

Rate of digesta passage in the Philippine flying lemur, *Cynocephalus volans*

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Accepted: 7 January 1994

Abstract. The rate of digesta passage was measured in five captive Philippine flying lemurs (*Cynocephalus volans*). These animals were force fed capsules containing known quantities of either particulate or soluble markers. The volumes of the gastrointestinal tracts of three flying lemurs were determined based on the wet weight of the contents of each section of the gut. The mean rate of digesta passage was 14.37 ± 3.31 h when determined using the particulate marker and 21.9 ± 0.03 h when determined using the soluble marker. The values based on the particulate marker are between 2% and 10% of similar values for other arboreal folivores. The morphology of the gastrointestinal system of the Philippine flying lemur is similar to that of other hindgut fermenters. Flying lemurs have a simple stomach and a large caecum. The total gut capacity of the Philippine flying lemur is similar to that of other herbivores, but is slightly smaller than that of either the koala (*Phascolarctos cinereus*), a hindgut fermenter, or the three-toed sloth (*Bradypus variegatus*), a foregut fermenter. These data suggest that flying lemurs deal with the problems of a folivorous diet very differently than some other arboreal mammals. *Phascolarctos cinereus* and *Bradypus variegatus* may represent one extreme with *Cynocephalus volans* representing the other extreme along a continuum of foraging strategies that are compatible with the arboreal folivore lifestyle.

Key words: Digesta passage – Arboreal folivore – Flying lemur – *Cynocephalus volans*

Introduction

Throughout tropical forests leaves provide an abundant resource for herbivores, yet very few mammals have taken advantage of this resource. It appears that the high fiber content and the spatial and temporal complexity of tropical forests may have restricted the use of this resource to only a few mammalian species (McNab 1978; Cork et al. 1983).

Mammalian arboreal folivores represent a unique group of herbivores owing to the constraints under which they forage. The spatial arrangement and complexity of the food resource represent additional constraints on this group in relation to other herbivores. The arrangement of forage trees results in a patchy distribution of forage resources even on a large spatial scale. The production of foliage at the terminus of a branch limits the size of the animals that can reach this resource (Grand 1978). Leaves, although plentiful, are also a low quality forage resource (owing to high fiber and lignin content) and often contain secondary plant compounds (eg. tannins, alkaloids, etc.) (Janzen 1978; Langer 1986).

Small herbivores are generally restricted to high quality forage (forage containing low amounts of fiber) because gut capacity is directly proportional to body size, while mass-specific MR is inversely proportional to body size (Demment 1982; Demment and Van Soest 1985). In order for small herbivores to meet their nutritional requirements they increase their intake by reducing the residence time of digesta. Reducing the residence time reduces the ability to digest fiber, which necessitates the consumption of rapidly digestible, low-fibre forage (Van Soest et al. 1981; Demment and Van Soest 1985).

Eisenberg (1978) ranked mammalian arboreal folivores in terms of their degrees of folivory and arboreality based on gut morphology and the natural history of the animals. Of the species with the highest rankings in both categories, only two, the koala (*Phascolarctos cinereus*) and the three-toed sloth (*Bradypus variegatus*), have been previously studied in detail. Both of these small mammals (<15 kg) differ from other small herbivores in that

Abbreviations: bw, body weight; EDTA, ethylenediaminetetraacetic acid; MR, metabolic rate; t , mean rate of passage; t_{exp} , expected time to appearance; t_0 , time to first appearance

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they have extremely slow rates of digesta passage (Montgomery and Sunquist 1978; Warner 1981; Cork and Warner 1983). Although the slow rate of digesta passage increases their ability to digest fiber it also limits their forage intake and ultimately their energy intake. Both of these species balance their low forage intake with very low energy requirements (McNab 1978; Montgomery and Sunquist 1978; Eberhard 1978).

We were interested in whether other mammalian arboreal folivores were somehow constrained by the same digestive physiology to use a similar foraging strategy. The Philippine flying lemur (*Cynocephalus volans*) is an arboreal folivore restricted to six islands in the Republic of the Philippines. It differs from most other arboreal folivores in its extensive gliding ability (Wharton 1950; Medway 1978; Wischusen 1990). We hypothesized that the ability of this species to easily move long distances through the forest might allow it to utilize a different foraging strategy from either the sloth or koala. In this paper we describe the rate of digesta passage and the gastrointestinal morphology in the Philippine flying lemur. We then compare these data to data for other species of arboreal folivores to determine if the Philippine flying lemur differs from other arboreal folivores in its digestive physiology. The implications of these data for the foraging and energetic strategies of the Philippine flying lemur are discussed.

Materials and methods

Five adult Philippine flying lemurs (three males and two females) were maintained in small outdoor cages which provided shelter from both the sun and rain. These were free-ranging animals that were captured just prior to the start of these experiments. They were supplied with fresh young leaves from tree species on which animals were commonly observed foraging (*Shorea squamata*, *Ficus* spp., *Artocarpus heterophylla*, *Palaquium* spp.) at least twice a day (06:00 and 17:00 hours). In addition to the leaves water was also provided by spraying water on the leaves and in dishes.

The rate of digesta passage was measured using both particulate and soluble markers. Two types of markers were employed because of the different rates of passage for different fractions of digesta observed in other animals (Warner 1981). The particulate marker used was a plastic pellet 2–4 mm in length, 1 mm in diameter, with a specific gravity of 1.3 (Stevens et al. 1987). Fifty pellets were placed in a gelatine capsule to facilitate feeding to the experimental animals. The soluble marker was LiCr EDTA which was synthesized following the methods of Uden (1978). A known weight of the marker was placed in a gelatine capsule.

Only animals that had been maintained in captivity for at least 2 weeks and whose weight had stabilized were fed the markers. The capsules were force fed to the animals just prior to sunset (the beginning of their natural active period). During the following days the cages were checked at approximately 2-h intervals for the presence of feces. The feces were then collected and either the pellets were recovered and counted, or the feces were dried for storage. The dried feces were later analyzed for Cr concentration using an atomic absorption spectrophotometer (Uden 1978). The trials using the soluble and particulate markers were conducted independently of each other.

Several measures of the rate of digesta passage were then calculated from these data. The time to first appearance (t_0) of the markers was calculated as the midpoint of the interval during which the feces containing the marker first appeared. The mean rate of passage (t) for both types of markers was determined as:

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

where m_i is the quantity of marker excreted in the i^{th} defecation at time t_i , the midpoint of the collection interval after dosing (Cork and Warner 1983). The mean rate of passage for the largest gut segment or T_{exp} was calculated by fitting an exponential curve ($y = Ae^{-kt}$, where A is a constant) to the declining portion of a marker excretion curve and then taking the reciprocal of k (Cork and Warner 1983).

The gut capacity of flying lemurs was determined by removing the gastrointestinal tracts from three female flying lemurs. These were free-ranging animals that were collected during their active period. The contents of the different sections of the gastrointestinal tract were weighed to the nearest 0.01 g following the methods of Demment (1982). Although there is a tendency for this method to underestimate the gut contents of small animals it has been extensively used in previous studies (Demment 1982).

Results

The mean rates of passage (t) for the trials conducted using the particulate marker averaged 14.37 ± 3.31 h (range 11.26–22.78 h). This is much shorter than the estimated rate of passage (24.6 h) for other non-ruminant herbivores of the same size, based on the relationship between bw (1.75 kg) and rate of passage for non-ruminant herbivores (Van Soest et al. 1983) (Table 1). The

Table 1. Measures (mean \pm SD) of the retention of digesta in the gut of Philippine flying lemurs (*Cynocephalus volans*)

Measure	Plastic pellets (15)	Cr EDTA (2)
t_0 (time to first appearance)	7.1 ± 3.61	4.0 ± 1.41
t (mean rate of passage)	14.4 ± 3.31	21.9 ± 0.03

All times are in hours and the numbers of replicates are in parentheses

Table 2. Mean gut retention time for the Philippine flying lemur (*Cynocephalus volans*) based on trials using particulate marker

Animal	Sex	Number of trials	Mean retention time ^a (hours)
1	M	1	11.26
1	M	2	11.57
1	M	3	11.62
1	M	4	11.71
1	M	5	14.35
2	F	1	16.40
2	F	2	11.00
2	F	3	11.78
3	F	1	22.78
3	F	2	13.49
3	F	1	15.52
4	F	2	14.73
4	F	3	14.51
5	M	1	15.48
Mean for all trials			$14.37 (\pm 3.31)$

^a Calculated following Cork and Warner (1983)

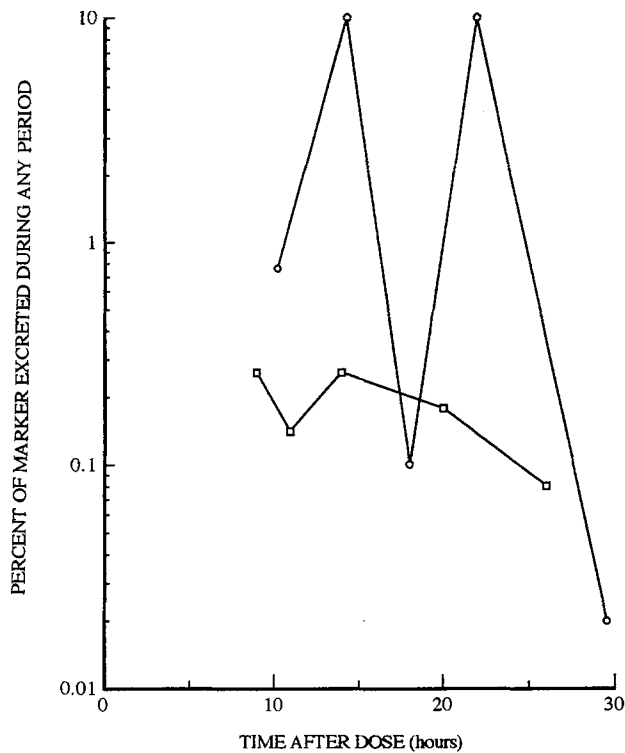


Fig. 1. Excretion curves for two different trials conducted with the same Philippine flying lemur (*Cynocephalus volans*) using a particulate marker

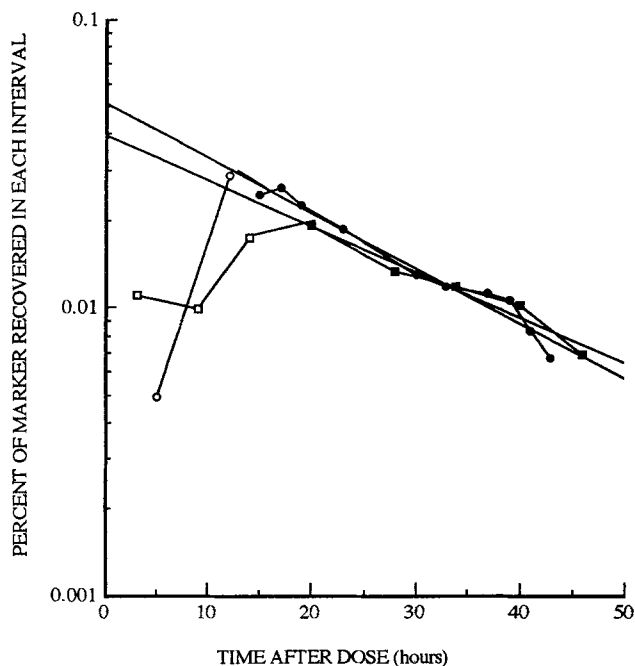


Fig. 2. Excretion curves for the Philippine flying lemur (*Cynocephalus volans*) using the marker LiCr EDTA. Lines were fitted to the declining portion of each line (filled points). The equations for the lines were: $y = 0.051 \cdot e^{(-0.044 \cdot x)}$, $r = -0.98$; and $y = 0.040 \cdot e^{(-0.037 \cdot x)}$, $r = -0.98$, for the two trials, respectively

Table 3. Capacity of the gastrointestinal tract of the Philippine flying lemur (*Cynocephalus volans*). The numbers in parentheses are the percentage of the body weight

Section	Capacity (g)		
	I-12	I-4	II-7
Stomach	47.6 (2.4)	48.9 (2.9)	18.2 (1.6)
Small intestine	22.1 (1.1)	12.9 (0.8)	5.9 (0.5)
Caecum	77.4 (3.9)	88.5 (5.2)	45.6 (4.2)
Colon	136.6 (6.8)	105.3 (6.2)	70.0 (6.4)
Total	283.7 (14.2)	255.6 (15.1)	139.7 (12.7)

mean rates of passage (t) for the trials conducted using the soluble marker were much longer than for the particulate marker with a mean of 21.9 ± 0.03 h versus 14.37 h (Table 1).

In the trials conducted using the particulate marker there was a trend in rate of passage based on the sex of the individual (Table 2): males (12.66 ± 1.79 h) tended to have faster rates of passage than females (15.51 ± 3.68 h); however, these differences were not statistically significant (ANOVA, $df = 1$, $F = 3.043$, $P = 0.10$).

The particulate marker did not show a consistent pattern of excretion even within one individual. In some trials the initial increase in marker concentration in the feces was followed by a steady decline and in others the increase was followed by a bimodal pattern (Fig. 1). The soluble marker (LiCr EDTA) showed a consistent excretion pattern consisting of an initial increase in marker concentration followed by a steady decline (Fig. 2). The decline in marker excretion followed a simple exponential decay pattern.

The contents of the gastro-intestinal tracts represented 14% of the bw of these animals (Table 3). Of the different segments of the gastrointestinal tract the colon had the greatest capacity, containing approximately 46% of the total contents, followed by the caecum (32%), stomach (16%), and finally the small intestine (6%). The site of fermentation (caecum and colon) represented 78% of the total gut capacity for this species (Table 3).

Discussion

The overall mean rate of digesta passage of the Philippine flying lemur was not only shorter than expected for a non-ruminant herbivore of its size but was also very short when compared to the rate of passage for other

Table 4. Comparison of the mean rates of digesta passage for several mammalian arboreal folivores

Species	Mean retention time (hours)	Source
<i>Bradypus variegatus</i>	632	Montgomery and Sunquist (1978)
<i>Cynocephalus volans</i>	14	This study
<i>Phascogalea cinerea</i>	100–213	Cork and Warner (1983)

arboreal folivores (Table 4). In experiments conducted using particulate markers the mean rate of digesta passage for the three-toed sloth and the koala are both extremely long for animals of their size (Table 4) (Montgomery and Sunquist 1978; Cork and Warner 1983). The mean rate of digesta passage for the Philippine flying lemur using a particulate marker was much shorter than that of either of these species, being approximately only 2% and 10% of the mean rates of passage for the other species, respectively (Table 4).

This relatively fast rate of passage indicates that they consume much greater quantities of forage, but have a reduced ability to digest fiber (Van Soest et al. 1983). These data suggest that flying lemurs may select forage low in fiber. Milton (1979) showed that young leaves for a variety of tropical tree species contained 33% less fiber than mature leaves. Our observations of forage choice by the Philippine flying lemurs support this prediction. Of 312 foraging bouts recorded for Philippine flying lemurs all were of animals consuming young leaves. Koalas, in contrast, have been observed feeding extensively on old foliage (Eberhard 1978) which tends to be much higher in fiber and therefore more difficult to digest.

A comparison of the data from the trials conducted using the soluble marker suggests that there is either a single mixing compartment or several mixing compartments functioning in parallel, rather than in series. If the mixing compartments were functioning in parallel t_{exp} would be expected to be equal to or greater than t , but this result is not expected if several mixing pools are functioning in series (Table 5) (Cork and Warner 1983). Data for the soluble marker also suggest that the solute and perhaps very fine particulate matter is being mixed in a pool, owing to the exponential decline in marker excretion over time, while data for the particulate marker suggests that the large particulate matter may often bypass that pool and leave the gut. This type of pattern has been

seen in koalas and may result in a reduction of the duration of the "gut-filling" effect of the diet (Cork and Warner 1983).

The total gut capacity of the three measured flying lemur digestive tracts ranged from 139.7 to 283.7 g, or from 12.7 to 15.0% of the individuals bw (Table 6). The percentage of the bw of flying lemurs composed of digestive tract was within the range exhibited by other herbivores (Parra 1978). The total gut capacity was slightly smaller than the capacities of either the three-toed sloth or the koala, although it was not possible to test for the significance of these differences (Table 6).

The morphology of the gastrointestinal system of the Philippine flying lemur was similar to that of other hindgut fermenters (Bauchop 1978). All of these animals have relatively simple stomachs and either large caeca or colons, or both. The total gut capacity of flying lemurs was similar when compared to herbivores in general, but it was slightly smaller than that of either the koala or the three-toed sloth. Considering the very long rates of passage of both the koala and sloth the larger gut volumes would allow these species to increase their intake.

These comparisons suggest that the Philippine flying lemur is very similar in gut morphology to other species of hindgut-fermenting herbivores and in rate of digesta passage to other species of herbivores. However, when the comparisons are restricted to other species of arboreal folivores it appears that there are major differences between flying lemurs and both the koala and the three-toed sloth.

How do these differences influence the foraging strategies of these species? The three-toed sloth and the koala are both species with very long rates of passage, increasing the amount of fiber which can be digested compared to species with shorter rates of passage. The greater digestibility may have allowed these species to feed on foliage with a greater range of fiber content, including old foliage, which in addition to being the most abundant source of foliage in the forest also contains high levels of fiber. Because this food resource (high-fiber foliage) is very abundant, the animals do not need to move from one location to another very often and, therefore, exhibit limited movement on a daily basis. Species such as the Philippine flying lemur and perhaps others which have short rates of passage are not able to digest fiber as well as the species with the longer rates of passage (Bosque and de Parra 1992). The flying lemurs must therefore select only readily digestible foliage, or foliage low in fiber such as young foliage. Young foliage, however, is not only much less common in the forest than old foliage, but the spatial distribution of young foliage is often much more scattered owing to the leafing phenologies of the various tree species. In order for flying lemurs to find enough appropriate forage, they must move much greater distances than either the sloth or koala. The large daily movement pattern observed in the proboscis monkey may be the result of a similar situation (Salter et al. 1985).

Coprophagy would be one method of increasing the digestibility of forage for hindgut fermenters. In the case of the Philippine flying lemur even though the soluble marker has a longer mean retention time than the partic-

Table 5. Comparison of mean rate of passage t and the estimated mean rate of passage for the largest gut compartment t_{exp} for individual flying lemurs (*Cynocephalus volans*)

Animal	No. of trials	t	t_{exp}
1	1	22.00	22.76
2	1	21.96	27.30

All data were collected using LiCr EDTA as the marker, and all times are in hours

Table 6. Comparison of the site of fermentation and size gastrointestinal tracts of several mammalian arboreal folivores

Species	Fermentation site	Gut capacity (percent of bw)	Source
<i>Bradypus variegatus</i>	Forestomach	~20	Parra (1978)
<i>Cynocephalus volans</i>	Hindgut	14.0	This study
<i>Phascogalea cinereus</i>	Hindgut	20.0	Cork and Warner (1983)

Table 7. Summary comparison of the foraging strategies of arboreal folivores

Species	Method of locomotion	Fermentation site	Rate of passage	Distance moved	Species consumed
<i>Bradypus variegatus</i>	Non-gliding	Forestomach	Long	Short	Many
<i>Cynocephalus volans</i>	Gliding	Hindgut	Short	Long	Many
<i>Petauroides volans</i>	Gliding	Hindgut	?	?	Few
<i>Phascolarctos cinereus</i>	Non-gliding	Hindgut	Long	Short	Few
<i>Nasalis larvatus</i>	Non-gliding	Forestomach	?	Long	Many

ulate marker, a finding which would be expected if the animal was practicing coprophagy, the difference in the mean retention times was relatively small compared to differences seen in animals known to practice coprophagy regularly such as rabbits (Uden 1978). However, the proportional difference in retention times between the soluble and particulate markers was similar to that observed for the koala, which has been observed reingesting its feces (Waring et al. 1966). Unfortunately, the extent of coprophagy practiced by koalas and the impact of coprophagy on its nutrition are not known.

The similarities in the capacity of the fermentation chamber and the overall gut capacities was not surprising owing to the work of Parra (1978) who showed that, although there was a lot of variability between species, generally all herbivores have the same gut capacities when scaled to bw. This similarity in gut capacity relative to bw implies that the species with slower passage rates take in less forage over time than the species with the faster rates of passage. Mertens (1973) showed that the rate of digesta passage was the most important factor in predicting the intake and digestibility of forage for herbivores.

Overall, the inferred digestive physiology of the Philippine flying lemur appears to be very similar to that expected for a small hindgut-fermenting herbivore and very different from either the koala or the three-toed sloth. Arboreal folivores have been thought to use similar foraging strategies owing to the many environmental constraints under which they forage (McNab 1978; Cork et al. 1983). Data from this study suggest that within this group of animals there is considerable variation in the digestive physiology and probably the foraging strategies of these animals. These comparisons reveal two strategies used by arboreal folivores (Table 7): one, which has been previously described for the three-toed sloth and the koala, is an energy-conserving strategy involving long gut retention times, the ability to utilize low quality forage, and little daily movement (Montgomery and Sunquist 1978; Cork and Warner 1983). The other, which is used by the Philippine flying lemur and potentially by other species, consists of a much shorter gut retention time, high intake of forage, selection of high quality forage, and great daily movement. The need to select low fiber forage may in part be responsible for the long distances moved on a daily basis. This strategy appears to involve a higher energy expenditure, which may be responsible for the shorter retention time.

This comparison also points out the need for additional information about various aspects of the foraging

ecology of arboreal folivores (Table 7). Detailed information about the diet composition of the koala and the greater glider as well as information about the rate of digesta passage for the greater glider and the proboscis monkey would greatly enhance this type of comparison. As additional information about these species becomes available researchers may find a continuum of foraging strategies employed by different species of arboreal folivores in which there is not one or two optimum strategies, but rather a continuum of strategies.

Acknowledgements. We would like to thank Brian McNab and an anonymous reviewer for their critical reviews of an earlier draft of this manuscript; O. Babao, N. Basoc, Jr., E. Cedilla, and J. Villarosa for their assistance in the field; and the Ferrazini family for providing us with a house to stay in and permission to work on their land. This study was generously supported by the Chicago Zoological Society, Wildlife Conservation International, and the U.S. Fish and Wildlife Service.

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