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The Digestive Strategy of the Common Marmoset, *Callithrix jacchus*

J. M. Caton,[1] *D. M. Hill,*[2] *I. D. Hume,*[3] *and G. A. Crook*[4]

[1]Department of Archaeology and Anthropology, The Australian National University, Canberra ACT Australia; [2]Environmental Science Program, Australian Nuclear Science and Technology Organization, Menai NSW Australia; [3]School of Biological Sciences, The University of Sydney NSW Australia; [4]Division of Human Nutrition, Commonwealth Scientific and Industrial Research Organization, O'Halloran Hill SA Australia

ABSTRACT. Digestive tract morphology and function were studied in the common marmoset (*Callithrix jacchus*), a small (350 g) exudivore with a well-developed caecum. Transit times (times of first appearance of the markers in the faeces following a pulse dose in the food) were similar for Co-EDTA, which marks the fluid phase of the digesta, and Cr-mordanted cell walls, which marked the large (600–1200 μm) particulate phase of the digesta. However, mean retention time (the average time taken for the markers to transverse the whole digestive tract) for Co-EDTA was significantly longer than for Cr-cell walls, indicating selective retention of fluid digesta relative to large particles, probably in the caecum. These data are consistent with a digestive strategy of the common marmoset that appears to be based on rapid digestion of higher quality foods (animal prey, fruits) in the small intestine, followed by microbial fermentation of the complex polysaccharides of plant exudates in the caecum, which would allow for considerable dietary flexibility in its natural habitat of scrub forests. COMP BIOCHEM PHYSIOL 114A;1: 1–8, 1996.

KEY WORDS. Common marmoset, exudivore, caecum, digestive strategy, digesta retention

INTRODUCTION

The common marmoset, *Callithrix jacchus* (family Callitrichidae), is a small monkey from the xerophytic forests and drier woodlands of north-east and central Brazil, which are considered by Rylands (26) to be harsher environments than the rain forests of Amazonia where most other members of this family are found (26). C. *jacchus*, with a body mass of 350 g, is an exudivore that feeds on gums harvested from a number of species of trees (6,17,29). The dry matter of these gums is predominantly nonstarch polysaccharide (14,18,26), which is mainly processed indirectly by mammals. As with other nonstarch polysaccharides, digestion of gums is accomplished by microbial fermentation at sites within the gastrointestinal tract where digesta are retained long enough to allow significant growth of the microorganisms involved (14). Mammals of small body size, particularly less than 500 g, have to cope with high energetic requirements that are associated with rapid heat loss from high surface area to volume ratios (14,22). Thus, it would be expected that a diet of slowly processed gums could present problems for the common marmoset. This paper describes the digestive strategy of C. *jacchus* in relation to its predominantly exudivorous diet and the energetic costs of its small body size and unusually high reproductive output.

Reproduction in the common marmoset, as in all callitrichids, is unusual among primates in that multiple births are the norm, with females usually producing twins every 5 months. Thus, female marmosets are almost continually pregnant or lactating. The neonates are large, being 25% of the mother's mass at birth (26). The total costs of reproduction for the female are reduced somewhat by the evolution of a social structure that relieves her of caring for and carrying the young, which are the duties of the male and the older siblings. Callitrichids live in small family groups of 3 to 7 animals, with one breeding pair and their young of various ages (17,29).

The family groups occupy home ranges of 2.5 to 6.5 ha (29). The animals spend most of the day in core areas of 1.0 to 1.5 ha, which are the focus for their feeding activities, particularly those that are centred on trees that produce exudates (gums and saps). Scanlon *et al.* (29) found that the core areas contained 54 to 151 exudate-producing trees per ha, and estimated that a single marmoset group would need a minimum of 54 such trees per ha to survive. Exudate feeding peaks early in the morning and late in the

Address reprint requests to: Mrs. J. M. Caton, Dept. of Archaeology and Anthropology, The Australian National University, Canberra ACT 0200 Australia. Fax: 06 249 2711.

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afternoon. During the remainder of the day the marmosets disperse throughout the canopy to hunt insects. They also eat fruit, but that is not a major component of their diet (27). C. *jacchus* is strictly diurnal, retiring to sleeping sites at dusk and remaining there until morning (17). Power (22) reported that callitrichids lower their body temperatures at night to reduce heat loss when ambient temperatures are lowest.

The marmosets exhibit a range of anatomical features that enable them to exploit exudates as a food source. These include the following:

1. Pointed and keeled nails on all digits, except the hallux, that enable them to grip the bark of the trunks and larger branches of trees while feeding or preparing exudate holes (19,25);
2. A well-developed tooth-scraper, with mandibular incisors that are procumbent and equal to the canines in length for gouging holes through the cambium layer of exudate-producing trees, releasing a flow of gum for harvesting (19);
3. A well-developed caecum, of equal calibre to the colon, that is blunt-ended and U-shaped in form (2,9–12). Two taeniae extend from the colon to midway along the length of the caecum, producing the haustrations that are clearly seen in freshly killed animals (Caton, personal communication).

Similar adaptations are seen in the fork-crowned lemur, *Phaner furcifer*, and the needle-clawed bushbaby, *Euoticus elegantulus* (19).

When looking at the physiological mechanisms needed for processing the polysaccharides of exudates, the concept of optimal digestion can be used to predict the strategy that would allow an animal of a given size to maximize energy release from ingested food (14). Based on this concept, three important factors have implications for a small marmoset:

1. Optimal digestion time will vary among foods, being longer for poor quality foods, such as exudates and other items containing complex polysaccharides that are only degraded by microbial fermentation, than for higher quality foods, such as fruit and animal prey that are rapidly digested by the animal's own enzymes;
2. If gut capacity is limiting, as in many small mammals (7), the optimal strategy will be to maximize digestion rate by selecting higher quality foods;
3. At any given level of intake, an animal should maximize the retention of food so as to maximize the rate of obtaining energy. This will be longer for the poorer quality foods requiring microbial fermentation.

At 350 g body mass, these factors present marmosets with a dilemma, for they have a need for both slow and fast digestive processes within the gut to meet their high mass-specific energy requirements. Resolution of their dilemma is facilitated by reference to chemical reactor theory, which considers optimal gut structure and the constraints that apply in terms of the principles of chemical reactor engineering (20). Animal digestive tracts can be considered to be a series of chemical reactors. First, a marmoset gut must be capable of digesting and absorbing nutrients rapidly. This is the role of the small intestine, which functions in a way that is best modelled as a plug-flow reactor (PFR). These reactors are characterised by an orderly flow of material through a tubular reaction vessel. Reactant concentrations and reaction rates are high near the entrance to the reactor, but they decline along its length. Plug flow provides the greatest rate of digestive product formation in the minimum of time and volume under most conditions, although the extent of digestion may be low unless the reactants are easily digested. Thus, high quality foods can be processed rapidly in PFR-like organs such as the small intestine, providing the animal with a readily available source of nutrients. The slower process of microbial fermentation usually takes place in organs that are best modelled as continuous-flow stirred-tank reactors (CSTR), in which reactants are diluted immediately upon entry by material recirculating in the reactor—in the case of the gut, residues from previous meals. Reaction rates, in general, are lower than in PFR, but can still be relatively high if flow through the reactor is low enough. Hume (14) considered the mammalian caecum to be a modified CSTR, and in the case of the common marmoset this idea is supported anatomically by the size of the organ and by the well-developed haustrations that serve to mix the contents of this fermentation chamber.

To investigate the importance of the caecum to the digestive strategy of C. *jacchus*, both morphometric and digesta marker studies were undertaken. Two digesta markers were administered at the same time in one pulse dose. These markers when used together, can provide valuable insights into gut function, particularly potential sites within the gut for retention of different digesta components. Fermentation chambers may be found in either the forestomach or the hindgut (*i.e.*, the caecum and colon). For each of these digestive strategies, involving microbial fermentation in the forestomach or regions of the hindgut, there are distinctive patterns of marker excretion (14). In small caecum fermenters, the fluid phase of the digesta is often retained for a longer period than in the particulate phase (15,31). We predicted that this would be the case in C. *jacchus* if the caecum was likely to be the principal site of fermentation of exudates.

MATERIALS AND METHODS

The study was conducted in the marmoset colony maintained by the Division of Human Nutrition of the Commonwealth Scientific and Industrial Research Organization, O'Halloran Hill, South Australia.

Morphology and Morphometrics of the Digestive Tract

Three freshly killed adult female common marmosets *Callithrix jacchus* (343 g mean body mass), were made available for dissection. All of the animals were healthy and had been maintained on the same diet as the three animals used in the digesta marker experiment. Each animal was weighed, then its digestive tract exposed through a ventral midline incision. The tract was removed from the body, cleared of mesenteric attachments, and divided into stomach, small intestine, caecum and colon; it was not possible to clearly distinguish between the proximal and distal sections of the colon. Each section of the tract was then weighed, emptied of contents and reweighed. The length of each section, including the stomach along its long axis (not along its greater curvature), was measured immediately after its removal from the body, while still filled with digesta, and without stretching the tissue.

Animals, Housing and Diet

The three adult C. *jacchus* (two females and a male) of 348 g average body mass (Table 4) used in the marker transit study were housed individually in barred aluminum cages (46 × 34 × 60 cm high) for the duration of this part of the study. The barred floors to the cages allowed faeces to fall through onto stainless steel trays. The animals were held in an air-conditioned room (25° ± 2°C) on a 12-hour light/12-hour dark cycle, with lights on at 0700 h and were maintained on the usual colony diet of 30 g marmoset pellets (Commonwealth Scientific and Industrial Research Organization, Division of Human Nutrition marmoset colony formula) plus 10 g banana, 20 g fruit, nuts or vegetables per day and water ad libitum throughout the experiment. The composition of the marmoset pellets and their nutrient analysis are given in Tables 1 and 2, respectively.

TABLE 1. Composition of pelleted marmoset diet (air dry)

	g/100 g diet
Wheat grain	38.9
Field peas	13.9
Meatmeal	8.5
Oat grain	8.0
Rice pollard	8.0
Soybean meal	6.0
Fishmeal	5.0
Cottonseed meal	4.0
Sunflower oil	1.9
Commercial calcium source	1.5
Commercial phosphorus source	1.0
Binder	1.2
Tallow	1.0
Vitamin/mineral premix	0.4
Salt	0.2
Choline chloride	0.2
L-lysine	0.17
Flavouring	0.1
Ascorbic acid (heat stable)	0.01

TABLE 2. Nutritional analysis of pelleted marmoset diet (oven dry air)

	g/100 g diet
Crude protein	24.4
Crude fat	11.7
Ash	8.2
Crude fibre	4.9
Calcium	2.15
Total phosphorus	1.48
Available phosphorus	1.11
Sodium	0.25
	mg/100 g diet
Iron	11.6
Zinc	7.3
Manganese	5.8
Copper	1.7
Cobalt	0.12
Iodine	0.12
Niacin	6.9
Thiamine	6.5
Riboflavin	3.5
Pyroxidine	2.3
Folic acid	0.58
Vitamin A	0.96
Vitamin E	10.4
Vitamin K3	0.52
	μg/100 g diet
Vitamin D3	36.1
Biotin	34.7
Vitamin B12	1.2

Fresh food was presented between 0800 and 0900 h each day; the animals tended to eat the fruit first, then ate the pellets at frequent intervals throughout the rest of the light phase.

Measurement of the Rate of Digesta Passage

Two digesta markers were used. The fluid phase of the digesta was marked with cobalt-ethylene diaminetetraacetic acid (Co-EDTA), which has been shown by Uden *et al.* (34) to associate virtually exclusively with fluid. The particulate phase was marked with chromium mordanted on to cell-wall constituents (Cr-CWC) prepared from chopped oaten (*Avena sativa*) hay (8). The cell walls were prepared by the neutral-detergent fibre technique of Van Soest and Vine (33), then washed through a set of Endicott (London, U.K.) screens. Those particles that passed through a 1200-μm screen but were retained on a 600-μm screen were collected for the mordanting procedure. Mordanting renders the particles indigestible (34).

The marker dose was given by mixing 0.1 g Co-EDTA and 0.2 g Cr-CWC with mashed banana and presenting this to the marmosets at 0830 h, before their regular feeding. The marmosets were more cautious when the banana, a favoured food, was rendered bright purple in colour by

the Co-EDTA, and it took variable amounts of time for them to consume the markers. Thus, the time of dosing was taken to be the mid-time between the presentation of the markers and their complete consumption. A fourth marmoset, M469, would not eat the marked banana, and was removed from the experiment. The collection trays beneath the holding cages were then checked usually at two-hour intervals during the light phase (daylight), and many faeces present were collected. This was done for a total of 3 days. Marmosets, like most monkeys, are diurnal animals, and no faeces were produced during the dark phase (Fig. 1). Time of faeces collection (Ti) was taken as the midpoint between the time the faeces were collected and the previous time the collection trays were checked during daylight hours.

Analytical Methods

The faeces were collected onto small squares of aluminium foil for drying and transport, then dried at 40°C for 48 hours. They were prepared for analysis Co and Cr concentrations in a flame atomic absorption spectrophotometer (Varian AA/400P) by the wet-ashing procedure routinely used by Hill at the Environmental Chemistry Laboratories, Australian Nuclear Science and Technology Organization, for the extraction of metals from oxidisable material. Samples of up to 1.5 g taken from the dried faeces were weighed into 150-mL conical flasks. Ten millilitres of a 1 : 1 solution of concentrated nitric acid (HNO_3) : H_2O were added to each of the flasks, which were then covered with a watch glass and warmed on a hotplate for 10 min. The flasks were removed from the hotplate, 5 mL concentrated HNO_3 was added to each one, and then they were returned to the hotplate; the temperature was raised slightly to start them gently refluxing. After 30 min they were again removed from the hotplate so that a further 5 mL HNO_3 could be added. Refluxing was continued in the covered flasks for a further 30 min, at a slightly higher temperature than previously to ensure that the contents were boiling rapidly. At the end of this time, the watch glasses covering the flasks were moved to the side to provide an opening for escaping steam and nitrous oxide. The volume of the contents of the flasks was reduced to approximately 5 mL by again raising the temperature of the hotplate slightly, taking care to avoid boiling the flasks dry. The flasks were then removed from the hotplate and cooled before adding 3 mL hydrogen peroxide (H_2O_2) plus 2 mL water to each one in order to complete the oxidation reaction. Further H_2O_2 was added 1 mL at a time (up to 10 mL total, including the original 3 mL) if needed to clear the solution of any remaining organic matter. The contents were again evaporated to approximately 5 mL, with the flasks remaining partially covered. The solutions then were transferred quantitatively to 100-mL volumetric flasks and diluted to 100 mL. Two 20 mL samples were retained from each of the volumetric flasks, one for the total analysis of Co and Cr concentrations and one as a back-up.

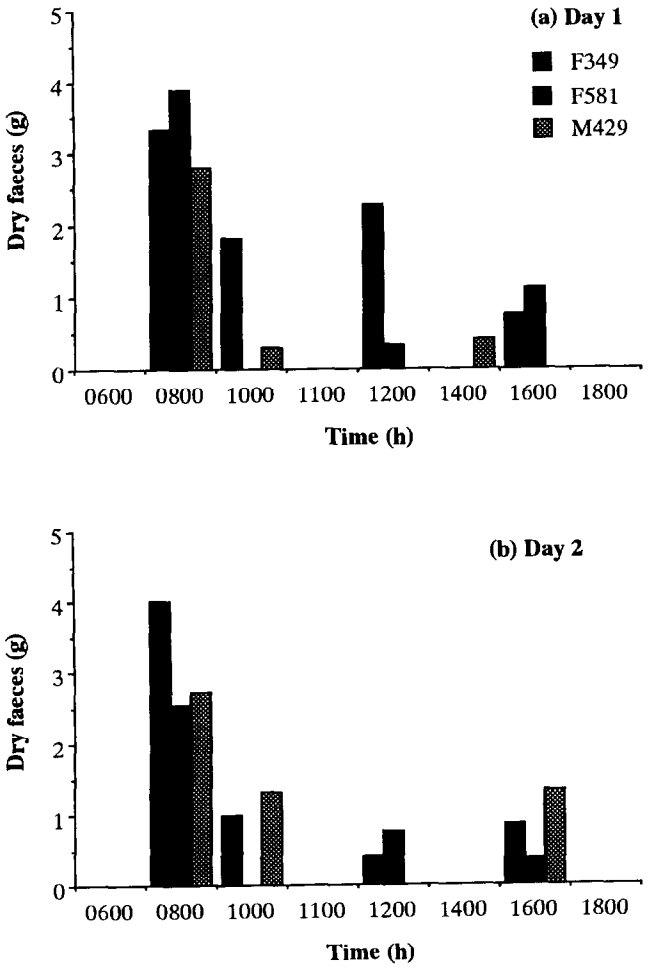

FIG. 1. Pattern of faecal production throughout the day in the three common marmosets.

Calculations

Transit time (TT) was taken to be the time of first appearance of the marker in the faeces (35). Mean retention time (MRT), the best single measure of the rate of passage through the entire digestive tract (35), is the average time taken for each of the markers to be excreted. The MRTs were calculated by the formula:

$$MRT\ (h) = \frac{\Sigma_{i=1}^{n} M_i T_i}{\Sigma_{i=1}^{n} M_i}$$

where M_i is the amount of the marker excreted in the ith defaecation at time T_i, and n is the total number of defaecations (4). Differences in transit time and MRT between markers within animals were tested statistically by paired t-tests (30).

RESULTS

Morphometrics of the Gastrointestinal Tract

The gut region with the greatest capacity in terms of wet weight of contents was the stomach, and the longest region was the small intestine (Table 3). Although only a small proportion of the total gut, the caecum contributed 25% of the total length of the hindgut (caecum plus colon) and 35% of its total capacity.

Rate of Passage of Digesta

The pattern of marker concentrations in collected faeces with time of dosing is shown in Fig. 2, and the cumulative excretion of the two markers is shown in Fig. 3 for the three animals that consumed the dose. The general form of the marker concentration curves (Fig. 2) was similar in all animals, with a rapid increase in concentration to a peak 2 to 8 hours after dosing for both markers, followed by a slower decline in the concentration of Co (the fluid marker) than in that of Cr (the particle marker) over the following 40 h. Cumulative excretion curves (Fig. 3) were characterized by lags that corresponded with the dark phase of the light/dark cycle, approximately 8 to 20 h and 32 to 44 h after dosing.

There was no significant difference in transit time between the two markers, the average time of first appearance being 3.6 h (Table 4). However, the mean retention time for Co-EDTA was significantly greater ($P < 0.05$) than that for Cr-CWC.

DISCUSSION

On the basis of both the morphological and marker retention data from this study, it appears that the common marmoset is a caecum fermenter. By comparison with other small mammals that feed on nonstarch polysaccharides (3), it can be concluded that in C. *jacchus* fluid digesta are separated from large particles in the proximal colon. Fluid digesta are selectively retained in a caecum that, although only a small proportion (8%) of total gut capacity (Table 3), is 35% of total hindgut capacity. It is noteworthy that several other small mammals, including other species of primates, that feed on gums also have well-developed caecum (11–13,21).

Although the difference in MRTs between the two markers was only 2.5 h, it is statistically significant (Table 4). When compared with the MRT values of 14.8 and 12.4 hours for the two markers in this study, the difference is likely to be biologically significant as well. It should also be remembered that MRTs are measured from mouth to anus, and are thus the net result of retention events in at least three different sites along the digestive tract. The first site is the stomach, which retains particulate digesta longer than fluid in all mammals (31). This partially counterbalances the selective retention of fluid digesta, which occurs virtually only in the caecum, together with the proximal colon (15). The third site of significant digesta retention is the rectum (if present) and distal colon in animals that defaecate episodically. This is the case with marmosets, which are strictly diurnal animals in the wild (17) and in captivity. Our animals spent the entire dark phase of the 24-hour cycle in their nest boxes, and never defaecated in the boxes.

The biological significance of the selective retention of the fluid marker in C. *jacchus* is related to characteristics of gums. Gums are composed principally of β-glucans, which are unavailable to mammalian digestive enzymes but are highly fermentable (32). They are usually partially soluble in water, forming viscous solutions (1), and therefore can be expected to travel with the fluid component of the digesta. Small particles (<75 μm) have also been shown to travel with the fluid marker in rabbits and possums (28). This would include small food particles and bacteria (3). Selective retention of these fractions in the caecum of C. *jacchus*, as in many other small hindgut fermenters, concentrates digestive effort on the most fermentable components of the digesta leaving the small intestine, reduces washout of symbiotic bacteria from the hindgut, and excretes any large particles relatively rapidly, thereby reducing any limitations on food intake imposed by indigestible bulk.

Faecal production by all animals peaked in the hour after the lights were turned on in the colony, and there was a smaller secondary peak at the end of the light phase (Fig.

TABLE 3. Mean wet weights and mean lengths of contents of four regions of the gastrointestinal tract in three freshly killed common marmosets

	Wet Weight of Contents		Length of Gut Regions	
Gut region	Mean (g) (± SD)	Percentage of Total Tract (± SD)	Mean (cm) (± SD)	Percentage of Total Tract (± SD)
Stomach	17.0 ± 8.2	51.5 ± 5.0	6.7 ± 0.9	8.6 ± 0.9
Small intestine	8.8 ± 4.8	27.1 ± 13.7	49.0 ± 1.7	62.3 ± 2.3
Caecum	2.9 ± 2.2	7.5 ± 2.9	5.7 ± 0.8	7.2 ± 1.2
Colon	5.5 ± 6.8	13.9 ± 11.2	17.3 ± 2.6	21.9 ± 2.5

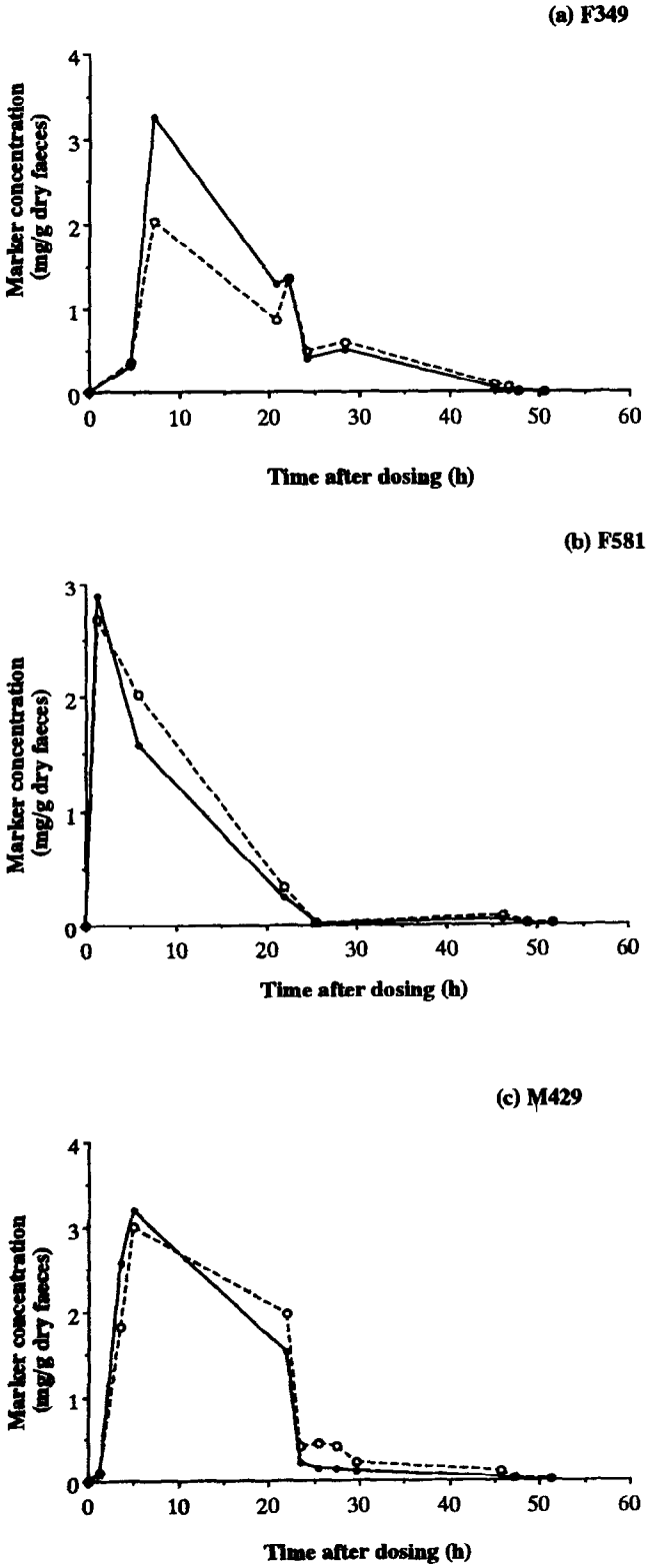

FIG. 2. Concentration versus time after dosing of Co (broken line) and Cr (solid line) in the dry faeces of three common marmosets. Cobalt (as Co-EDTA) represents the fluid phase of the digesta; Cr (as Cr-mordanted cell walls) represents large particles (600–1200 μm).

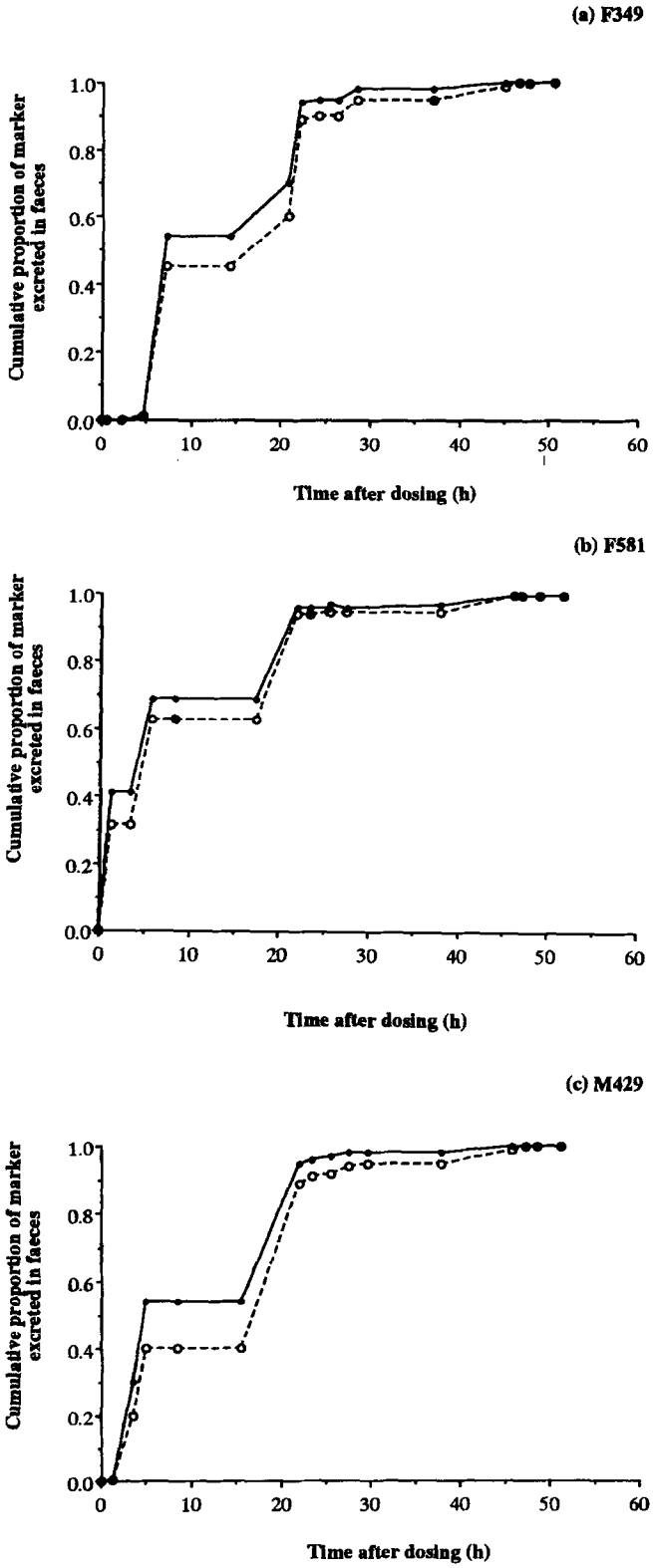

FIG. 3. Cumulative excretion versus time after dosing of Co (broken line) and Cr (solid line) in the dry faeces of three common marmosets.

TABLE 4. Transit times (TT) and mean retention times (MRT) of the two digesta markers in the gastrointestinal tracts of three common marmosets

Marmoset	Body Mass (g)	TT (Co, Cr) (h)	MRT Co (h)	MRT Cr (h)
F349	337	6.1	16.7	14.5
F581	343	2.3	11.5	9.7
M429	365	2.5	16.3	12.9
Mean ± s.d.	348 ± 14.7	3.6 ± 2.1	14.8 ± 2.9	12.4 ± 2.4

$t = 5.43$ (2 df) $P < 0.05$

1). Retention of faeces during the dark phase is evident in the marked lag phases in the cumulative excretion curves of the markers 8 to 20 h after dosing (Fig. 3). Retention of the faeces overnight, probably in the distal colon, would be expected to reduce the differences in the MRTs between the two markers. It also helps to explain why the concentrations of marker in the faeces (Fig. 2) do not fall more rapidly; a sharper decline after peak concentration would be more consistent with the expectation of an exponential decline in marker concentration in a system with a single large fermentation chamber (35).

Although direct evidence for microbial fermentation in the caecum of C. *jacchus* is not yet available, it would appear that the common marmoset employs a two-part digestive strategy that is typical of caecum fermenters (16), in order to maximize energy release from its food (5). This involves

1. rapid digestion of high-quality foods, such as insect prey and sweet fruits, in the long small intestine, which functions as a PFR. Any increase in the length of this region of the gut during the evolution of this species would have the added benefit of increasing the surface area, thus optimizing the rate of nutrient uptake from digesta.
2. selective retention in the caecum of the soluble polysaccharides from the exudates, bacteria and any very small food particles, principally from insect exoskeletons. This has the effect of concentrating digestive effort in the caecum on the most digestible fraction of the residues leaving the small intestine. Retention in the relatively large caecum, which functions as a modified CSTR, is probably considerable, based on compartmental analysis of digesta retention in various regions of the digestive tract in other small caecum fermenters, such as rodents (16).

The utilization of two reactors in series in this way would enable the animal to meet immediate energy requirements for daily activity from the rapid digestion of high-quality foods in a PFR (the small intestine) as well as maintaining a constant background production from the slower fermentation of polysaccharides in a CSTR, the caecum.

Previous studies of digestive tract function in callitrichids using digesta markers have dealt only with the estimation of transit times (*i.e.*, the first appearance of the marker in the faeces). Power (22) studied digestive tract function, energy intake and response to dietary gum in a range of captive callitrichid species, including the common marmoset. He used chromic oxide and polystyrene and cellulose acetate beads (1 mm in diameter), as both were easy to detect visually in the faeces, but unfortunately none of these materials can be relied upon to travel with specific phases of the digesta. He found in C. *jacchus* that there were no differences in the TTs of both markers, which averaged 1.6 ± 0.8 h on the basal diet and 4.1 ± 0.9 h on Power's (22) gum diet. Our results for TT in the common marmosets on a diet without gum are similar to those on the gum diet (Table 4). Price (23,24) also used chromic oxide to measure transit times in *Callithrix geoffroyi*, and his results (TT = 4.7 ± 0.34 h) were similar to ours and to Power's. However, transit times alone provide only minimal information on digesta kinetics. Much more informative are MRTs, especially when specific phases of the digesta are marked, as in the present study. Our results indicate that the fluid phase of the digesta, probably along with small particles, is selectively retained in the caecum of C. *jacchus*. This suggests that microbial fermentation of soluble nonstarch polysaccharides plays an important role in the total digestive strategy of this small primate.

The digestive strategy of C. *jacchus*, of rapid digestion of food in a PFR (the small intestine) followed by microbial fermentation of complex carbohydrate residues in a CSTR (the caecum), is an adaptation that allows for considerable dietary flexibility in meeting its energetic requirements. The diet of C. *jacchus* includes insects, fruit and gums (the main component) in the wild, but they are successfully maintained in captivity on diets that are predominantly fruit, vegetables and some form of processed food, supplemented with insects.

Rylands (26) noted that C. *jacchus* lives in xerophytic forests where the seasonal availability of insects and fruit may vary considerably. High numbers of exudate-producing trees in small home ranges (29) suggest that this food source is readily available throughout the year, and that harvesting of exudates can be done with minimal energy expenditure at times when insects are scarce. It would seem that this digestive flexibility is among the factors that have enabled C. *jacchus* to become established through introduction into areas where the destruction of natural forest ecosystems has occurred, as in the Atlantic forests of northeast Brazil, and there are populations in the cities of Rio de Janero and Buenos Aires (27). In forest areas where this has happened, *Callithrix jacchus* is known to have replaced other species of this genus (27).

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