Digesta Retention in the Gastro-intestinal Tract of the Orang Utan (*Pongo pygmaeus*)

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ABSTRACT. The diet of the orang utan *Pongo pygmaeus* consists of fruit, leaves, communal insects, and bark, and contains appreciable amounts of non-starch polysaccharides. These complex carbohydrates require microbial fermentation before they can be used as an energy source by the orang utans. The gastro-intestinal tract of *P. pygmaeus* consists of a simple or unipartite stomach, a relatively long small intestine, and a complex haustrated caecum and colon. This morphology suggests that the capacious proximal colon is the principal site of digesta retention and fermentation of non-starch polysaccharides. We measured several parameters of digesta retention by giving three captive adult *P. pygmaeus* a pulse dose of inert markers specific for the solute and particulate phases of the digesta and collected their faeces at regular intervals over 192–338 hours. Transit times (times of first appearance of the markers in the faeces) and mean retention times (MRT) were long, consistent with a large complex gastro-intestinal tract. MRTs for the particulate marker were longer ($p=0.032$) than for the solute marker, indicative of selective retention of large particulate digesta. These results are consistent with the patterns of marker excretion in other mammals that use the digestive strategy of colon fermentation.

Key Words: Orang utan; *Pongo pygmaeus*; Digesta retention; Haustrated colon; Colon fermentation.

INTRODUCTION

There are two subspecies of orang utan, *P. pygmaeus abelii* from northern Sumatra and *P. pygmaeus pygmaeus* from Borneo (FLEAGLE, 1988; GROVES, 1989). Both subspecies of *P. pygmaeus* live in primary rain forests with continuous canopies that provide pathways which will take the weight of these large arboreal apes (RIJKSEN, 1978; FLEAGLE, 1988). Adult orang utans exhibit a high degree of sexual dimorphism in body size, with males averaging 80 kg and females 40 kg (FLEAGLE, 1988). The diet of *P. pygmaeus*, which is largely plant-based, includes ripe fruit, leaves, bark, and insects (RODMAN, 1977; RIJKSEN, 1978; HAMILTON & GALDIKAS, 1994). Two Sumatran orang utans and a hybrid animal were included in this study, as the relationship between subspecies is so close that major differences in morphology, physiology, and ecology are unlikely (RIJKSEN, 1978; RODMAN, 1988; GROVES, 1989).

The diet of *P. pygmaeus* is largely plant-based, requiring microbial fermentation for processing the structural polysaccharides (cellulose, hemicelluloses, and pectins consumed) (RIJKSEN, 1978; RODMAN, 1988; STEVENS & HUME, 1995). The morphology of the gastro-intestinal tract of *P. pygmaeus* is consistent with that seen in other mammalian colon-fermenting herbivores; viz. a simple (unipartite) stomach, a relatively long small intestine and a voluminous haustrated colon, which is the principal site of fermentation (CHIVERS & HLADIK, 1980; STEVENS & HUME, 1995;

CATON, 1997). Digesta marker studies were used to test the hypothesis (based on gut morphology and diet) that the orang utan uses the digestive strategy of colon fementation (CATON, 1997).

For mammals using colon fermentation as their digestive strategy the passage of both fluid and particle phases of the digesta from a single meal is relatively long (≥24 h), and there is generally selective retention of the particle phase relative to fluid and solutes in the proximal colon (HUME, 1989). This can be demonstrated by the administration of a pulse dose of a particle and a solute marker (WARNER, 1981). The results of a digesta marker study with three adult *P. pygmaeus* in two Australian zoos are presented in this paper.

METHOD

The three adult orang utans included in this study were the adult Sumatran male from Adelaide Zoo (*male 1*), aged 21 yr, and the adult male, also Sumatran and 16 yr old (*male 2*), and a 15 yr old female hybrid (*female 1*) from Melbourne Zoo. Cobalt-ethylene diaminetetraacetic acid (Co-EDTA) was used to mark the fluid phase of the digesta (UDÉN et al., 1980). Chromium mordanted to cell wall constituents of 600−1,200 μm (Cr-CWC) prepared from chopped oaten (*Avena sativa*) hay was used to mark the particle phase of the digesta. The particle marker was prepared according to the technique described by CATON et al. (1996).

Male 1 (82 kg body mass) was given marker doses of 7 g of Cr-CWC and 3 g of Co-EDTA, mixed together in three jam sandwiches, prior to his first meal of the day. These were eaten immediately, resulting in a pulse dose. His diet was primate cake (Adelaide Zoo's recipe made from dog chow, marmoset meal, and fruit pulp) with fruit and vegetables in the morning, and a second meal of fruit and vegetables in the afternoon. *Male 1* was housed on his own and faeces were collected twice a day for 14 days; in the morning before the night den was cleaned and in the late afternoon when he returned to his night den. The faeces were oven dried at 45°C to constant weight.

The two orang utans at Melbourne Zoo were fed fruit and vegetables in the morning before being let out from their night den, and fruit, vegetables, primate cake and milk in the late afternoon after they returned to their night dens. Faecal collections were coordinated with these two sets of movements. The particle marker was mixed into a small amount of freshly prepared primate cake (Melbourne Zoo's recipe of milled mixed cereals, crushed nuts with vitamin and minerals supplements); the solute marker was mixed with water and black currant cordial. The markers were given to the orang utans prior to their morning meal. *Male 2* (91 kg body mass) was also housed on his own. He was given 6 g of Cr-CWC and 3 g of Co-EDTA. This animal was easily stressed and if upset the result was loose faeces. This happened on days 2−4 of the experiment, before he was let out in the morning. Faeces were thus collected from this animal over a shorter period (9 days), as it was estimated that all of the markers would have been cleared from his gut by this stage. *Female 1* shared an enclosure with her infant daughter. She was given blue food dye in black currant syrup every morning, commencing on the day before the markers were administered, in order to identify her faeces during marker collection. She was only given 4 g of Cr-CWC and 1g Co-EDTA, as her body mass was estimated to be half that of the male's (i.e. approximately 40 kg). Faecal collection continued for 11 days with this animal. The markers were consumed immediately by both animals, resulting in a pulse dose. All faeces were initially dried in shallow open boxes in the boiler room of the Ape House due of the large quantities involved, on average a total 1 kg of faeces per day from the both apes. The faeces were subsequently dried to constant weight in smaller batches at 45°C in a laboratory oven.

Subsamples (1.0–1.5 g) of the faeces were wet-ashed using the technique described by CATON et al. (1996). The concentrations of Co and Cr in the clear digests were measured with an atomic absorption spectrometer (Varian model AA/400P). Three measures of the rate of digesta marker passage were calculated from the patterns of appearance in the faeces. Transit time was taken to be the time of the first appearance of the markers in the faeces; times were midtimes between collections, expressed in time (h) after dosing. The time of peak maximum marker elimination from the gastro-intestinal tract (T_{max}) was calculated from the product of marker concentration and dry faecal output at each collection time. Mean retention time (MRT), which is the best single measure of rate of passage through the gastro-intestinal tract (WARNER, 1981), was calculated using the formula:

$$\text{MRT (h)} = \sum_{i=1}^{n} MiTi \,/\, \sum_{i=1}^{n} Mi$$

where Mi is the amount of marker excreted in the ith defaecation at time Ti and n is the total number of defaecations (BLAXTER et al., 1956). Differences between the MRTs of the two markers were tested statistically with paired t-tests (Microsoft Excel 4.0, Macintosh version).

RESULTS

The marker elimination curves of *male 2* and *female 1* were similar in form (Fig. 1). The effect of stress in *male 2* was minimal, as comparison of the marker elimination curves indicates (Fig. 1). With *male 1*, little of either marker appeared during the first 45 h after dosing, then the bulk of the markers were eliminated from the gastro-intestinal tract within the next 50 h (Fig. 1). Separation of the markers is clearly seen in the elimination curves of *male 2* and *female 1*, with the solute marker excretion peaking ~20 h before that of the particle marker (Table 1). Negligible amounts of the markers (0.1±0.05% Co-EDTA; 0.5±0.5% Cr-CWC) remained in the gastro-intestinal tract at the final collection.

Transit times were similar in all three orang utans, averaging 24.2 h, and are the same for both markers (Table 1). A trace (less than 0.1%) of both markers was present in the first faecal sample of *female 1*. This was not considered to be the transit time, as appearance of the markers in amounts equivalent to those in the males' faeces were not recorded until the next morning. In the Melbourne Zoo orang utans the time of peak elimination (T_{max}) of the particle marker was considerably longer than that of the solute marker (Table 1). The mean MRT of Cr-CWC was significantly ($p<0.05$) longer than the MRT of Co-EDTA in these three animals (Table 1),

Table 1. Transit time (TT), time of maximal elimination (T_{max}), and mean retention time (MRT) of a solute marker (Co-EDTA) and a particle marker (Cr-CWC) from the gastro-intestinal tracts of three adult *Pongo pygmaeus*.

		Transit time (h)		T_{max} (h)		MRT (h)	
Orang utan	Body mass (kg)	Co-EDTA	Cr-CWC	Cr-CWC	Co-EDTA	Cr-CWC	Co-EDTA
Male 1	82	25.3	25.3	72.3	75.0	91.4	72.3
Male 2	90	23.6	23.6	72.0	57.3	63.6	47.2
Female 1	40	23.7	23.7	99.9	79.4	91.4	76.2
Mean±S.D.	70.7±21.9	24.2±0.8	24.2±0.8	81.4±13.1	70.6±9.5	73.7±15.5	65.2±12.8

The difference between the MRTs of the two markers was statistically significant ($p=0.032$) by paired t-test ($t=3.750$, 2 df).

indicative of selective retention of particulate digesta relative to fluid and solutes in the orang utan gastro-intestinal tract.

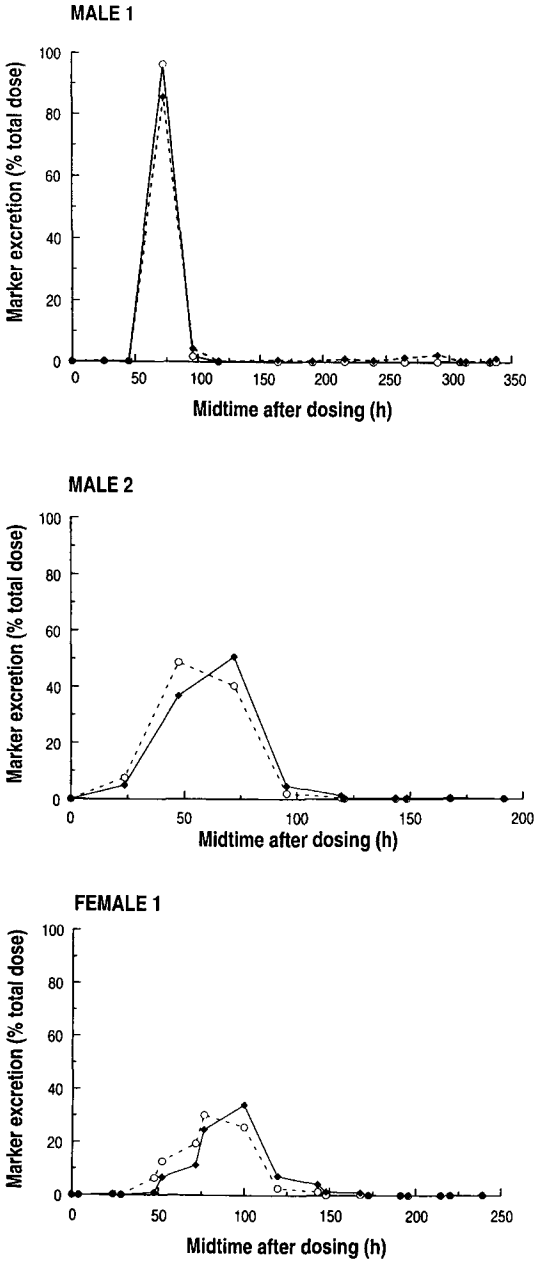

Fig. 1. Elimination (expressed as percentage of the total dose) versus midtime after dosing of Co (broken line) and Cr (solid line) in the dry faeces of three adult *Pongo pygmaeus*. Cobalt (as Co-EDTA) represents the solute phase of the digesta; chromium (as Cr-mordanted cell walls) represents large particles (600–1200 μm). The differences in the scales on the axes of the elimination curve of *male 1*, compared with *male 2* and *female 1*, are due to differences in the doses of the markers and the longer collection time for this animal.

DISCUSSION

This digesta marker study was undertaken to test the hypothesis (based on diet and gastro-intestinal morphology) that *P. pygmaeus* uses the digestive strategy of colon fermentation to process the structural polysaccharides in its diet. In his review of the digestive strategies of mammalian herbivores, HUME (1989) showed that there are characteristic patterns of fluid and particle digesta marker elimination in the faeces of herbivores using different digestive strategies. For large (mature body masses above 20 kg), plant-eating species, like *P. pygmaeus*, with simple stomachs and complex hindguts, digesta transit times are long and there is selective retention of particle markers relative to solute markers, allowing extensive microbial fermentation of food particles in the proximal colon (HUME, 1989). With a body mass of 40–80 kg *P. pygmaeus* is one of the largest extant primates.

The pattern of marker retention seen in the gastro-intestinal tracts of the three *P. pygmaeus* in this study is similar to that seen in other mammalian colon fermenters (STEVENS & HUME, 1995; CATON, 1997). The transit times recorded were long (24 h), and most of the fluid and the particle markers were retained for longer than 72 h, i.e. three days after the administration of the pulse dose of the markers. The MRT of Cr-CWC, the particle marker, was significantly longer than that of Co-EDTA. The temporal separation in the elimination of the two markers in the faeces of these orang utans can be seen in their marker elimination curves of *male 2* and *female 1* (Fig. 1). There was no separation of the markers at T_{max} in *male 1* (Fig. 1), but the recorded values of T_{max} were within the range of those of the other two orang utans (Table 1). This result

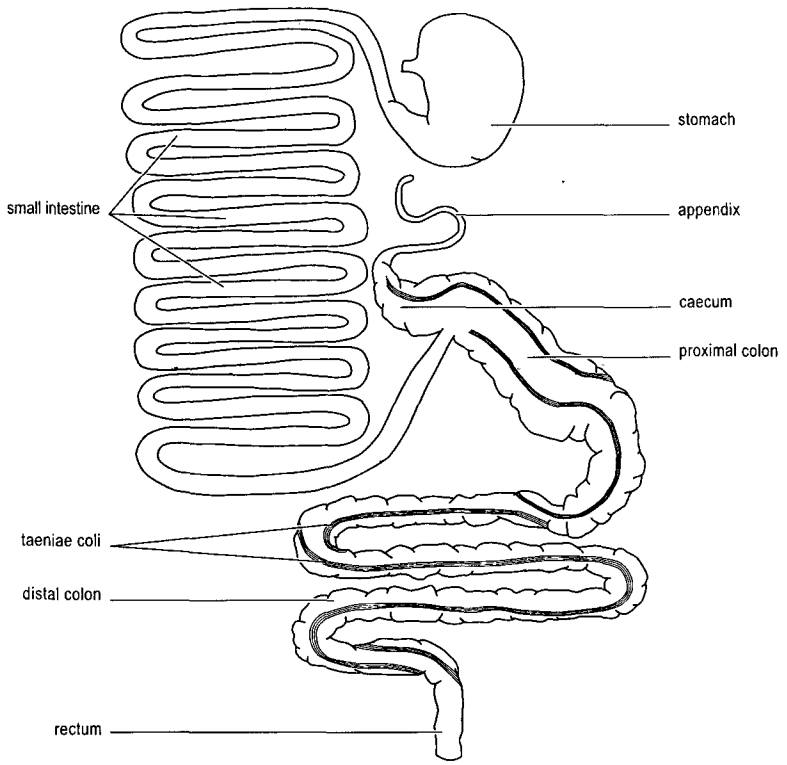

Fig. 2. The morphology of the gastro-intestinal tract of *Pongo pygmaeus* (after STEVENS & HUME, 1995). The head and body length of adult males is 97 cm and adult females 78 cm.

may have been due to a number of causes, e.g. differences in zoo diets, differences in routines, or differences in defecation patterns. The MRTs of the markers in *male 1* show a clear separation and the values recorded are very similar to those of *female 1* (Table 1). The shorter MRTs recorded for *male 2* are the result of abnormal gut function under stress.

Several limitations to this digesta marker study can be identified, the most important being the small number of orang utans available; only limited numbers of orang utans are kept in captivity under conditions suitable for digesta marker experiments, especially quantitative collection of faeces. A second limitation relates to the defecation pattern of *P. pygmaeus*, which like other hominids and primates in general, has a 24-hour defecation cycle (CATON, 1997). Most faeces are eliminated in the early morning, with markedly reduced faecal production by early afternoon, and none during the night. Faeces are thus stored in the rectum for considerable periods of time prior to elimination. Rectal storage of faeces increases transit time, and mean retention times of digesta markers may also be extended (WARNER, 1981; HUME, 1989).

Another problem encountered in this study was the inclusion of cobalt in the commercially-prepared mixes used to prepare the primate cakes in both Adelaide and Melbourne Zoos (CATON, 1997). It was not possible to avoid this situation; however, the amount of cobalt included was calculated to be negligible relative to that in the Co-EDTA doses (CATON, 1997). It is also likely that most of the soluble Co salts incorporated into the diet were absorbed in the gastro-intestinal tract, while the Co-EDTA was not. This is supported by the general form of the two excretion curves, characteristic of pulse dose/total collection digesta marker experiments (WARNER, 1981). These limitations not withstanding, the results of the digesta marker passage experiment provide important insights into the digestive strategy of *P. pygmaeus*.

Models for describing the optimal gut structure and function for processing specific diets can be based on reactors used in chemical engineering (DENBIGH & TURNER, 1971; PENRY & JUMARS, 1987). Microbial fermentation of plant structural polysaccharides is a relatively slow process, and is most likely to occur in a continuous-flow stirred-tank reactor (CSTR), in which retention of digesta is longer and the mixing of contents is thorough (CATON, 1997). In contrast, digestion by endogenous enzymes (or catalysis) secreted by a range of digestive glands emptying into the lumen of the gut, occurs most efficiently in a plug flow reactor (PFR), in which flow is unidirectional with little axial mixing. Compartmentalization of the mammalian gastro-intestinal tract increases its functional efficiency through separation of these two broad types of digestive reaction, i.e. catalysis and microbial fermentation or autocatalysis (PENRY & JUMARS, 1987). Identification of the reactor types found in the gastro-intestinal tract of a given mammalian species is based on: (1) the diet and its processing requirements; (2) the results of digesta marker transit studies; and (3) the arrangement of the longitudinal and circular muscle coats of the tunica muscularis in each of the gut compartments.

The musculature of the tunica muscularis is particularly important as it determines the pattern of flow of reactants, in a manner characteristic of each type of reactor (CATON, 1997). Gut reactors are classified as either simple or complex depending on the musculature and the pattern of flow (CATON, 1997). Simple reactors, like the small intestine, have two complete coats in the tunica muscularis and the flow pattern is similar to that of ideal reactors (i.e. those that can be described accurately by simple equations). Complex reactors, like the proximal colon of *P. pygmaeus* and other hominids, have the longitudinal coat of the tunica muscularis divided into discrete bands, or taeniae. The taeniae produce haustra in the walls of these compartments (Fig. 2), which function as localized mixing cells (CATON, 1997). Complex reactors allow for microbial fermentation of plant structural polysaccharides, and retention of digesta markers is longer in mammals that have complex reactors in their gastro-intestinal tracts (STEVENS & HUME, 1995; CATON, 1997).

In the wild *P. pygmaeus* eats fruit, leaf material, insects (mostly ants and termites) and bark.

Such a diet contains considerable quantities of polysaccharides that require microbial fermentation before they can be used as an energy source (RIJKSEN, 1978; HAMILTON & GALDIKAS, 1994). *P. pygmaeus* in both Sumatra and Kalimantan is highly selective in its choice of food items. Ripe fruit is preferred and it comes from a variety of sources ranging in size from large spiny durians to figs measuring 1−2 cm in diameter (RIJKSEN, 1978). Leaf material, which includes buds, shoots, young and mature leaves, is also selected carefully (HAMILTON & GALDIKAS, 1994; RIJKSEN, 1978). Pith and bark from stems and branches form a third category of plant foods. Bark is stripped off and the vascular tissue on the underside and the exposed surface is scraped away with the incisors and eaten (RODMAN, 1977; RIJKSEN, 1978). The bark is often chewed to extract soluble materials, then the apes spit out the resulting wad of fibre (RODMAN, 1977). Parts of a number of latex-producing plants are consumed (RIJKSEN, 1978).

Details of the plant parts eaten by *P. pygmaeus*, plus data from the chemical analyses of dietary items (HAMILTON & GALDIKAS, 1994), indicate that these apes select parts that have a high concentration of fermentable polysaccharides other than cellulose, e.g. from fruit, vascular tissues, young leaves, gums (intra-cellular and extra-cellular), and avoid those parts with a high content of lignified cellulose (RIJKSEN, 1978; HAMILTON & GALDIKAS, 1994). Their diet is thus of relatively high quality for most of the year. The low levels of alkaloids also recorded in these chemical analyses suggest that these too play a significant role in food choice, rather than the levels of tannins (HAMILTON & GALDIKAS, 1994). The relatively low protein levels in fruit, the orang utan's dietary staple, might help to explain why they supplement their diets with insects (HAMILTON & GALDIKAS, 1994). It was not possible to measure the fibre content of the zoo diets of *P. pygmaeus*, but they probably had a lower total fibre or structural polysaccharide content than in the wild.

The relative proportions of the gut compartments, calculated from the raw data of CHIVERS and HLADIK (1980), can be used illustrate the importance of different gut compartments in the digestive strategy of *P. pygmaeus*. The surface areas of the small intestine (49% of the total) and the hindgut (44%) are large, facilitating the absorption of digestive end-products in these compartments. The volume of the hindgut (caecum and colon) is double that of the small intestine (55% and 28% of the total respectively). In general, gut compartments that function as fermentation chambers have greater relative volumes than surface areas (CATON, 1997). The entire colon is haustrated by three taeniae coli (Fig. 2) and its morphology is similar to that of the human hindgut. This suggests that the function of the hindgut in the two species is similar. Alternating bouts of peristalsis and antiperistalsis, together with localized contraction of the haustra, facilitate the retention and mixing of digesta, allowing time for fermentation of the plant structural polysaccharides eaten by *P. pygmaeus* (ELLIOTT & BARCLAY-SMITH, 1904; CATON, 1997). The caecum is probably too small to be anything more than an extension of the proximal colon (Fig. 2).

CONCLUSIONS

The results of the study on digesta passage in the gastro-intestinal tract of *Pongo pygmaeus* demonstrated that there was: (1) prolonged retention of both markers of the solute and particle phases of the digesta within the gastro-intestinal tracts of these individuals; and (2) selective retention of the particle marker.

This is in accordance with the need of wild orang utans to process diets with a large fermentable component made up of structural polysaccharides from plant material and chitin from insect exoskeletons. Microbial fermentation of these compounds occurs in the proximal hindgut, which is capacious and has musculature adapted for retention and mixing of digesta.

The pattern of digesta retention in the gastro-intestinal tract of *P. pygmaeus* is similar to that in other large herbivores with the digestive strategy of colon fermentation.

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