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Article in *Integrative Zoology* · June 2012

DOI: 10.1111/j.1749-4877.2012.00282.x · Source: PubMed

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ORIGINAL ARTICLE

Digestive retention times for Allen's swamp monkey and L'Hoest's monkey: data with implications for the evolution of cercopithecine digestive strategy

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Abstract

Primates access energy from plant fiber via bacterial fermentation in either a modified forestomach ('foregut'), a caecocolic ('hindgut') chamber of the large intestine, or both. Longer digestive retention times allow for more complete fermentation; as such, primates that consume an herbivorous diet high in fiber are expected to have both relatively and absolutely longer retention times than those mammals that rely on more readily digestible plant foods, such as fruit. We used particulate markers to measure the digestive retention times of captive Allen's swamp monkeys [*Allenopithecus nigroviridis* (Pocock, 1907)] ($n = 3$) and L'Hoest's monkey (*Cercopithecus lhoesti* P. Sclater, 1899) ($n = 2$). Results indicate mean retention times of 23.2–29.4 h and 23.2–24.0 h for *C. lhoesti* and *A. nigroviridis*, respectively. Results from this study, in combination with previously published data on digestive retention times in other primate species, indicate that cercopithecines differ from other primate taxa by having lengthier retention times that can be predicted by body mass alone. These data are consistent with the hypothesis that relatively lengthy retention times are a primitive trait for Cercopithecinae.

Key words: Cercopithecinae, digestive retention time, evolution of diet, fermentation, plant fiber

INTRODUCTION

Plant dietary fiber comprises carbohydrate polymers with chemical bonds that vary in their breakdown by autoenzymatic digestion (van Soest 1994; Stevens & Hume 1998). Herbivorous vertebrates access usable components of plant fiber via fermentation, a process by

which symbiotic microbes degrade the structural polymers of plant cell walls under anaerobic metabolism (Chivers 1994; Kay & Davies 1994). Fiber components requiring fermentation include the polysaccharides cellulose and hemicellulose as well as more easily fermented fiber components, such as β -glucans, pectins, inulins and oligosaccharides. The degree to which fiber can be fermented is influenced by several variables, including the diversity and abundance of the microbe community, the size of the fermentation chamber and, as evaluated here, the digestive retention time of a food bolus. Longer digestive retention times facilitate more thorough microbial processing and are generally associated with higher concentration of fermentation byproducts,

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such as short chain fatty acids (mmol/L), which are used by the host for energy (Milton & McBees 1983; Stevens & Hume 1998; Lambert & Fellner 2011). Differences in digestive retention times have been used to explain diet and feeding ecology among primate taxa. For example, the fact that howler monkeys [*Alouatta palliata* (Gray, 1849)] commonly consume a substantially more fibrous diet than similarly-sized, sympatric spider monkeys (*Atel Geoffroyi* Kuhl, 1820) is argued to be a consequence of their considerably longer digestive retention times (20.4 vs 4.4–5.3 h; Milton 1984).

The relationship between body mass and digestive retention times is linear and positive, although size explains only a portion of retention time variance. In a regression analysis of transit times using data from 41 primate species in 9 extant families, Lambert (1998) estimates that body size mass explains approximately 30% of the variance in retention time. The remainder of the variance is influenced by other factors, including anatomy (e.g. gut form and size), physiology (e.g. metabolic rate, peristalsis and hormonal stress) and behavior (e.g. activity budget, age and reproductive status) (Warner 1981; Lambert 1998). An interesting pattern to emerge from this analysis is that all species studied to date in the genus *Cercopithecus*, in the tribe Cercopithecini (guenons) and in the subfamily Cercopithecinae more generally, have considerably longer retention times than could be predicted by body size alone. Mean retention times for *Cercopithecus* species often exceed 24 h, a pattern more consistent with larger and more folivorous hindgut fermenting mammals or foregut fermenting primates (Alexander 1993; Stevens & Hume 1998).

Given this pattern, Lambert (2002a, 2007) proposes that relatively and absolutely longer digestive retention times might be primitive to Cercopithecinae. An ideal model taxon to test this hypothesis is Allen's swamp monkey [*Allenopithecus nigroviridis* (Pocock, 1907)]. In most cladistic reconstructions, this species lies close to the cercopithecine split (Disotell 2000), so close that Groves (2000) questions its inclusion in the Cercopithecinae entirely. Purvis (1995) estimates that the *Allenopithecus/Cercopithecus* lineage diverged approximately 5.0–5.2 million years ago, at approximately the terminal Miocene and pre-dating the radiation of *Cercopithecus*, estimated to be 1.00–0.25 million years ago (Leakey 1988; Fleagle 1999).

Here, we measure and compare the digestive retention times of *A. nigroviridis* with another more derived guenon species, L'Hoest's monkey (*Cercopithecus lhoesti* P. Sclater, 1899). These taxa were selected

for their potential to provide insight into the evolution of long digestive retention times in cercopithecinae. Our goals were to determine: (i) whether the digestive strategy of *C. lhoesti* is consistent with other *Cercopithecus* species, and (ii) whether *A. nigroviridis* exhibits a similar digestive strategy to other guenon species (tribe Cercopithecini). We found that *A. nigroviridis* do indeed have long digestive retention times: both absolutely and relative to body mass. Although our sample size is small, we view these results as being consistent with the hypothesis that this feature predates the divergence of the *Allenopithecus/Cercopithecus* lineages.

MATERIALS AND METHODS

Study site

Approval for this study was granted by the Institutional Animal Care and Use Committees of the Oregon Zoo and the University of Oregon. Data were collected at the Oregon Zoo, Portland, Oregon, USA in June and September 2002. The study animals included 1 adult male and 1 adult female captive *C. lhoesti* and 1 adult male and 2 adult female captive *A. nigroviridis*. The 2 species were housed in separate exhibits. *C. lhoesti* resided in an indoor climate-controlled exhibit maintained at a constant temperature (26 °C). *A. nigroviridis* were housed indoors overnight and outdoors during the day; daytime temperatures ranged from 16 to 30 °C and nighttime temperatures were held constant at 21 °C. *A. nigroviridis* shared their enclosure with 2 juvenile and 1 infant *A. nigroviridis* and 2 adult female *Colobus guereza* Rnppell, 1835. No changes to the regular diet were made during the study (Table 1). The 2 monkey species consumed a diet comprising fresh plant parts (*C. lhoesti*: 670 g/individual; *A. nigroviridis*: 340 g/individual) and extruded diet (*C. lhoesti*: 20 biscuits Marion Zoological Leaf Eater Diet = 22.3% crude protein, 5.2% crude fat and 11.1% crude fiber/individual ration; *A. nigroviridis*: 1 biscuit Purina Monkey Chow = 25.0% crude protein, 5.0% crude fat and 7.0% crude fiber/individual ration) (Table 1).

Marker administration and recovery

We undertook feeding trials on subsequent days for a total of 3 trials per animal over 3 days. A trial consisted of feeding the animal 20 plastic markers in either a small piece of banana (*C. lhoesti*) or approximately 10 g of seeded blackberry jam (*A. nigroviridis*), depending on the preferences of the group. We prepared the markers by cutting non-toxic plastic mono-filament into

Table 1 Macronutrient content of diet, including extruded diet and the vegetative parts (leaves and petioles), reproductive parts (fruits and seeds) and modified roots of domesticated plant species

Food category	Food type	Gross energy (kcal/g)	Crude protein (%)	Crude fat (%)	Crude fiber (%)	NDF (%)	ADF (%)	Individual portion (<i>C. lhoesti</i>)	Individual portion (<i>A. nigroviridis</i>)
Extruded	Marion Zoological Leaf Eater Diet	3.1	22.6	5.23	11.1	23.3	14.5	20 biscuits	—
	Purina Monkey Chow	4.0	25.0	5.0	7.0	—	—	—	1 biscuit
Vegetative plant part	Romaine lettuce, raw (<i>Lactuca setiva</i>)	4.06	31.8	3.9	33.4	16.3	14.1	165 g	85 g
	Spinach, raw (<i>Spinacia oleracea</i>)	3.99	34.0	4.2	32.1	20.1	11.7	165 g	85 g
Reproductive plant part	Apple, raw with peel (<i>Malus sylvestris</i>)	4.2	1.2	2.2	16.8	10.2	6.0	100 g	50 g
	Orange, raw with peel (<i>Citris sinensis</i>)	4.15	7.1	0.9	18.1	18.1	—	65 g	35 g
	Grapes, raw with peel (<i>Vitis vinifera</i>)	4.26	3.4	3.0	5.1	8.5	—	60 g	30 g
	Banana, raw with peel (<i>Musa sapientum</i>)	4.17	4.0	1.9	9.3	5.4	—	85 g	40 g
Modified plant root	Carrot, raw (<i>Daucus carota</i>)	4.04	8.4	1.6	—	9.7	8.9	30 g	15 g

Data are from NRC (2003) and from guaranteed analyses from Marion Zoological and Purina. Nutritional content of extruded diet is expressed as percent of ration and nutritional content of plant diet expressed as percent of dry matter (100% DM). ADF = Acid Detergent Fiber; NDF = Neutral Detergent Fiber; — = data not available.

uniform size ($1 \times 2 \times 1$ mm), following previous studies (Lambert 2002a; Remis & Dierenfeld 2004). Plastic markers were administered at the standard morning feeding times (07.30 hours for *C. lhoesti*, 08.00 hours for *A. nigroviridis*) after overnight fast. Fecal specimens were recovered over the course of the day and evening. Color coding allowed overlap of the plastic marker trials.

The animals were monitored constantly between 06.00 and 20.00 hours every day and the time and location of each defecation noted. For samples that occurred

overnight (88/342 samples from *C. lhoesti* and 0/212 samples from *A. nigroviridis*), the age of the defecation was estimated by the degree of desiccation of the specimen after training consisting of comparison of specimens of unknown age to specimens of known age. Operator estimations were 86% accurate to within 1 h of defecation and underestimated true age 96% of the time. Fecal specimens were then washed to recover the plastic markers.

Calculations and statistical analysis

Three measures of marker retention, expressed in time (h) after dosing, were calculated based on their concentration and time of appearance in fecal samples. Using standard definitions (Warner 1981), transit time (TT) is defined as the first appearance of a plastic marker in feces. The mean retention time (MRT) is generally viewed as the single best measure of the rate of passage through the GI tract (Blaxter *et al.* 1956; Warner 1981; Lambert 1998) and is calculated as:

$$MRT = \frac{\sum_{i=1}^n m_i t_i}{\sum_{i=1}^n m_i},$$

in which m_i = the quantity of marker excreted at the i th defecation at time t_i after dosing. The time of maximum marker elimination (T_{\max}) is defined as the final appearance of a plastic marker in feces.

Statistical analysis was performed using the statistical software JMP IN v7.0 (SAS Institute, 2004). Comparisons of TT and T_{\max} were performed using descriptive statistics. MRT was analyzed using analysis of variance. A χ^2 -test was performed to look for differences in the timing of defecations throughout the day. A linear regression analysis of retention time data was performed using analysis of covariance (ANCOVA). The covariates include previously published species average TT using plastic marker methodology and the average body mass for the species (Clemens & Phillips 1980; Milton 1984; Nash 1986; Crissey *et al.* 1990; Sakaguchi *et al.* 1991; Dierenfeld *et al.* 1992; Maisels 1993; Kay & Davies 1994; Cabre-Vert & Feistner 1995; Overdorff & Rasmussen 1995; Caton *et al.* 1996; Power & Oftedal 1996; Norconk *et al.* 1998; Edwards & Ullrey 1999; Kirkpatrick *et al.* 2001; Lambert 2002a; Remis & Dierenfeld 2004). A logarithmic transformation was necessary for regression covariates to fit a normal distribution to meet the assumptions of ANCOVA.

RESULTS

A total of 189 fecal samples for *C. lhoesti* and 237 for *A. nigroviridis* with markers present were collected over 275 observation hours. All animals defecated most often between 06.00 and 09.00 hours (*C. lhoesti*, $P < 0.001$; *A. nigroviridis*, $P < 0.001$). While fecal specimens were more frequent during this time, the dried mass of individual specimens did not differ over the course of the day ($P = 0.9998$).

Table 2 reports results from each trial of plastic markers. The recovery rate of markers was 21/120 (17.5%) from *C. lhoesti* and 120/180 (66%) for *A. nigroviridis*. The low fecal recovery rate, particularly in *C. lhoesti*, is due to the oral processing and spitting behavior of the animals. Similar behavior has been observed in both wild and captive cercopithecines and is a function of cheek pouch use and fine oral processing (Lambert 2001, 2005; Lambert & Whitham 2001). In an earlier study using identical methods to the current study, a low marker recovery rate was found in all *Cercopithecus* species (Lambert 2001). During feeding trials, *C. lhoesti* were observed to spit out many of the plastic markers from their mashed banana vehicles. The use of seeded blackberry jam precluded cheek pouch use in *A. nigroviridis* and appeared to improve marker recovery rate for these animals.

The regression analysis of Lambert (1998) was repeated using previously published data as well as results presented here (Table 3; Fig. 1). Linear regressions comparing the published average body weight (in grams) against the transit time (in hours) for the species average were generated for cercopithecines and non-cercopithecine primate taxa. The regression lines for body weight and TT were significant for both groups (for cercopithecines, adjusted $r^2 = 0.345$, $P = 0.026$; for non-cercopithecine primates, adjusted $r^2 = 0.366$, $P < 0.001$). The effect terms for body weight and the interaction effect were non-significant for both groups. A significant effect was detected between the cercopithecine and non-cercopithecine groups ($P = 0.006$). To verify that this effect was not affected by outliers (i.e. taxa with unusually short retention times), analyses were performed isolating each taxon (e.g. hominoids, ceboids, colobines and prosimians); once cercopithecines were excluded, no significant differences were detected among these taxa and the mean primate regression.

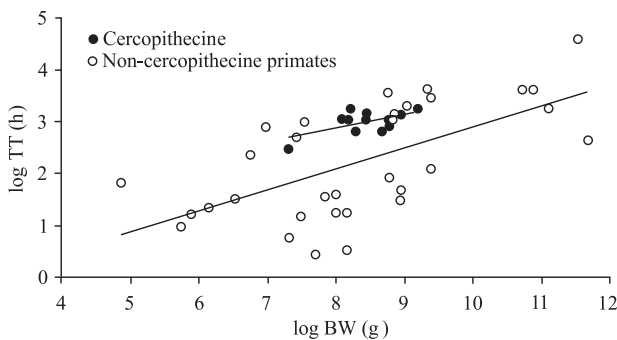
DISCUSSION

Conclusions derived from these results are limited by the small sample size and low marker recovery rate. The results for *C. lhoesti* in particular should be viewed as preliminary. Marker recovery was complicated by many logistical factors, especially spitting behavior. Spit markers were not recoverable as their small size made locating a single marker in the zoo exhibit virtually impossible, particularly for *A. nigroviridis*, where the daytime enclosure was lined with grass. Marker recovery for *A. nigroviridis* was improved by the use of seeded blackberry jam. Why this was the case is not clear.

Table 2 Digestive retention times of markers: includes animal identification, trial number, number of markers recovered/trial, transit time (TT), mean retention time (MRT) and maximum retention time (T_{\max})

Animal	Trial	Plastic Markers recovered	TT (h)	MRT (h)	T_{\max} (h)
<i>Cercopithecus lhoesti</i>					
Male	1	3 (15%)	23.0	23.2	46.0
	2	1 (5%)	—	27.2	—
	3	9 (45%)	23.5	29.4	36.1
Female	1	1 (5%)	—	24.5	—
	2	3 (15%)	25.0	25.9	26.5
	3	4 (20%)	22.9	25.9	39.6
<i>Allenopithecus nigroviridis</i>					
Male	1	12 (60%)	17.0	23.2	25.0
	2	14 (70%)	23.0	24.6	25.0
	3	15 (75%)	22.0	23.2	24.0
Female 1	1	19 (95%)	22.0	23.6	24.0
	2	12 (60%)	22.0	23.8	24.0
	3	14 (70%)	23.0	23.4	24.0
Female 2	1	8 (40%)	23.0	23.6	24.0
	2	12 (60%)	23.0	23.4	24.0
	3	14 (70%)	23.0	23.2	24.0

Transit time (TT) is determined as the first appearance of a marker per trial. Mean retention time (MRT) is calculated from the weight average of marker recovery and time. Maximum time (T_{\max}) is determined from the final appearance of a marker per trial. — = data were not collected.

**Figure 1** Correlation of body weight to digestive transit time, cercopithecines vs noncercopithecine primates.

However, it is possible that the blackberry seeds (which were similar in size and shape to the markers) overwhelmed oral perception of the experimental markers. Selective eating of the food over the brightly colored markers did not occur, as in no case were the monkeys

seen to visually examine the vehicle before consuming it.

Caveats noted, the retention times presented here for both *C. lhoesti* and *A. nigroviridis* are similar to those of other cercopithecines. The observation that *A. nigroviridis* exhibits lengthy digestive times supports the hypothesis that lengthy retention times are an adaptation shared among cercopithecines. Because long digestive retention times can result in greater production of short chain fatty acids (and, hence, usable energy) from structural polysaccharides, results presented here add to our understanding that cercopithecines do not conform to dietary expectations based on body size.

Cercopithecines are well-known for their diverse and eclectic diet and overall flexible feeding strategy (Rudran 1978; Struhsaker 1978; Gautier-Hion 1988; Beeson 1989; Richard *et al.* 1989; Altmann 1991; Maisels 1993; Lambert 2001, 2002a,b; Chapman *et al.* 2002). In comparisons of diet between African monkeys and sympatric chimpanzees, cercopithecines consistently main-

Table 3 Digestive retention times and body mass in primates, from published literature

Primate taxon	TT (h)	BW (g)	Reference
Cercopithecinae			
<i>Allenopithecus nigroviridis</i>	25.8	9800	
<i>Cercocebus albigena</i>	16.9	5900	a
<i>Cercopithecus ascanius</i>	16.6	4000	a,b
<i>Cercopithecus erythrotis</i>	20.6	3250	a
<i>Cercopithecus lhoesti</i>	20.6	3550	
<i>Cercopithecus mitis</i>	25.4	3740	a,c
<i>Cercopithecus neglectus</i>	20.6	6500	b
<i>Cercopithecus pogonias</i>	12.0	1500	a
<i>Chlorocebus aethiops</i>	22.7	7700	c
<i>Macaca mulatta</i>	23.5	4710	d
<i>Miopithecus talapoin</i>	18.4	6540	b
<i>Papio anubis</i>	21.2	4655	c
Non-cercopithecine primates			
Lemnoidae			
<i>Eulemur mongoz</i>	2.2	1510	e
<i>Eulemur fulvus</i>	1.6	2215	e
<i>Eulemur rubriventer</i>	3.3	1800	e
<i>Lemur catta</i>	4.8	2530	e,f
<i>Hapalemur griseus</i>	18.2	1080	e
<i>Varecia variegata</i>	1.7	3500	f
Galaginae			
<i>Galago crassicaudatus</i>	10.5	860	g
Cebinae			
<i>Cebus capucinus</i>	3.5	3000	h
<i>Cebus apella</i>	3.5	3500	h
Pitheciinae			
<i>Pithecia pithecia</i>	15.0	1740	i
<i>Pithecia monachus</i>	20.0	1900	h
<i>Cacajao calvus</i>	5.0	3000	h
<i>Chiropotes albinasus</i>	5.0	3000	h
Atelinae			
<i>Alouatta palliata</i>	20.4	6900	h
<i>Alouatta seniculus</i>	35.0	6400	j
<i>Ateles geoffroyi</i>	4.4	7600	h
<i>Ateles paniscus</i>	5.3	7800	h
<i>Lagothrix lagothrica</i>	6.8	6500	h
<i>Brachyteles arachnoides</i>	8.0	12 000	h
Callitrichinae			
<i>Saguinus fuscicollis</i>	2.7	310	k
<i>Saguinus oedipus</i>	3.9	470	k
<i>Leontopithecus rosalia</i>	4.6	680	k
<i>Callithrix jacchus</i>	3.4	360	k,l
<i>Cebuella pygmaea</i>	6.3	130	k
Colobinae			
<i>Nasalis larvatus</i>	14.0	120 000	m
<i>Trachypithecus auratus</i>	22.7	7080	d
<i>Colobus guereza</i>	38.0	11 350	n
<i>Pygathrix nemaeus</i>	31.5	12 100	o
<i>Rhinopithecus bieti</i>	27.0	8500	p
Hominoidea			
<i>Pongo pygmaeus</i>	37.0	53 000	h
<i>Gorilla gorilla</i>	97.0	103 000	h
<i>Pan troglodytes</i>	37.0	45 250	b
<i>Homo sapiens</i>	26.0	67 000	h

Transit Time (TT) is the time of first appearance of a marker after feeding. While MRT is a better measure of retention time, far more reports of TT are available in the literature. Body weight (BW) is reported from published values. Data from (Fleagle 1999) was used to adjudicate discrepancies. Sources: a (Maisels 1993); b (Lambert 1998); c (Clemens & Phillips 1980); d (Sakaguchi *et al.* 1991); e (Overdorff & Rasmussen 1995); f (Cabre-Vert & Feistner 1995); g (Nash 1986); h (Milton 1984); i (Norconk *et al.* 1998); j (Crissey *et al.* 1990); k (Power & Oftedal 1996); l (Caton *et al.* 1996); m (Dierenfield *et al.* 1992); n (Kay & Davies 1994); o (Edwards & Ullrey 1999); and p (Kirkpatrick *et al.* 2001).

tain a more diverse diet that includes an overall greater percentage of fiber and plant secondary metabolites (Conklin-Brittain *et al.* 1998; Wrangham *et al.* 1998; Lambert 2002b). There have been few ecological studies published on the diets of wild *A. nigroviridis* or *C. lhoesti* to determine the breadth of feeding behaviors that may correlate with these observations. The most exhaustive investigation of *C. lhoesti* (Kaplin 2001) over a 9 month period documented an eclectic omnivorous diet, with almost one-third composed of fibrous, herbaceous plant material. Lambert (2002a) suggests that cercopithecine diets are in part facilitated by a flexible digestive strategy that includes a simple acid stomach (which does not preclude consumption of high-quality but acidic foods, such as ripe fruit) as well as hindgut fermentation and long digestive retention times that facilitate access to foods of higher fiber concentration (e.g. leaves and petioles).

The mechanism behind lengthy retention times in cercopithecines relative to similarly sized animals remains uninvestigated. The cercopithecine large intestine is more expanded than predicted based on anatomical measurements in comparably sized primate taxa (Chivers & Hladik 1980). However, the true measure of the capacity of the gut is not just volume but surface area, which is exceptionally difficult to measure in living tissues as it requires careful preservation and specialized anatomical analysis (Young Owl 1994). However, other mechanisms beyond gross anatomy are almost certainly involved in the lengthy retention times observed in cercopithecines. For example, in humans it is known that the neurohumoral regulation of peristalsis is carefully regulated by the parasympathetic nervous system as well as various gastrointestinal hormones, including motilin. One to 3 mass peristaltic movements per day, usually initiated by eating, propel digesta towards the rectum; changes in the frequency or force of these propulsive movements can increase retention duration (Binder 2006). Until more data on the digestive physiology of nonhuman primates are available, a description of the mechanisms behind lengthy retention times in cercopithecines remains speculative and incomplete.

Several final caveats should be noted. First, it is important to note that digestive retention in captive animals may not be representative of digestive retention in wild animals; indeed, it is known that there can be a 'captive effect' (Martin *et al.* 1985). In addition, captive primates tend to be less active than wild animals, and differences in energy expenditure can play a role in retention time (Warner 1981; Kleiman *et al.* 1997). Fi-

nally, marker recovery for *C. lhoesti* was suboptimal, suggesting that these data should be viewed as preliminary, and that the digestive strategies of cercopithecines specifically, and primates more generally, would benefit from further investigation.

ACKNOWLEDGMENTS

We are grateful to Tricia Calhoon, KO Ottenstein and Megan Ayars for help collecting the fecal specimens. Logistical assistance at the Oregon Zoo was provided by Dave Thomas, Anna Michel and Jan Steele. The study was supported by funding from the University of Oregon. The protocol was approved and conducted in compliance with the Institutional Animal Care and Use Committees of the University of Oregon and the Oregon Zoo.

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