergent fiber = 61.6%, acid detergent fiber = 46.6%, Remis et al., unpublished findings).

No changes were made to the housing conditions or diet of the subjects during this study. Only the principal investigator and keepers were permitted in the area adjacent to the night quarters, as a health precaution, and to minimize any stress to the animals that might affect gut retention times.

Gut passage trials

Four experimental trials were conducted on each study animal. A trial consisted of the administration of 20 nontoxic colored plastic markers. The markers (measuring 4 × 2 × 1 mm) were concealed in a banana and offered to the subjects in an AM feed and PM feed. The methods, size, and type of marker were chosen to be directly comparable to the methods used during the study of gut passage rates of cercopithecines and chimpanzees by Lambert (1997). The markers are similar in size and weight to small seeds typically swallowed by monkeys and apes. Each animal was fed loaded bananas once in the morning and once in the late afternoon just before or after each feeding for a total of four doses of markers over 2 days. For all trials, each individual was assigned its own unique marker color.

Animals were observed from March 23, 1999 at 16:00 hr–March 29, 1999 at 8:00 AM, 136 hr after the initial AM trial. The gorillas were observed by two observers from 7:30–18:00 hr daily (with up to seven additional observers posted adjacent to the outdoor exhibit), and the time of all observed defecations was recorded. In addition, standardized estimates of defecation time were made by observing and gauging the dryness and hardness of several feces of known defecation time. Estimates of time of unobserved defecations were made using standardized means of fecal age based on appearance.

All fecal material was collected immediately or during enclosure cleaning, and washed and screened to determine whether colored markers were present. The number of markers and color(s) of markers were recorded. A total count of all defecations was maintained throughout the entire project. Three measures of gut passage were calculated. These include time of first marker appearance or transit time (TT), time of last appearance (TLA) of a marker, and mean retention time of markers (MRT). Mean retention time is considered to be the single best estimate of digesta movement through mammalian gastrointestinal tracts and is a measure of the average time of retention of all the elements of the digesta being studied. MRT is calculated:

$$t = \sum_{i=1} m_i t_i \Big/ \sum_{i=1} m$$

where m_i = *the amount of marker excreted at the* ith defecation at time t_i *after dosing (Warner, 1981; Lambert, 1997).*

RESULTS

Administration of markers

The marker-dosed bananas were generally readily and immediately consumed by the gorillas; no spitting of markers was observed. Animals did not typically detect the presence of the markers. In two cases, animals manually removed several markers from bananas; at least five markers fell on the cage floor during marker administration (6%) and were promptly removed from the enclosure. Thus, the gorillas apparently swallowed a total of 475 markers during this study.

Defecation of markers

The gorillas defecated 193 times between March 24, 1999 at 8:00 hr and March 28, 1999 at 16:00 hr, resulting in an average of 7.3 defecations per individual per 24-hr day. On average, 1.6 markers were excreted per individual defecation (range, 0–8). The number of different color markers per defecation ranged from 1–4, so considerable mixing of the gut contents occurred. A total of 309 markers was excreted and collected (65% of 475 swallowed) (Fig. 1). As in other studies, a considerable number of markers were not recovered during the study period (Warner, 1981; Lambert, 1997). Some unrecovered markers may have been overlooked in the fibrous dung during the screening process. Other markers may have temporarily adhered to the intestinal walls; a small number of markers were still appearing in stools, albeit infrequently, at the end of the study period. Gorilla feces were typically large, fibrous, and well-formed. However, on the evening following administration of the first two trials of markers, the silverback produced a single defecation of loose stool when he responded aggressively with chases and bark vocalizations to a brief challenge from the large blackback for first access to the door to the indoor quarters. The conflict may have influenced the relatively rapid transit time of both males (see below). Thus, gut transit and retention times reported here should likely be considered as minimum estimates.

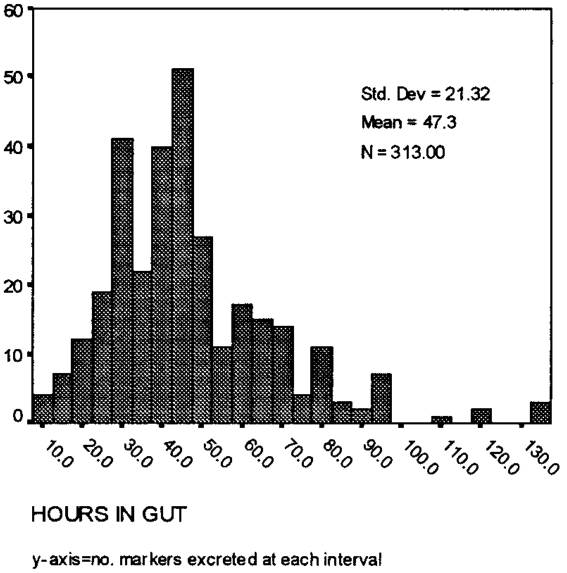

Fig. 1. Passage of markers fed to gorillas at the San Francisco Zoo, 1999.

TABLE 3. Gastrointestinal passage times in hours of gorillas at the San Francisco Zoological Gardens

Individual	Age/sex	Body weight (kg)	Percentage of markers recovered	Transit time	Mean rate of transit	Time of last appearance of marker
Pogo	Ad F	109	59	36.0	56.6	96.0
Bawang	Ad F	87	53	24.0	54.7	120.0
Zura	Ad F	77	41	31.2	61.9	136.0
Mkubwa	Ad M	170	54	17.0	38.6	112.0
Shango	SAd M	150	100	22.0	43.4	96.0
Barney	J M	50	79	8.0	36.3	70.0
Group Mean		110	64	23.0	47.1	109.3
Adult Mean		118	61	25.9	50.0	112.0

Gut passage time

The gorillas in this study exhibited considerable individual variation (see also Warner, 1981) in transit time (TT), mean gut passage time, i.e., mean rate of transit (MRT), and time of last appearance of markers (TLA) (ANOVA MRT, F = 15.52, P = 0.000) (Table 3). MRT of markers also varied by trial (ANOVA F = 4.162, $P < 0.007$), and may have been affected by minor dietary variation. MRT for all trials for the adult gorillas in this study was 50 hr (range, 16.5–136 hr). As expected, the juvenile gorilla had the shortest MRT (36.3 hr, n = 63 markers). The silverback and blackback did not differ in MRT (independent samples t-test t = −1.5, $P < 0.133$). As a result, data for the silverback and blackback were combined and data on adult-sized animals were analyzed for sex differences. Contrary to body-size expectations, the MRT for the large males (MRT = 41.74, n = 123 markers) was shorter than the MRT for the three females in this study (MRT = 57.38, n = 122 markers, independent samples t-test, t = −5.3, P =0.000).

DISCUSSION

The five adult-sized gorillas in this study had similar mean transit times and mean retention times to those recently reported for other captive gorillas, chimpanzees, and orangutans (Caton, 1999; Milton, 1999), suggesting that gut retention may be a phylogenetically determined trait. Nevertheless, the San Francisco Zoo gorillas had longer mean gut retention times and mean time of last appearance of markers than the two adult chimpanzees studied by Lambert (TT = 23.2, MRT = 31.5, TLA = 63.3 hr). This difference may be significant, as this study was more comparable in methods and diet to the study by Lambert, 1997 (chimpanzee diet consisted of 700 g Mazuri Leaf Eater Chow and 1.8 kg mixed produce daily) than to those described in other studies. The single juvenile gorilla in this study was similar in both body weight (50 kg) and mean retention time (MRT = 36 hr) to the adult chimpanzees in Lambert's study.

Dietary intake, the proportion of fiber in the diet of captive animals, feeding frequency, ambient temperature, pregnancy, activity level, age, and exposure to medications which could destroy natural gut fauna and flora all affect gut passage rates (Warner, 1981; Milton, 1999). Our efforts to understand the digestive physiology of hominoids are just beginning, and sample sizes remain small. Therefore, the relative contributions of ecological niche, phylogeny, body size, sex, and dietary intake to gut retention have yet to be determined (Lambert, 1997; Milton, 1999). Future research will seek to expand the sample size of this study to include chimpanzees and additional gorilla subjects. It will also investigate the effects of an ad libitum all-fruit (low-fiber) or high-fiber diet on gut retention times. This research should provide clues as to whether seasonal dietary flexibility among gorillas corresponds to changes in digestive strategies and efficiency, as has been found for other taxa (Gross et al., 1986; Lee and Houston, 1993; Afik and Karasov, 1995; Afik et al., 1997; cf. Milton, 1999).

The results of this study confirm expectations of the effects of body size on ape gut retention times, but not expectations of body-size-related sex differences in gorilla MRT. The male and female subjects in this study were fed different amounts of fruit and chow, although vegetables and browse were consumed ad libitum. Differences in fixed-intake as well as the social factors discussed above may have affected sex differences in MRT.

Between species, the large size of gorillas permits a high-fiber diet, relative to smaller-bodied chimpanzees, although more work on both species at various intake rates is warranted. Gorillas may also retain foods longer than chimpanzees fed similar diets. Nevertheless, relative to body size, great apes have shorter gut passage times than might be expected based on the gut passage times of much smaller-bodied cercopithecines and the morphologically specialized colobine folivores (Lambert, 1997; Milton, 1999). These data support the hypothesized divergence between ape and monkey digestive strategies and corresponding differences in dietary quality relative to body weight (Andrews, 1981; Temerin and Cant, 1983; Lambert, 1997; Wrangham et al., 1998). Proportionately longer transit times appear to represent an alternative means by which small simple-stomached catarhines consume foods containing high levels of fiber and secondary compounds (Lambert, 1997, 1999).

Gorillas eat large quantities of fleshy fruit across study sites, but rely on fibrous fruits and foliage as staples or fallbacks (Williamson et al., 1990). The nutritional profiles of gorillas reveal selection of foods high in proteins or sugar relative to fiber and tannins (Casimir, 1975; Goodall, 1977; Calvert, 1985; Rogers et al., 1990; Watts, 1990; Plumptre, 1995; Remis et al., unpublished findings). Consumption of tannins varies with habitat and presumed variability of investment of plants in secondary compounds (see also Reynolds et al., 1998).

Wrangham et al. (1998) demonstrated that, despite body size differences, the nutrient and biochemical profiles of foods eaten by sympatric primates at Kibale were similar (see also Conklin et al., 1998). Likewise, chemical analyses of fruits consumed by gorillas, chimpanzees, and grey-cheeked mangabeys at Bai Hokou, Central African Republic (CAR) during a poor fruit season show similar site-specific biochemical profiles of fruits consumed by all species (Remis et al., unpublished findings). Large body size and surface area of the gut and long retention of foods in the gastrointestinal tract may work together, or separately, to facilitate dietary flexibility and the consumption of foods containing digestion inhibitors.

This study provides further preliminary insights into the physiological bases of food choice among gorillas. Gorillas share a generalized hominoid morphology and physiology and a penchant for fleshy fruit with the smaller-bodied apes. Nevertheless, gorillas' body size lends them flexibility to subsist on alternate foods as staples or fallbacks whenever necessary. Large body size also spells some disadvantages for gorillas, as they need absolutely large amounts of foods and occasionally face constraints on their access to arboreal resources (Remis, 1995, 1999).

Research on dietary strategies and physiology also provides insight into the possible ecological factors mediating species diversification among the African apes and between the African apes and monkeys. For example, during the evolutionary diversification of the African hominoids, increasing body size from a smaller highly frugivorous ancestor probably lent gorillas dietary flexibility. Consumption of fibrous fallback or staple foods likely facilitated gorilla group cohesion (Wrangham, 1979; Remis, 1997a,b) as well as coexistence with sympatric chimpanzees, and permitted gorillas to expand their range or retreat into high-altitude areas where fruit is scarce (Groves, 1986; Yamagiwa et al., 1996).

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