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Article in *International Journal of Primatology* · January 2002

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Digestive Retention Times in Forest Guenons (*Cercopithecus* spp.) with Reference to Chimpanzees (*Pan troglodytes*)

Joanna E. Lambert¹

Received March 13, 2001; accepted September 10, 2001

Because the length of time food is maintained in the gut influences fermentation rates and its overall digestibility, information on digestive passage rates is critical to explain the overall feeding and foraging strategy of a species. I present results from digestive passage experiments conducted on captive *Cercopithecus ascanius*, *C. mitis*, *C. neglectus*, *Miopithecus talapoin*, and *Pan troglodytes*. I recorded several measures of digestive passage time, including transit time (time of first marker appearance; *TT*), mean retention time of markers (*MRT*), and time of last appearance of a marker (*TLA*). I conducted 4 trials on each of the 10 subjects. A trial consists of the administration of 20, non-toxic colored plastic markers. Overall, the 5 species varied in digestive times ($p < 0.01$), but there is no difference between *Cercopithecus neglectus* and *Pan troglodytes* ($p = 0.131$) or between *C. mitis* and *C. ascanius* ($p = 0.661$). When the effect of body size is removed (by computing the ratio y/x , where x = body mass, and y = *MRT*), *Pan troglodytes* exhibits a low ratio, suggesting relatively slow retention times in the 4 cercopithecines. My findings and other published digestive passage rates suggest that lengthy digestive retention times may be characteristic of cercopithecines. These data may help to interpret how the smaller-bodied guenons are able to consume a higher percentage of fiber than that of chimpanzees, a specialized frugivore. Small body size, in combination with long digestive passage times may be an adaptation on the part of *Cercopithecus* species to consume a high fiber diet, while maintaining a greater capacity to detoxify secondary metabolites.

KEY WORDS: digestive ecology; body size; plant secondary metabolites; feeding niche; primate diet; *Miopithecus*.

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INTRODUCTION

The degree to which the structural carbohydrates (fiber) of plant cell walls can be used as a source of energy depends in part upon the length of time that they are retained in the fermenting chamber(s) of the gastrointestinal tract. Holding anatomy and diet constant, longer retention times result in higher levels of fermentation. Since many plant parts, e.g., leaves, petioles, bark, and gum, require considerable fermentation before they are useful as an energy source, information on digestive retention times can provide considerable insight into the dietary options and feeding flexibility of primates (Lambert, 1998; Milton, 1984, 1993; Remis, 2000).

With several key exceptions, there are few data on primate digestive retention times (Lambert, 1998). Data are particularly lacking for *Cercopithecus* species (guenons). Indeed, while Caton (1999) compared the digestive strategy of *Trachypithecus* to that of *Cercopithecus neglectus*, Maisel's (1993) study is the only previously published work devoted of forest guenon digestion. Guenons consume a wide variety of foods (Cords, 1986; Gautier-Hion, 1988; Kaplin and Moermond, 2000; Tutin, 1999), and despite their small body size, are generalist feeders that consume a high percentage of high-fiber foods during times of low fruit availability (Gautier-Hion, 1988; Rudran, 1978). Information on digestive kinetics would help considerably to understand their niche breadth (Lambert, 2002; Milton, 1998).

I present results from digestive experiments designed to investigate the rates at which digesta are passed through the gastrointestinal tract. I provide data on digestive retention times for 4 forest guenons: *Cercopithecus ascanius*, *C. mitis*, *C. neglectus*, and *C. (Miopithecus) talapoin*. I conducted this experiment to evaluate whether the passage retention times published by Maisels (1993) for *Cercopithecus erythrotis*, *C. pogonias*, and *C. ascanius* are part of a general pattern for forest guenons (or the Cercopithecinae more generally) or are unique to them or due to the methods employed by Maisels (1993).

Larger mammals are generally predicted to retain foods longer in the gut and to consume lower-quality diets than is characteristic of smaller mammals with similar gastrointestinal anatomy (Cork and Foley, 1991; Feer, 1995; Kay, 1985; Kay and Davies, 1994; Parra, 1978; Remis, 2000; Van Soest, 1996). In order to gain a comparative understanding of the digestive retention times of *Cercopithecus* species versus larger bodied (and often sympatric) catarrhines, I also present data on *Pan troglodytes*. The gastrointestinal tracts of great apes and cercopithecines is little modified from the ancestral mammalian pattern (Milton, 1986; Mitchell, 1905). *Pan troglodytes* and *Cercopithecus spp.* have similar digestive anatomy and are characterized in having a simple, acidic stomach, a C-shaped duodenum, a globular, reduced caecum

and an emphasis on fermentation in the colon (Chivers and Hladik, 1980; Hill, 1958; Martin, 1990). The colon in both lineages is capacious and haustrated by 3 taenia, and there is no major difference in the relative proportions in surface area in any of the gastrointestinal components: stomach, small intestine, colon, and caecum (Chivers and Hladik, 1980; Hill, 1958; Stevens and Hume, 1995). While Milton and Demment (1988) undertook an exhaustive analysis of the digestive passage kinetics of chimpanzees, their research involved different methods and thus may not be directly comparable to my results. I discuss digestive passage data in terms of how retention times might influence cercopithecine capacity to consume foods high in structural polysaccharides or secondary metabolites or both.

METHODS

Study Subjects

I conducted gut passage trials with 10 subjects, including two individuals each of 5 species (Table I). All 10 subjects were active and in good condition. I studied one adult male and one adult female blue monkey (*Cercopithecus mitis stuhlmanni*), one adult male and one adult female De Brazza's monkey (*C. neglectus*), and two adult male talapoins *C. (Miopithecus) talapoin* August 8-15, 1995, at the Henry Doorly Zoo, Omaha, Nebraska. I studied one adult male and one adult female red-tailed monkey (*Cercopithecus ascanius schmidtii*) December 27-30, 1995, at the Fort Wayne Children's Zoo, Fort Wayne, Indiana, and one adult male and one adult female chimpanzee (*Pan troglodytes*) January 25-30, 1996 at the Saint Louis Zoo, St. Louis, Missouri.

Feeding Trials

I conducted 4 trials on each subject. In each trial I administered non-toxic colored plastic markers ($4 \times 2 \times 1$ mm) in a banana. I fed each animal a loaded banana containing 20 markers once in the morning and once in the late afternoon for a total of 4 trials (80 total markers/individual) in two days. In order to distinguish among the defecation of markers from each trial, I assigned each animal 4 (one color/trial) uniquely colored markers over the 2 days; all colors among 10 subjects were different. Following the *am*-marker feed, the subjects ate their principle meal of the day (Table II). The *pm*-marker feed occurred after the subjects had been fed a late afternoon snack.

I paid particular attention to the timing of defecation. I monitored all blue monkey, De Brazza's monkey, and talapoin monkey feces for 168 h

Table I. Sex, body mass (kg), DOB (date of birth), birth place, and housing conditions at the time of the study

Species	Sex	Body mass (kg)	DOB	Birth place	Housing	Enclosure dimensions	Average temperature and humidity	Hours of light
<i>Cercopithecus ascanius</i>	Male	5.7	1988	Fort Worth, TX (captive)	Fort Wayne Children's Zoo, IN	4 × 4 × 3m	69° F 40%	0630–2200h
<i>Cercopithecus ascanius</i>	Female	4.7	1983	Birmingham, AL (captive)	Fort Wayne Children's Zoo, IN	4 × 4 × 3m	69° F 40%	0630–2200h
<i>Cercopithecus mitis</i>	Male	9.8	1985	Omaha, NE (captive)	Henry Doorly Zoo, NE	Diam = 6.5m Height = 5m	85° F 75%	0600–2130h
<i>Cercopithecus mitis</i>	Female	7.4	1988	Monroe, LA (captive)	Henry Doorly Zoo, NE	Diam = 6.5m Height = 5m	85° F 75%	0600–2130h
<i>Cercopithecus neglectus</i>	Male	6.9	1980	Unknown (wild caught)	Henry Doorly Zoo, NE	4 × 5 × 5m	75° F 60%	0700–2000h
<i>Cercopithecus neglectus</i>	Female	6.1	1981	Phoenix, AZ (captive)	Henry Doorly Zoo, NE	4 × 5 × 5m	75° F 60%	0700–2000h
<i>C. (Miopithecus) talapoin</i>	Male 1	1.9	1987	Omaha, NE (captive)	Henry Doorly Zoo, NE	3.5 × 5 × 5m	75° F 60%	0700–2000h
<i>C. (Miopithecus) talapoin</i>	Male 2	1.3	1975	Washington, D.C. (captive)	Henry Doorly Zoo, NE	3.5 × 5 × 5m	75° F 60%	0700–2000h
<i>Pan troglodytes</i>	Male	57.3	1967	Unknown (wild caught)	St. Louis Zoo, MO	100 × 50m	75° F 60%	0730–1800h
<i>Pan troglodytes</i>	Female	59.5	1967	Sierra Leone (wild caught)	St. Louis Zoo, MO	100 × 50m	75° F 60%	0730–1800h

Table II. Schedule of administration of marker-dosed bananas ('a.m./p.m. feed'), quantity (kg) and quality of morning meal and afternoon snacks (per animal) for red-tailed monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), De Brazza's monkeys (*C. neglectus*), talapoin monkeys (*Miopithecus talapoin*), and chimpanzees (*Pan troglodytes*)

Species	'a.m. feed'	'p.m. feed'	Morning meal	Afternoon snack
<i>C. ascanius</i>	0730	1930	0.25 kg monkey chow [◊] 0.25 kg fresh produce*	0.10 kg monkey chow
<i>C. mitis</i>	0800	1630	0.15 kg monkey chow ^{◊◊} 0.25 kg fresh produce**	0.15 kg monkey chow; 0.10 kg fresh produce
<i>C. neglectus</i>	0800	1630	0.15 kg monkey chow ^{◊◊} 0.25 kg fresh produce**	0.15 kg monkey chow; 0.10 kg fresh produce
<i>C. (M) talapoin</i>	0800	1630	0.08 kg monkey chow ^{◊◊} 0.06 kg fresh produce**	0.08 kg monkey chow; 0.06 kg fresh produce
<i>P. troglodytes</i>	0800	1630	0.35 kg monkey chow ^{◊◊◊} 0.9 kg fresh produce***	0.35 kg monkey chow; 0.9 kg fresh produce

Note. *broccoli and carrots; **carrots, apples, celery, potato; ***collared greens, grapefruit, bananas, sweet potatoes, kale, orange, apple, carrots; [◊]HMS High Fiber Primate Diet (diet# 9021; Bulffton, Indiana), consists of 23% crude protein, 4% crude fat and 10% crude fiber; ^{◊◊}High Protein Monkey Diet (diet# 5045 PMI Feeds, Inc., St. Louis, Missouri), consists of 25% crude protein, 5% crude fat, and 7% crude fiber; ^{◊◊◊}Mazuri Leaf Eater Primate Diet (diet# 5M02, PMI Feeds, Inc., St. Louis, Missouri), consists of 23% crude protein, 5% crude fat and 14% crude fiber.

after the onset of the first trial. I monitored red-tailed monkey feces for 84 h and chimpanzee feces for 124 h after the initial *am* trial. I observed blue monkeys, De Brazza's monkeys and talapoin monkeys directly from 0630 h until 2200 h. I observed red-tailed monkeys from 0630 h to 2200 h, and chimpanzees from 0800 h to 1700 h. Due to the constraints of access to animals while the zoo facilities were closed, I had to estimate times of defecation that took place between 2200 h and 0630 h (blue monkeys, De Brazza's monkeys, talapoin monkeys, red-tailed monkeys) and 1700 h to 0800 h (chimpanzees). To standardize the estimates, for each species I observed several feces of a known defecation time and gauged the relative levels of dryness and hardness. This procedure allowed for a standardized means by which to estimate fecal age based on appearance.

I washed and screened all fecal material to determine whether the sample contained colored markers. The markers were highly visible and readily identified and quantified. I recorded the time of defecation and the number and color(s) of markers. I maintained a total count of all defecations throughout the project and weighed and measured the fecal samples.

I assessed 3 measures of gut passage: time of first appearance of a marker or transit time (TT), time of last appearance of a marker (TLA), and mean retention time of markers (MRT). MRT is the best estimate of digesta movement through mammalian gastrointestinal tracts (Warner, 1981). It is a measure of the average time of retention of all the elements of the focal digesta,

e.g., colored markers. MRT is calculated as:

$$t = \sum_{i=1}^n m_i t_i / \sum_{i=1}^n m_i$$

in which m_i = the number of markers excreted at the i th defecation at time t_i after dosing.

There are several caveats regarding my methodology and the constraints of working with zoo animals. First, because of the relative scarcity of guenons in captivity, my sample sizes are small. Second, zoo curators/keepers, concerned with the well-being of their animals, are naturally reluctant to interrupt animal feeding regimes. Thus, in my experiment diet was not completely standardized among the study species: while the guenon diets were similar, the chimpanzees had almost 3 times as much fresh produce than manufactured chow. Third, there is evidence that captivity can influence the intestinal surface areas of some-but not all-primate species (Hladik, 1967; Martin *et al.*, 1985). Among primate species whose guts are reported to differ as a consequence of zoo diets, the trend is for surface area to decrease. Finally, the markers were a standard size, and not scaled according to gut proportions. This means that markers passing through a talapoin monkey gut are relatively larger than markers passing through the gut of a blue monkey or chimpanzee; this scaling factor has the potential to influence digestive kinetics (Milton, personal communication, 1997). Nonetheless, my methods and sample sizes are consistent with those employed by other researchers who studied primate digestion (Maisels, 1993; Milton, 1984; Remis, 2000). Methodological concerns are mitigated by the fact that relatively few data points can help substantially to identify the influence of digestion on feeding and foraging ecology (Maisels, 1993; Milton, 1981, 1984; Overdorff and Rassmussen, 1995).

RESULTS

Marker Administration

The subjects readily consumed the marker-dosed bananas. The cercopithecines typically reached for the bananas manually and then immediately stuffed the fruit into their cheek pouches and retreated to a corner of the enclosure to process the food. While eating, the monkeys manipulated the markers with their tongues and sometimes spat out a few. I promptly removed spat markers from the enclosure to prevent the monkeys from re-swallowing them. The percentage of spat markers differed among species. The blue monkeys and De Brazza's monkeys spat .33% of the markers.

Talapoin monkeys spat .60%, and red-tailed monkeys spat .20% of the markers. Cheek pouch use, processing and swallowing of the banana took 1–10 min.

The chimpanzees also readily consumed the bananas. They placed a banana, often with skin intact, directly into the mouth and manipulated it against the lower incisors with the lower lip; eventually, the bolus was pushed to the back of the mouth and swallowed. Processing and swallowing of the banana typically took 1–3 min. The chimpanzees spat out or dropped, one-third of the markers, which I removed from the enclosure. The percentage of spat markers is comparable to the percentage of similarly-sized seeds spat by wild chimpanzees and *Cercopithecus* spp. in Uganda (Lambert, 1999, 2001).

Marker Recovery

Information on defecation frequency, fecal weight and marker recovery is in Table III. The total recovery rate of markers swallowed by blue monkeys is 80% (85/106), by De Brazza's monkeys 78% (74/106), by talapoin monkeys 70% (46/66), by red-tailed monkeys 90% (115/128), and by chimpanzees 89% (94/128). The fate of the unrecovered markers is not clear. Although unlikely, it is possible that they were overlooked in the dung screening process. A more probable explanation is that they were spat by the animals, but not found on the enclosure floor. It is also possible that the markers adhered to intestinal villi and were simply not defecated with the majority of the markers. A lack of 100% recovery of markers is common in mammals (Dierenfeld *et al.*, 1992; Warner, 1981).

Although defecation of markers occurred throughout the day and night, there were peaks in defecation frequency. I divided the 24-h day into 8 3-h periods, and evaluated differences in defecation frequency among them. Red-tailed monkeys defecated more markers during 0600 h and 0900 h than at any other time ($\chi^2 = 29.3$; $p < 0.01$; $df = 7$), as did blue monkeys ($\chi^2 = 167.7$; $p < 0.01$; $df = 7$), De Brazza's monkeys ($\chi^2 = 107.6$; $p < 0.01$; $df = 7$), and talapoin monkeys ($\chi^2 = 86.7$; $p < 0.01$; $df = 7$). For chimpanzees, no single 3-h period accounted for significantly more defecations than any other time ($\chi^2 = 17.2$; $p = 0.06$; $df = 7$), though most defecation (79%) occurred between 0600 h and 1500 h.

Excretion curves are in Fig. 1. Overall, the 5 species varied in mean retention times (ANOVA $F = 18.7905$, $p < 0.01$), but there is no difference between De Brazza's monkeys and chimpanzees (two-tailed t-test $t = 1.52$, $df = 169$, $p = 0.131$) or between blue monkeys and red-tailed monkeys (two-tailed t-test $t = -.44$, $df = 191$, $p = 0.661$) (Table IV).

However, these analyses ignore body size differences among the taxa. Evaluating these differences in passage rate data in variably sized primates is

Table III. Summary of chimpanzee (*Pan troglodytes*), red-tailed monkey (*Cercopithecus ascanius*), blue monkey (*C. mitis*), De Brazza's monkey (*C. neglectus*), and talapoin monkey *C. (Miopithecus) talapoin* fecal measurements and marker presence

Species	Mean # feces/indv/24h	Mean fecal length (cm)	Mean fecal width (cm)	Mean mass (gms)	# Markers/feces	# Different colored makers/feces	Total #feces/species	# Feces with markers
<i>Cercopithecus ascanius</i>	12.8	4.5	1.7	9	Range: 1–10 Mean: 2.45 SD: 2.76	Range: 1–3	84	48/84 (57%)
<i>Cercopithecus mitis</i>	10.4	^a	^a	11	Range: 1–7 Mean: 1.63 SD: 1.03	Range: 1–2	135	50/135 (37%)
<i>Cercopithecus neglectus</i>	9.5	^a	^a	9	Range: 1–6 Mean: 1.72 SD: 0.98	Range: 1–2	123	50/123 (41%)
<i>Cercopithecus (Miopithecus) talapoin</i>	9.6	^a	^a	4	Range: 1–5 Mean: 1.9 SD: 2.11	Range: 1–2	125	21/125 (17%)
<i>Pan troglodytes</i>	6.6	10	3.8	109	Range: 1–15 Mean: 4.31 SD: 2.05	Range: 1–3	66	42/66 (64%)

^aMeasurement not recorded.

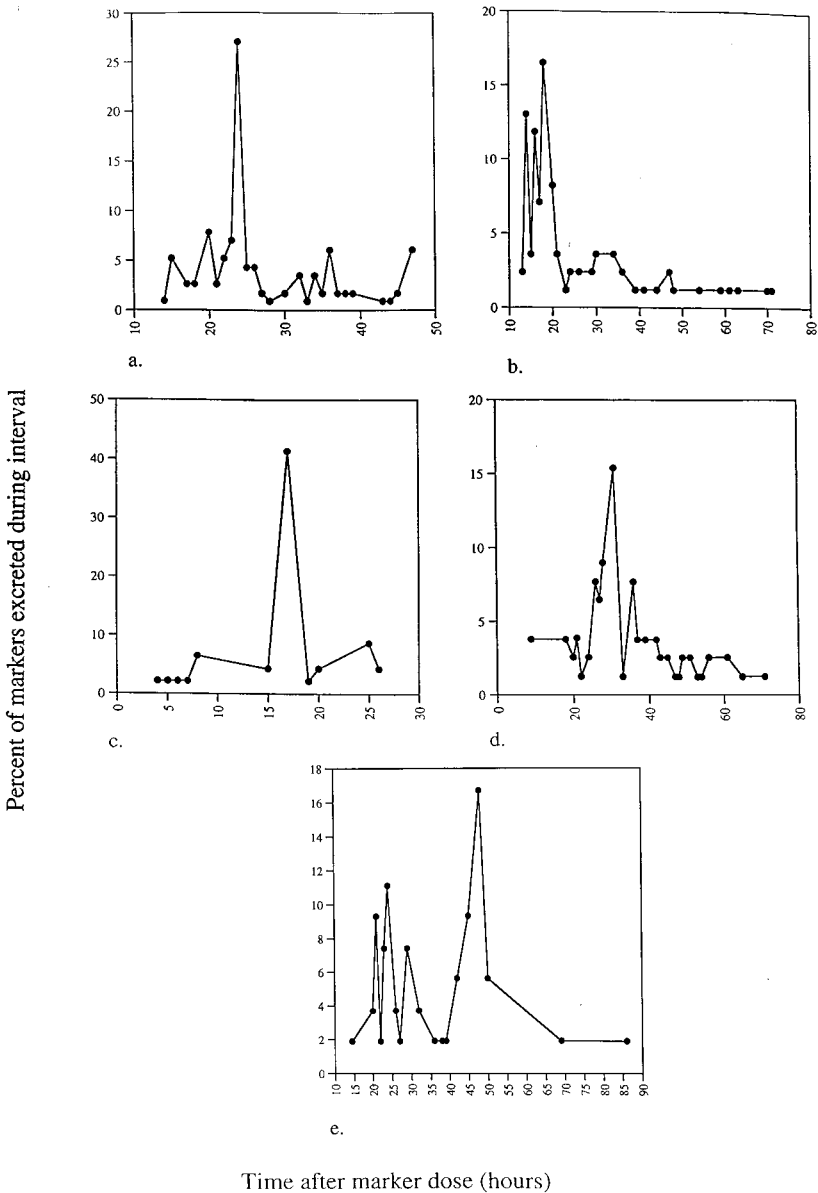


Fig. 1. Timing of marker recovery in (a) *Cercopithecus ascanius*; (b) *C. mitis*; (c) *C. (Miopithecus) talapoin* *Miopithecus talapoin*; (d) *Cercopithecus neglectus*; (e) *Pan troglodytes*.

Table IV. Mean retention time (MRT), mean transit time (TT), mean time of last appearance (TLA) of markers, and range in timing of appearance of marker^a

Species	MRT	TT	TLA	Range in timing of marker appearance
<i>C. ascanius male</i>	24.9 (6.6)	19.9 (4.6)	35.6 (9.3)	
<i>C. ascanius female</i>	29.4 (9.8)	19.4 (0.1)	42.1 (5.7)	14–47h
<i>C. ascanius specific average</i>	27.2 (8.6)	19.7 (3.4)	38.9 (8.9)	
<i>C. mitis male</i>	29.7 (14.6)	17.2 (2.9)	54.8 (12.7)	
<i>C. mitis female</i>	20.6 (12.8)	16.5 (3.4)	42.8 (19.8)	13–71.5h
<i>C. mitis specific average</i>	25.0 (14.4)	16.9 (3)	48.8 (16.7)	
<i>C. neglectus male</i>	33.9 (10.8)	21.7 (2.5)	56.0 (12.7)	
<i>C. neglectus female</i>	34.4 (16.6)	19.1 (3.4)	63.1 (10)	9–71h
<i>C. neglectus specific average</i>	34.1 (14.3)	20.6 (5.9)	58.4 (11)	
<i>C. (M.) talapoin male 1</i>	17.6 (5.8)	12.0 (5.8)	26.4 (2.3)	
<i>C. (M.) talapoin male 2</i>	13.6 (7)	12.1 (1.5)	26.5 (5.7)	4–26
<i>C. (M.) talapoin specific average</i>	16.8 (5.2)	12.0 (5.4)	26.4 (0.7)	
<i>P. troglodytes male</i>	31.1 (10.5)	20.8 (4.2)	60.5 (25.4)	
<i>P. troglodytes female</i>	31.8 (14.1)	25.6 (19.1)	66.0 (21.2)	14.5–86h
<i>P. troglodytes specific average</i>	31.5 (12.1)	23.2 (7.6)	63.3 (21.8)	

^aStandard deviation follows in parentheses. All measures in hours.

challenging for several reasons: One, the length of the gastrointestinal tract does not reliably indicate volume and thus the capacity of the gut (Young Owl, 1994). Two, intestinal surface area is the best means by which to determine fermentation capacity, but there are few data on the surface area of most primate species. Three, as discussed by Hladik (1967) and Martin *et al.* (1985), in some cases intestinal surface area of captive primates may be modified as a consequence of the provisioned diets. Finally, at present there is no consensus on the scaling of the gastrointestinal tract; most authors (Cork and Foley, 1991; Demment and Van Soest, 1983; Milton, 1998; Parra, 1978; Schmidt-Nielsen, 1997; Van Soest, 1996) argue that the mammalian gastrointestinal tract scales isometrically to body size. However, other authors (Chivers and Hladik, 1980; Martin *et al.*, 1985) suggest more complex allometric relationships.

Using the few data points on gastrointestinal tract surface area that are available for primate species whose digestive times are also known, Lambert (1997) found that body mass accounts for 97% of the variance in gut surface area. Thus, given that gut length is not a good indicator of volume, the paucity of data on gut surface area, that surface area can shift developmentally, and the lack of consensus regarding the allometry of primate digestive anatomy, I used bodily mass to compare the passage rate data. A calculation of the ratio y/x (where x = bodily mass, and y = gut passage time) effectively removes the influence of bodily mass on the measures and allows for a comparison across

Table V. Ratios (gut passage time/body mass) of gut passage measures in the subjects^a

Species	MRT	TT	TLA
<i>C. ascanius</i>	7.8	5.6	11.1
<i>C. mitis</i>	4.3	3.0	8.4
<i>C. neglectus</i>	5.2	3.2	9.0
<i>C. (Miopithecus) talapoin</i>	11.2	8.0	17.6
<i>P. troglodytes</i>	0.7	0.5	1.4

^aBased on species average.

differently sized taxa (Table V). The chimpanzee ratios stand out in how small they are relative to the guenon calculations. Indeed, after body size adjustment, relative to the chimpanzees, blue monkeys have $5.9 \times$ longer transit times, $6.2 \times$ longer MRT, and $6 \times$ longer TLA. DeBrazza's monkeys have $6.3 \times$ longer transit times compared to those of chimpanzees, $7.5 \times$ longer MRT, and $9 \times$ longer TLA. In comparison to chimpanzee ratios, the red-tailed monkeys have $11 \times$ longer transit times, $11.3 \times$ longer MRT, and 7.9 longer TLA. Talapoin monkeys have $15.7 \times$ longer transit times, $16.2 \times$ longer MRT, and $12.6 \times$ longer TLA than those of chimpanzees.

DISCUSSION

We have very few data on the digestive rates of primates. So, despite the constraints imposed by working with captive animals, the data presented here contribute important information for an overall understanding of the digestive ecology of forest cercopithecines. Milton and Demment (1988) reported longer MRT in chimpanzees (37.7-48 hours) compared to my subjects. These researchers evaluated the liquid and particulate passage of the diet via cobalt EDTA and chromium markers and thus it is difficult to make a comparison to my findings. For example, their methods may or may not result in comparably longer MRT calculations with *Cercopithecus* spp. Remis (2000) employed identical methods to mine on *Gorilla gorilla gorilla* and reported a range of MRT ($n = 6$ indiv) of 36.5-61.9 (mean = 47.1). She suggests that unexpectedly fast (from a body size perspective) retention times in great apes may be phylogenetically determined.

Regardless of the comparison with larger-bodied apes, my results, in combination with previously published digestive passage rates, suggest that lengthy digestive retention times may be characteristic of the Cercopithecinae in general. For example, Maisels (1993), found that *Cercopithecus pogonias*, *C. erythrotis*, and *Lophocebus albigena* had MRTs of approximately 27, 26.7, and 38 h respectively. Caton (1999) reported an MRT of 32 ± 6

h for *Cercopithecus neglectus*. *Cercopithecus aethiops* had a time of first appearance (TT) of 31.5 h (Clemens and Moloiy, 1981), and *Papio anubis* had an MRT of 37 h (Clemens and Phillips, 1980). Moreover, in an analysis regressing transit times (MRT not available for most species) as a function of body size using all reported primate transit times, Lambert (1998) found that the cercopithecines were significantly further above the regression line than any other primate taxon.

Data on passage rates are critical to determine primate digestive strategies and their capacities to deal with foods high in structural carbohydrates (Milton, 1981, 1984, 1986, 1993). Since "both the total capacity of the digestive tract and the capacity available for microbial fermentation are almost directly proportional to body mass" (Cork and Foley, 1991, p. 139), it is commonly held that only an increase in body size would allow longer retention times (Kay and Davies, 1994). Accordingly, it is generally asserted that smaller primates have both absolutely and relatively faster food passage rates than larger species, which limits their capacity to ferment fibrous plant components (Cork and Foley, 1991; Kay, 1985; Kay and Davies, 1994; Parra, 1978; Van Soest, 1996). These generalizations are based upon the well-known negative allometric relationship between mammalian body size and metabolism and its affects on feeding and foraging ecology: the Jarman/Bell principle (Bell, 1971; Gaulin, 1979; Jarman, 1974).

Yet, a pattern is emerging that suggests that *Cercopithecus* spp., and perhaps cercopithecines in general, do not conform to the expectation that they have fast digestive passage rates and should, accordingly, have a lower fiber diet than those of larger primates. Further, contrary to what might be predicted by the Jarman/Bell principle, wherever the diets of wild cercopithecines have been studied in comparison to chimpanzee diet, chimpanzees are invariably dietary specialists relying on readily digestible ripe fruit versus more generalist cercopithecines. Forest cercopithecines exhibit a high degree of flexibility in feeding; they often concentrate on common species and maintain a higher percentage of non-fruit plant parts regardless of fruit abundance (Cords, 1986; Kaplin *et al.*, 1998; Lambert, 2002). For example, in the Kanyawara area of the Kibale National Park, Uganda, Rudran (1978) recorded wide intermonthly variation in consumption of fruit by *Cercopithecus mitis* (range 17.3–75.5%), leaves (2.5–57.8%) and seeds (0–11.7%), and Wrangham *et al.* (1998) reported that for every month studied over an 11-mo period, chimpanzees had more ripe fruit in their diets than in those of *Cercopithecus ascanius*, *C. mitis* and *Lophocebus albigena*.

In addition to consuming a greater percentage of more commonly distributed and higher-fiber plant parts, cercopithecines are noted for their capacity to consume plant foods with greater secondary metabolite loads than plants consumed by sympatric chimpanzees (Lambert, 2000; Waser, 1977;

Wrangham *et al.*, 1998). Wrangham *et al.* (1998) reported that the annual diets of *Cercopithecus ascanius*, *C. mitis*, and *Lophocebus albigena* contain absolutely more condensed tannins, monoterpenoids, and triterpenoids than those of chimpanzees.

How do my data help to refine understanding of the effect of body size on forest guenon and chimpanzee diet and foraging? Gut motility is responsible for digesta retention and rate of transit through the gastrointestinal tract (Stevens and Hume, 1995). In colonic fermenters such as cercopithecines and apes, digesta retention takes place via antiperistalsis and haustral contractions in the colon. Species differ in intestinal motor activity, hence their digestive passage times (Stevens and Hume, 1995). Thus, while surface area, gross morphology, gastrointestinal length, and volume of the fermenting chamber contribute to the rate of digestive passage, even species with similar morphology can differ as a function of motility. In other words, retention times can be under selective pressure regardless of body size.

At the same time, because rates of enzymatic activity scale negatively with mammalian body size (Freeland, 1991; Walker, 1978), staying small may allow guenons to access plant foods high in secondary metabolites. Mammals without the advantage of forestomach microbial activity rely heavily on microsomal enzymes to detoxify plant metabolites (Freeland and Janzen, 1974). Accordingly, Freeland (1991) suggested that smaller mammals are at an advantage for detoxifying plant secondary metabolites and that the larger the mammal, the greater the preference for foods with low amounts of toxic plant metabolites. These assertions rest largely on results by Walker (1978), who has expressed rates of enzyme activity in rats as a function of liver mass relative to body mass.

The facts that longer retention times result in greater fermentation capacity and that smaller body size can facilitate relatively greater rates of detoxification suggest that forest guenons have adopted a strategy in which they have altered digestive motility to extract nutrients out of a high-fiber diet, while at the same time maintaining a smaller body size to detoxify plant metabolites that their larger ape counterparts cannot afford to process. This is counter to many body-size generalizations that predict that the best way manage a low-quality diet is via an increase in body size (Bell, 1971; Gaulin, 1979; Jarman, 1974; Kay and Davies, 1994; Parra, 1978; Van Soest, 1996).

Identifying the variables that contribute to dietary differences among taxa is of considerable interest to researchers concerned with the evolution of animal feeding strategies and niche divergence (Illius and Gordon, 1992; Milton, 1998; Remis, 2000). The relatively long mean retention times in cercopithecines, in combination with their smaller body size, may help to explain their dietary flexibility and their capacity to fall back on low-quality foods.

But, we clearly have much to learn. Are long retention times a primitive trait in cercopithecines? Or, is it a labile trait with high levels of modularity as in other taxa (Afik and Karasov, 1995; Bjorndal, 1989; Prop and Vulink, 1992)? Evidence from American robins that eat a diet predominated by insects during part of the year and fruit at other times of the year have retention times that shift significantly according to the digestibility and nutrient load of the diet (Levey and Karasov, 1992). This begs a series of questions, mirroring those posed by Levey and Karasov (1992): to what degree does diet determine retention times and vice versa, and how fixed are retention times in primates? These are important questions, particularly as we attempt to evaluate the niche breadth and differentiation in African monkey and apes.

ACKNOWLEDGMENTS

For assistance at the Henry Doorly Zoo, Omaha, Nebraska, I thank Dan Morris, John Bradley, Steve Casey, Elizabeth Pyle, Rachel Wither- spoon, Laura Flynn, Darlene Klimek, Laura Krause, Steve Walinski, Kevin Brown and Mike Mitchell. At the Fort Wayne's Children's Zoo, Indiana, I gratefully acknowledge the help of Mark Weldon. At the St. Louis Zoo, Missouri, I thank Ingrid Porton, Meg White, Bob Merz and Rich Rouggy. Early on, Judith Caton and Katharine Milton offered their advice on transit time methods and primate digestion, and I am thankful for their input. Stephen Wooten's assistance was invaluable and I am deeply indebted to him for his support. I thank Darcy Hannibal and Melissa Remis for their input on this manuscript, and I thank Paul Garber, Stan Ambrose, Colin Chapman and Steve Leigh for commenting on earlier versions of this work. This work was supported by a Sigma Xi Grant-in-Aid-of Research and the University of Illinois.

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