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PJBS

ISSN 1028-8880

Pakistan Journal of Biological Sciences

ANSInet
Asian Network for Scientific Information
308 Lasani Town, Sargodha Road, Faisalabad - Pakistan

Pakistan Journal of Biological Sciences 6 (17): 1564-1573, 2003
ISSN 1028-8880

Fiber Digestion in Mammals

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Abstract: Animal models are viewed to understand the major types of fiber digestion. Faunivores, omnivores and granivores differ in their amounts of fiber digestion. These differences are partially due to the morphology of the gut and opportunities in abundance and Sacristy of food stuffs. The funivore model is the anteater, who utilizes autoenszymes to deal with the chitin in the diet. The frugivor model is the bat, who has to deal with cellulose and seeds. The herbivore model is the rabbit, who must consume large amounts of dietary fiber as dose the grazer. Adaptions vary in gut and selection

Key words: Fiber, American consumption, fanuivores, omnivores, graminivores, autoenzymacit, alloenzymatic

In the United States human nutrition is taught in the form of a food pyramid with four levels. The bottom of this food pyramid includes grains; fruit and vegetables on the next tear; and dairy, meat and fats at the top. As Americans become more overweigh the low-fat foods on the bottom of the food pyramid are emphasized even more. The majority of these fruits, vegetables, and grain foods naturally contain higher amounts of fiber content.

Humans often mill their grains and cook their vegetables and fruits, reducing the fibrous nature of their food. This processing creates easily digestible, caloric rich foods. In an effort to cut calories, yet not compromise satiety, nutritionists have explored the bulking effect of fiber rich foods. To understand the nutrient impact of fiber, science often turns to animal models. Animals, unlike humans, depend on more specific diets. Therefore to understand the nutrient value of fiber it is productive to look at mammals first, understanding their unique strategies of managing fibrous diets.

In the nutritional process, the digestive system must confront different materials and attempt to break them down into molecular forms that can then be transported and utilized by the body. This process of digestion becomes complicated by the presence of thick-walled cellular components that are not easily broken down. In order to utilize the components of the cell wall, or the material within, the organism must develop ways to maximize nutrient extraction. Because dietary niches highly vary, the consumption practices, digestive physiology, and digestive strategies of the organisms in those niches also vary.

To understand different mammals' digestive niches, we must first examine the different categories of diet within the animal kingdom. Biologist Chivers (1989) postulated four dietary classes. The first group, faunivores, encompasses the mammals that consume the tissues of other animals. Faunivores include the subgroups: crustavivores, carnivores, and insectivores, among other animal-eating groups. Second, is the group called omnivores; this group includes species that eat foods of both animal and plant origin. Flurivores consume plants and include groups such as nectarivores, frugivores, gumivores, granivores and herbivores. The last group also consumes solely plant material but they are called the grazers or graminivores. Grazers differ from Flurivores because they represent a large group of mammals that eat solely grasses.

Grazers are often consuming large amounts of their foodstuffs: To complement the different dietary niches there are digestive strategies that are also divided into four major classes. The first group uses autoenzymatic digestion. Autoenzymatic digestion means that the mammals use their own set of digestive enzymes to digest their food. The next three groups differ from the first in that they utilize microbes to ferment their food; these groups are, therefore, called alloenzymatic. The first of these three alloenzymatic groups differs from the second two because the majority of its digestion occurs in its hindgut. The last two alloenzymatic forgut fermentors differ because group four uses rumination, or repeated chewing of the cud to repeatedly break down the contents of the fore stomach while group three does not. The different digestive strategies evolved in response to the different dietary niches of animals. Gut morphology becomes defined by its sub-units that are divided between three types of reactors. Batch reactors are chambers where contents are filled then emptied after a given reactor time. The second type of reactor includes continuous flow stirred tank reactors. Plug-flow reactors are tubular reactors. In these reactors materials continuously flow through and there is little mixing of the content.

It should be mentioned that digestive physiology is impacted by an animal's size. Factors called integrated processing response (IPR) include the change of intake, reaction time, gastrointestinal size, and content of the diet due to energy demand of indigestible content of the diet. It is thought that smaller animals (for example, rodents) are not able to meet their energy requirements on low caloric dense diets, such as grass, due to IPR.

The indigestible fiber to which this paper will frequently refer includes the plant cell walls, and chitin. Cell walls comprise 20-80% of forage dry weight and serve to allow land plants to keep an upright posture. The matrix of a cell wall is comprised of cellulose, hemicellulose, pectins, lignin and small amounts of bound protein. Cellulose is the most common compound in plants and is constructed of glycosidic linkage of monomeric sugars into phoysaccharide chains. Hemicellulose a non-cellulose polysaccharide fraction that is readily hydrolyzed with acid. Pectin is comprised of chains of galactouronic acid, galactans, and arabinans. Lignin, the last component mentioned is the toughest part of the cell wall; it is a polymer of phenylpropaniod units and defends against the microbe's modification on the cell walls. Lignin and cellulose are the two most abundantly distributed polymers on earth (Wilson, 1994). The term "fiber" used in the paper will refer to dietary fiber or roughage; this is usually composed of contents of plant cell wall. Similar to cellulose in structure, chitin is a polysaccharide comprising chains of N-acetyl-D-glucosamine, a derivative of glucose. Chitin serves as a supportive structure in invertebrates and fungi. Both cell components and chitin create challenges for the digestive track of mammals.

This paper examines several mammals representing examples of different dietary niches. The mammals will be investigated to see how each cope with the indigestible matter in its food. Starting with a faunivore, an insectivore, and the anteater. The anteater faces the indigestible chitin shell of its prey and must overcome its indigestibility to take in enough energy to sustain a positive energy balance. Secondly, a frugivor bat. Not only do frugivors face digestion of cellulose in the plant tissue, but frugivores also have to deal with seeds in the fruit. Next, the koala will exemplify an extremely specific herbivore that deals with a plant source high in fiber. The rabbit, like the koala is a hindgut fermentor that deals with large amounts of dietary fiber. However, the rabbit's dietary habits of coproghagy are a unique method of dealing with fermentation processes in its hindgut. The last animal is a grazer, also dealing with high levels of fiber in its diet. The grazer, unlike the koala and rabbit is a forgut fermentor that utilizes rumination to contend with the fiber in its diet.

Anteater: The anteater consumes a very specific insectivore diet. Anteater, the common name, encompasses 22 animals including the pangolin, aardvark, encidna, antbear, or any animal that consumes a diet of primarily ants. In this paper the term "anteater" (Tamandua, Myrmecophaga, and Tachyglossus, respectfully). The anteater will exemplify a faunivor that deals with indigestible matter in its diet.

Studies done on the enchina, or spiny anteater, have shown on average that they consume a diet about 50% ants, and 50% termites, yet these ratios vary between and within the seasons (Griffiths *et al.*, 1990). The other anteaters that this paper will be discussing also consume a diet that includes terminates. Calculating the nutritious value of arthropods is difficult, due to the presence of their hard exoskeleton that serves to protect their bodies. The exoskeleton and its chitin component provide a relatively indigestible substance. In addition to the difficulties of digesting the actual chitin, chitin surrounds and protects the softer nutrients within. The "primitive" systems of anteaters do not include the use of the enzyme chitins to breakdown the insect's exoskeletons; therefore, only the "soft parts" of the insect are actually utilized. The soft internal parts of invertebrates along with their flesh do contain protein and fat. These parts of the insect provide the nutrients needed by the anteaters. Ants, compared to other insects and even termites have higher percentages of chitin (Redford and Dorea, 1984). Anteaters will often choose the larger members of the ant and terminate population (for example they will choose against the smaller workers); this decreases the percentages of chitin. Yet, overall, a significant problem with a diet of ants and termites is their low nutrient concentration. This limits the energy available to the anteater's metabolism.

Not only do these insectivores consume large amounts of this indigestible chitin, but they also intake large amounts of soil with their prey. Studies done with tamadua show feces the color if ingested termite nest (McNab, 1984). As much as 47% of the stomach content of the aardvark consisted of sand. This finding is consistent of other ant and termites eaters (Redford, 1983). The sand and ditrus add bulk to the digestive load of insectivores and reduce the caloric proportions of their digestive content.

No published information could be found on the actual digestive track of anteaters; therefore, this paper will look at the pre-digestive adaptive characteristics of anteaters. These adaptations must be efficient, successfully taking in enough food to compensate for the energy expenditure of hunting and digesting such low-calorie foods.

Using the research available, it is interesting to investigate anteater actives such as hunting, capture, and mashing of the interesting to investigate anteater actives such as hunting, capture, and mashing of the insects. The anteater possesses an acute sense of smell. It uses this sense of smell to find its prey. Using their strong forelegs and immensely sharp claws they dig into the anthill or termite mounds. This increases the anteater's exposure to these small insects, going to where the insects are most concentrated in their nests. The famous tongue of the anteater has been calculated to flick in and out faster then twice a second. These mobile tongues can extend eighteen inches long. Mucous on the tongue aids in grabbing the prey, then quickly pull it back into its mouth (Redford, 1983). A hard, back portion of the tongue then grinds the prey against the pallet on the roof a mouth (Griffiths *et al*., 1990). This crushing process breaks up the exoskeleton, increasing the surface to volume ratio. This exposes the inside of the insects to digestive juices in the anteater's digestive track. Because the anteater does not have teeth, it also compensates with heavy muscled portions of its stomach. This serves to further pulverize the insect (Redford, 1985). Such hunting and capturing techniques allow the anteater to capture up to 30,000 ants in a day (Cohan, 1984). By consuming large numbers of insects, the anteater can meet its caloric needs and offset the high concentration of indigestible chitin.

Post digestion, anteaters can also overcome the effects of a low caloric diet. One method of metabolic compensation is the low metabolic rate and lower bodies temperatures of these animals. This adjustment is partially due to the fact ants and termites are not always available enough for predators to maintain high-energy budgets. The anteater's energy expenditures are, therefore, maintained at levels when the insects are least available (McNab, 1984). Low on energy, anteaters also participate in daily torpor to reduce their energy expenditure. They can use their strong forearms to dig into the soil and bury themselves. By avoiding the hot harsh condition of day anteaters can reduce their energy expenditure.

The anteater is often though of as a primitive mammal, this is evident in the digestive adaptations of the anteater. Perhaps its poor food source caused the anteater to become evolutionarily trapped in its "primitive" characteristics. What adaptations that are seen in the anteater are mainly acute hunting skills. The low sluggish characteristics of the anteater are post-digestive metabolic consequences for it's dietary niche.

Flying fox: The flying fox is a frugivor, meaning that its diet consists of fruit materials. "Fruit bats", a more general term, refers to species in two families: the spear-nosed bat of the Americas (Phyllostomidae) and the Old World fruit bats (Pteropodidae). It is the "Old World" fruit bats that are also called the flying fox. The flying fox gets its name from its fox-like face, but it is actually a type of bat. The range of the flying fox includes Africa, Asia, Australia, and the Indo-Pacific Ocean. The genes Pteropodiadae contains over 100 species of fruit-eating bats. Some of these bats can grow quite large; it is reported that the flying fox can have wingspans of 5 feet. The diet of the flying fox consist of mainly fruits and sometimes pollen. These fruits not only include an indigestible fiber content in their pulp, but they also have large portions of seeds. These seeds are not digested at all and form bulk in the diet. One species, the Seabee's Short-tailed fruit bat, will eat about 36 piper fruit (of the pepper family), and 8-10 cecropia fruit (figs) in a single night (Fleming, 1987). Other studies showed that a dwarf bat could eat two times its body weight in fruit every night (Thomas, 1991). Seeds can constitute 30-40% of the total dry fruit mass (Martinez-Del Rio and Restrepo, 1993). Another study estimated that the fruit bat may consume as many as 60,000 seeds in one night (Rio *et al*., 1993). The diet of the fruit bat includes figs, peaches, mangoes, nectars and other commercial fruits. This becomes a problem for fruit farmers. One farmer reported having lost three-fourths of his peach and nectar crop due to these bats (Nowak and Federoff, 1998). The fruit bat has, consequently, become unpopular in Australia and farmers try to reduce the numbers of bats. To counter-balance these measures, conservationists have done studies on the bat's feeding habits. This is where the majority of the fruit bat research originates. Yet, as almost all the research emphasizes, because the seeds pass through the bat, bats play an extremely large role in seed dispersal. Evidence shows that seeds passed through the gut of a bat actually have a higher germination success them seeds merely falling from the plant itself (Thomas, 1991). Also often unacknowledged by these farmers, the fruit bat plays a significant role in the pollination of many commercial fruits. The bat's diet does, therefore, also contain pollen. Besides commercial fruits, favorite pollens of the flying fox include the pollen from Gum and Eucalyptus trees. Studies vary on the importance of pollen to the bat's diet. Some scientist claimed that without the pollen content in the bat's diet, the bat's diets would be lacking in nitrogen (Ratclift, 1932). The discrepancies on the significance of the role of pollen probably vary due to the large range of the bat and the variability of conditions in these areas.

In addition to the indigestible seed mass, fruits also have quite sizable indigestible fibrous content. For example, figs, a favorite of many flying foxes, contain not only 74%

seed but also 43.3% indigestible pulp. Frugivores must cope, like the herbivore, with the large amounts of fiber. The stomach of the bat does not easily digest even the pollen grains and pollen can be found in a collapsed form in the stomach of the bat and pollen can be found in a collapsed form in the stomach and small intestine (Ratclift, 1932).

Because fruits are seasonal, strict frugivores may have to deal with the lack of food sources during climatic changes. Fruit production also varies from year to year. Figs are one of the fruits of Africa that do not fluctuate in production through the coarse of the year, for this reason the fruit bat consumes a diet of primarily figs.

The digestive anatomy of frugivor bats not extremely adapted to the high fiber, seedy nature of its diet. Bats do posses teeth that allow them to grab and tear pieces of fruit. These teeth are not grinders; they only serve to tear pieces of food. Frugivors birds, such as the waxwing, have a craw or gizzard, which serves to grind the seeds and fibrous parts of the fruit, breaking down the hard cell walls. The stomachs of the fruit bats vary widely in shape. Frugivores depend very little on microorganisms for digestion. In this respect, fruigivore differ from herbivores. The gut of the flying fox, therefore, depends heavily on enzymatic pathways and metabolism in their nutrient assimilation and energy budget (Rio *et al*., 1993). The stomach of the flying fox is somewhat primitive. Compared to other flurivore animals, the flying fox has a short intestine. Yet, compared with other bats the intestinal size of the "fruit-eaters" is longer (Ratclift, 1932). This shows that although seemingly un-adapted in terms of fluivore, furgivore bats have adapted to diet when compared to insectious and vampire bats. The comparatively small size of the intestine and gut of the bat, to that of other mammal's mammals is probably due to the bat's ability fly. The small abdomen is an advantage to sometimes large, flying animals. Transit time through the short digestive track is also proportionally fast; this would also be compared to other plant eaters that usemicrobes for fermentation. Bats, consuming mostly juice can pass their food through quickly, not attempting to digest the fibrous content.

The adaptations of the flying fox to its diet are slight, yet numinous. These frugivorous bats simply avoid fruits high in indigestible fiber. When consuming large fruits, the bats carry the fruit off to be eaten in a more harbored environment. Consuming the fruit in a controlled environment allows the bat to be more selective and precise in consuming of the fruit. There are three steps in avoiding the high seed content of many of these fruits. First, bats tend to only consume the most edible part of the fruit. Consuming in small bites allows the bat to then spit the fiber and seeds out. Third, what seeds that are swallowed are separated from the more digestible parts and the seeds, and are then hurried through the gut. (Steele, 1989). On farms where nets were used to protect the fruit, bats still consumed the fruit by sucking out the juice and soft pulp. The quick transit time of their gut, previously mentioned, reinforce this reliance on the juice of the fruit. Because only a proportion of each fruit is utilized for energy, the bats are shown to consume rather large amounts of fruit (perhaps 40 in one night).

Yet, despite these small adaptations to the fibrous, low nutrient foods, the flying foxes also suffer metabolically. Bats are nocturnal, undergoing daily torpor and reserving energy for night activity. Also, when fruits are unavailable to the bat, they are less likely to produce young. By not having young when food is short, the females save themselves from the physical strain of growing and nurturing young. In some areas when crops fluctuate seasonally the "fruit bats" migrate. This allows for a consistency in caloric intake.

The flying fox does exhibit large sizes of a flying mammal, but its flying nature does limit its trunk size. Like the anteater, most of the adaptations of the flying fox are pre-digestive. By avoiding seeds, the flying fox cuts down the number of seeds that will "bulk" up its digestive track. One adaptation of the digestive track is the ability to separate the indigestible juice from the fruit, then extracting the excess, focusing on the foodstuffs that will provide energy.

Koala: Consuming an extremely specific folivorous diet, the koala is the third animal in this study. Not only do koalas' eat solely leaves of Eucalyptus trees, but of the 600 eucalyptus species, koalas prefer the leaves of only 35 species (Hume and Esson, 1993). This foliage contains particularly low nutrient concentration (especially nitrogen and phosphorus) when compared with other forest leaves elsewhere in the world. Thus, although eucalyptus fiber levels are not as high as the fiber content in grasses, they are high when compared to other types of Foliage. The mature form of Eucalyptus may consist of greater then 50% of highly lignite fiber (Cork and Warner, 1983). Lignite fiber is the most indigestible for of fiber and it is usually just passed on through the gut. Even the fruits of the eucalyptus tree are woody (Cork, 1996). Given the nutrient poor and fiber rich characteristics of the trees, the koala's digestive track must some how make the best of such a poor quality food source.

The koala is a hindgut fermentor. Hindgut fermentation can occur in the ceacum alone, the colon, or in both. Solutes and small particles are retained in the ceacum while larger particles are prefermentially excreted. These larger particles are primarily fragments of highly indigestible. By moving these particles through, the digestive track does not waste time and gut capacity on the indigestible particles. If an animal did not separate digesa there would not be sufficient intake and rate of passage for digestion to exhibit a productive digestion and liberate enough nutrients to meet energy needs. The efficiency of the koala's digestive track is revealed by the fact that although most large cellulose particles are passed through, koala are, in fact, highly successful at digesting ligand, with over 18.8% of the ligand being digested to some extent (Hume, 1982).

The first adaptation of these koalas exists pre-consumption and is revealed in their selection. As we previously mentioned, koalas are extremely picky about which eucalyptus leaves they consume. Perhaps this selectivity exists to maximize nutritional value by not wasting time-consuming leaves that are lesser in quality. Specific studies by Hume and Zoidis reveal that koalas also showed positive preferences higher ratios of nitrogen to fiber, and nitrogen to fiber and nitrogen to condensed tannins. This means that koalas select against fiber contend, which is, obviously, advantageous when considering the indigestibility of cellulose. The most important energy sources of the koala are lipids and phenolic compounds found in the eucalyptus oils. These nutrients counter-balance the hard to digest fiber content of these leaves.

The koala has also developed the morphological trait of having an extremely large hindgut. Zoologists have been quoted as saying that the ceacum and proximal colon of the koala are maximal development, more so than other mammal. Using morpho-metric data the surface area of the koala is measured, not only is the surface enlargement factor (SEF) the same as humans, but this data is placed in ratios to show the importance of the hindgut to other segments of the digestive track. In the koala these ratings are extremely high, a ration with the small intestine was calculated to be 5 (three times that of the rabbit, an animal previously calculated to have the largest ratio) (Snipes *et al*., 1993). Likewise, volume rations of he large intestine to the small intestine indicate high levels of fermentation activity. Here the koala received a value of 130, compared to the 71.2 of rabbits (once again previously the highest. Having a large gut means that the foodstuffs are exposed to more surface area of the gut, increasing the chance of microbial contact, enzyme contact, and absorption. Therefore, with this high surface area of its gut, the koala reduces the chance that nutrients will pass through undigested and unabsorbed.

Besides the enormous size of the koala's digestive track, the koala has also made three other adaptations to increase digestion. The caecal microflora of the microflora to the epithelium allows the membrane cells to maximize the absorption of the microflora to the epithelium. This close association of the micrflora to the epithelium allows the membrane cells to maximize the absorption of the fermentation by-products. A second adaptation, less understood, is the presence of a cardio-gastric gland on the stomach. This gland is significant because of its complex mucosal sacculations that open into the stomach. This gland is significant because of its complex mucosal sacculations that open into the stomach. About 4 cm. in diameter, the gland has a basal region composed of chief cells, parietal cells in the middle, and mucosal cells on the neck of the gland. This sectioned part of the stomach is not thought to be used for assimilation of large amounts of food and is, therefore, somewhat mysterious in function (Hume, 1982). The gland does increase the surface area of stomach and provides additional digestive cells. However, food is not kept long in the stomach so the surface are of the stomach may be an important factor. Finally, radioisotope markers revealed the overall long passage time in the koala's digestive track (99-213 h). The rate of digestion is slow. When examined more closely it was noted that while the food particles move somewhat quickly through the stomach and small intestine, the digestive passage of food through the hind-gut of a koala are comparatively slower (Cork and Hume, 1983). This time commitment of labor in the hindgut as compared to the for-gut reinforces the importance of the hindgut in eucalyptus digestion.

Beyond digestive phytsiology, the final adaptation of the koala to the high fiber, low energy, diet of eucalyptus leaves is the koala's slow metabolism. Studies done by Cork (1996) compare the digestible energy (DE) to metabolized energy (ME). Although this energy balance is slightly positive all year, koalas have lower BMR than even other marsupials. It is not known for sure if this metabolic rate is adaptive or pre-adaptive in relation to food types. It is a correlation, though, that koala's have an extremely low BMR and also happen to have a low caloric density diet (Hume, 1982).

Koalas exhibit several adaptations to the cellulose content in their diets. First, the koala is extremely selective in their leaf selection. This seemingly tedious task of the koalas just limits their range to the areas that contain the preferred tree types (eastern Australia) and allows their digestive track to have the best foliage available in their small dietary niche. The koala also has made several physiological digestive adaptations to its diet, creation an extremely efficient digestive track. Lastly, there appears to be a downfall to the low caloric dense diet because the koalas are sluggish animals.

Rabbit: The rabbit is a herbivore, consuming plant materials. Unlike the more specific diets of the anteater and the koala, the rabbit has a larger spectrum of foods that it eats. Its diet consists of many grasses and leaves, all of which have a high level of fiber due to the cellulose in the plant's cell walls. Yet, like the koala, the rabbit has a highly adapted digestive track that productively digests this fibrous plant material.

The rabbit, like the other animals examined in this paper, has a simple-stomach. Fermentation and the bulk of digestion take place in the hindgut of the rabbit. This significance, like the koala, the rabbit has a highly adapted digestive track that productively digests this fibrous plant material.

The rabbit, also, has a simple-stomach. Fermentation and the bulk of digestion take place in hindgut of the rabbit. This significance, like the koala, becomes apparent with the large size (of this relatively small animal's ceacum and large intestine. Yet, because the microbial fermenters are located near the end of the digestive tract, the rabbit does not obtain ample opportunity to digest the products of fermentation, and nutrients are lost in the faces. While the fatty acids produced are absorbed, when the micros pass out in the faces, protein and energy is lost.

Specific to lagomorephs, small rodents, and some other small mammals is the habit of coprophagy. Coprophagy is the practice of eating feces during the part of the day when they are no forging for fresh food. Obviously, it would be more productive for these animals to eat fresh food than already partially digested feces. As stated, coprophagy is practiced when the rabbit is inactive and, therefor, no energy is exerted to find food. The difference in these inactive faces is its softer nature. Soft feces is higher in protein and lower in fiber, it also has a larger water content (Alexander, 1997). This practice of eating a specific type of feces according to a circadian rhythm is caecotrophy.

Because the rabbit is used for so much medical testing, many of the fiber involved experiments are sophisticated and often times reveal more about the nature of fiber then the digestive track of the rabbit. Experiments have varied the amounts of fiber, type of fiber, and digestion rates. Fiber origin, particle size, and fiber level all have an effect on the ceacal microbial activity of the rabbit's hindgut. In testing the effects of fiber origin, biologist Gidenne (1992) kept his samples consistent in their ratios of cell wall constituents (lignin and cellulose). The three origins consisted of lucerne meal, sunflower meal, and wheat straw. Gideene found that fiber origin did affect fiber breakdown and ceacal fermentation. Yet a change in neutral-detergent fiber did not effect fermentation. These findings emphasize the importance of the cell will composition, not just the quantity. Testing fiber particle size included an earlier hypothesis that fiber digression would be improved by more contact between bacterial enzymes and the cell wall. It was found, though, that generally, particle size did not affect susceptibility of fiber to fermentation. The explanation given for this unpredicted finding is that, finer particles meant a longer retention time, this reduced the turnover rate of caecal contents. Thirdly, changes in fiber level also affect passage rate. Reduction of fiber level by 50% caused a voluntary food restriction by the rabbits of 25%. Although higher levels of DAPA and ATP were found in the low fiber diet, this increase in microbial fermentation was once again negated by a lower turnover rate (Bellier and Gidenne, 1996). When the digestible energy level fell, the consumption of foods by the rabbits increased.

This increase in "empty weight" showed a physical adaptation of the gut such with an enlargement of the ceacum and colon, increasing fiber digression (Gidenne, 1992). The anatomy of the rabbit's large intestine has been studied because of its use of colon separation mechanism. The contents from the ileum move into the ceacum are then mixed with the first few centimeters of the proximal colon. The proximal colon possesses three taenia and three rows of haustra. The second half of the colon contains one taenia and one row of haustra. A small section called the fusus coli connects these two sections. The fusus coli contains thick musculature and acts as a pacemaker for peristaltic movement in the colon. Differences between the hard and soft feces are due to its treatment in the proximal colon. In the regular treatment, increased muscular movement in the colon wall squeezes the liner, water-soluble particles towards the huastrum wall, forming a concentration of coarser matter in the middle. Peristaltic movements then move the finer particles along from huastrum to huastrum, back towards the ceacum, while coarser particles in the center of the lumen move toward the distal colon. When this coarser material reaches the distal colon it is formed into fecal pellets. This is how the smaller particles are separated for further fermentation while the coarse material is passed through clearing the gut for more productively digestible food material. The process forming fecal caecothrophes is different, when food particles proceed through the colon there is no mechanical separation. Each pellet is simply coated in a mucus coat, excreted, them consumed. Using a computer model, Alexander created four model animals and tested the efficiency of coprophagy for each gut system. Two of the models were forgut fermenters, while the other two were hindgut fermenters. The model gut systems from the two areas then differed in their size of continuous stirred-tank reactors to plug flow regulators. The four systems and the energy gained from two foods varying in fiber content. "a", "b", and "c" correspond to three daily patterns of feeding considered. In "a" the animal ate nothing during its rest period, but the gut contents continued to move and feces were passed. Category "b" included animals that ate nothing during their rest period and gut contents remained stationary. The last category, "c", the animals ate their feces during their rest period. From this experiment it can be seen that hindgut fermenters and foods which contain lower proportions of cell contents benefit more from coprophagy. This finding would be consistent with the characteristics of the rabbit and their practice of caecotrophy.

The rabbit, like the koala, demonstrates an adapted gut, that successfully ferments the high cellulose content of its diet and because of this can remain active and have a higher metabolic rate then other animals mentioned. Because the rabbit's fermentation occurs in the hindgut, some resources are lost in the feces. Therefore, when not active and conserving energy the rabbit consumes its feces in order to maximize absorption.

Cow: Of all the animals mentioned in this paper, the cow has had a tremendous amount of research done on its digestive system. This focus on the cow is primarily due to its importance in human consumption of milk and beef; therefore, there is interest in composition of the most productive feed for cows. But also, the cow exhibits a unique digestive track that provides interesting studies.

Ruminants are cloven-hoofed mammals that find their food by grazing. There are many ruminants, wild and domesticated. Although wild ruminates are found all over the world, we have increased the numbers of cattle and sheep, monopolizing the foods of other native grazers and consequently retraining their populations. The cow, and other grazers, are often large in size then the browsing flurivors. Grazers, like the cow, naturally consume grass foliage. More than 50% of the leaf's content is with in the specialized bundled sheath. Because grass is high in fiber, grain feeds have been produced for cattle that supply higher energy levels and are more digestible. Cell walls comprise 20-80% of the fry foliage consumed by cows. This cell wall content can vary in digestibility from 30-60% (Wilson, 1994).

Grazers are forgut fermentors. Their food is ingested rapidly, chewed, and mixed with salvia, forming a bolus. This bolus is then swallowed with some force into the anterior rumen. Ruminants are credited for having four stomachs when in actuality they have one stomach, which is divided into several sections. The time spent feeding is dependent on the type of feed and the time needed to reduce it to swallow-able material. Finer particles are swallowed right away. The coarser particles are chewed longer. Rumination includes the regurgitation of the ingested food and reforming of the bolus by emasculation. As ruminants re-chew their forestomach digesta, its cell walls are opened, making the cell contents more accessible. This re-chewing increases efficiency by allowing them to profit from the cell's internal abundance of energy, but to slowly release energy in cell wall polysaccharides (Chivers, 1989). The rumentation process is cyslic but may be interrupted by other activities. Once in the rumen there are contractions that mix the content. This mixing increases the turnover of indigestible residues. If rumen mixing and rumination did not occur, the indigestible content would clog the rumen. The finer components in the rumen then pass to the hindgut.

The lower gastrointestinal track is similar to non-ruminant herbivores. The ruminant's lower tract has often time been overlooked because of the fascination with the foregut; yet, water, minerals, and nitrogen is absorbed and perhaps VFA's. The large intestine of the ruminant is spiral, increasing the surface area. Also important is the job of the hindgut to absorb the microbes and their by-products so that they are not lost (like the rabbit) in the faces.

An experiment by Huhtanen and Vanhatalo (1997) attempted to examine this digestion in the hindgut using different ages of grass. The amount of cell wall carbohydrates digested in the caecum and proximal colon by microbial fermentation varies. Several factors, including physical processing, increased level of feed intake and supplementation with rapidly fermentable carbohydrates. To measure the amount of cell wall digestion in the large intestine, digestive flow measurements in the ileum is needed. This study found that much more hemicellulose then cellulose was digested in the hindgut.

Many kinds of microbes interact with the plant cell walls in the rumen of the cow. These microorganisms can include bacteria, protozoa, and even fungi. All of these rumen microorganisms have shown roles in plant cell wall digression. The major cellulolytric species include Ruminococcus albus, R. flavefaciens, and Bacteriodes succinogens. Variations do exist between adhering bacteria populations and different forages. While enzymes can degrade some cell walls, other s are tougher and require the adherence of bacteria (Federation Proceedings, 1983).

Experiments to study rumen fill in cows were done by placing water-filled plastic containers (500 ml each) to rumen. The added bulk comprising 25% NDF) the other diet being high-fiber (35% NDF). Feeds that contain large amounts of ballast are less filling because they pass through the rumen more quickly. Rumen-inert bulk played little of an adverse role in general function (Dado and Allen, 1995). Milk production was affected in that the cows on the low fiber diet produced more protein and lactose then the cows on the high fiber diet. Meanwhile mil-fat components were similar in the two diets (Dado and Allen, 1995). In conclusion, the addition of rumen-inert bulk decreased DMI for the high fiber diet but not on the lower fiber diet; the volume of rumen digesta was similar for both diets, regardless to if RIB was present or not.

The cow's large size means that it is going to consume larger amounts of food than smaller mammals, such as the rabbit. Rumination allows the larger bulk to be further ground and then re-swallowed. Smaller particles are not, therefore, held up by the large bulk, which is given a chance to be broken up. The forgut fementation assures that more of the products of fermentation and the microbes will be absorbed by the remaining digestive track. Perhaps it is the highly adapted nature of the cow's digestive track that provides the interest to scientist, and the milk and beef industry just provide financial sponsorship.

Humans: Humans are most commonly omnivores; therefore, food sources vary greatly. Indigestible roughage can be prevalent in components of human nutrition. The chitin on crustaceans is usually removed before eating. Fiber is also found in many human foods, especially those toward the bottom of the food pyramid. Foods such as fruits and vegetables provide about 2 grams of fiber per serving.

By looking at physical properties and physiologic roles, fiber is placed in tow groups in human nutrition; first, soluble fibers, including pectin's, gums, mucilage's, and some hemicelluloses. Soluble fibers are able to hold water and then form gels in the gut. Insoluble fiber includes cellulose, lignin, and some hemicelluloses. These fibers are often times highly indigestible by humans.

Most of the fiber nutrition research is done using mammals such as the rabbit that we have discussed; less material is available on actual human experimentation. Fermentation is not highly used by humans. Humans are not forgut fementors and do not posses a ceacum. This limits microbial fermentation to the large intestine; yet, most nutrients are absorbed in the small intestine. The large intestine does use bacteria to ferment fibers to an extent. Fiber fermentation leads to the production of gases (H_2,CO_2, and sometimes CH_4) and short-chain fatty acid (SCFA). These SCFA can have different effects including being used as energy, and having a productive role on mucosal cells and systemically interfere with carbohydrate and lipid metabolism (Bobin-Duigeon *et al.*, 1997).

Experiments done with humans usually test specific types of fiber to examine their digestibility. Therefore it should be noted that humans digest fiber to different degrees, depending on its origin and composition. Studies by Barry *et al.* (1997) have shown that cellulose and maize bran digestibility are very low (7.2 and 6.2, respectively). This compared to pectin and soybean fibers that were 97.4 and 91.1 percent digestible. Studies done by Bobin-Dubigeon *et al.* (1997) show that the sugar composition of dietary fiber is also a factor-determining digestibility.

Besides providing an indigestible bulk to the diet fiber can effect nutrient absorption. One experiment fed human subjects two diets. The first diet contained a low-fiber pasta (5.0 g) the second diet replaced 40% of the wheat flour with barley flour and contained a high fiber content (15.7 g). Overall, the study concluded the study concluded that carbohydrates were absorbed slower in the high fiber diets (Bourdon *et al.*, 1999). Because fiber does not play a large role in human calorie intake, the importance of fiber in human nutrition has taken on alternative functions. Like other animals discussed, fiber does effect the passage rate of human gut digesta. First, fiber can delay gastric emptying, giving a since of satiety. For this reason, fiber is often promoted in weight loss strategies. Once in the distal portion of the digestive track fiber increases passage rate. Adequate cellulose is often a remedy for human constipation. Interestingly, one study suggested that processed wheat fiber increases fecal output less than does raw unprocessed wheat fiber (Vukson, 1999).

Because fiber moves the colon contents through, it is thought to lower risks of diverticulotis and colon cancer. Research shows that not only does fiber benefit the colon but perhaps other types of cancers. It is estimated that dietary factors (including energy, fan and fiber) contribute to 35% of all cancers. Fiber, of all of these dietary factors, is more closely related to overall cancer death then any other individual factor (Anderson and Akanji, 1993). In the Netherlands cancer deaths were three folds higher in individuals with low fiber diets compared to individuals with high fiber diets (Kromhout *et al.*, 1989). Related are studies that correlate the higher cancer rates with the development of countries. Diets in "western" countries contain more processed foods and overall less fiber then diets of countries studied, such as Nigeria and Uganda (Spiller and McPherson, 1980).

Recent research has revealed a role of water-soluble fiber in lowering cholesterol. The study observed plasma glucose, cholecystokinin, and insulin concentrations from the two diets. The only immediate change in the plasma levels was prolonged elevation cholecystokinin is a hormone produced in the duodenal region of the small intestine that induces the gall bladder to contract and excrete bile. The soluble fiber actually binds bile and removes it in fecal waste. Cholesterol is then pulled from circulation to form new bile, lowering cholesterol. The cholesterol concentrations from a barley diet (compared with a wheat diet) were significantly lower (below fasting concentrations) (Bourdon *et al.*, 1999). Average US diets enriched with soluble fiber can produce net reductions in serum cholesterol concentrations of 15% and LDL cholesterol concentrations of 16% over three weeks; serum lipid improvements with such diets were sustained over the long-term with 26% reductions in serum cholesterol concentrations and 24% reduction in LDL cholesterol concentrations over 24 weeks (Anderson and Akanji, 1993). With heart disease the number one killer of males in the United States, lowering cholesterol is a major health concern.

The study by Bourdoun (1999) which revealed the slower carbohydrate absorption reaffirms the importance of fiber in diabetes. Diabetes is more prevalent in populations with low fiber intakes then those with high fiber intake (Anderson and Akanji, 1993). Some studies suggest high fiber foods have successfully enhanced glycogenic control, producing a lower glycogenic response relative to that predicated by the carbohydrate food (Furda *et al.*, 1990). Of 53 studies relating fiber intake to diabetes, 33 (62%) reported that high fiber diet improved glycogenic control (Anderson and Akanji, 1993).

Excessive consumption of fiber in the human diet (over 50 grams a day) can lead to a loss of minerals in feces. This is due to the expedient passage of fibrous materials through the intestine or colon where these minerals are to be absorbed.

The National Cancer Institute recommends a daily fiber intake of 25 to 35 gm. per day, or 10-13 gm. for every 1000 kcal. The new food labels suggest 25 gm of fiber for a 2000-kcal diet and 30 gm for a 22400 kcal diet. If the American public were following the food pyramid and consuming the minimal numbers of fruits and vegetables (equaling about 10 g of fiber) and the remaining from the base of the pyramid this would provide ample fiber in the diet.

Therefore, in the human fiber plays the role of bulk, regulating gut transit time, reducing cholesterol, and giving a sense of satiety with a low caloric concentration. Several different animals with vastly different diets have been reviewed. Fibrous compounds are quite prevalent in natural (unprocessed) fare and animals must maximize the digestion of such food sources. While each animal incurs roughage, his or her digestive strategies vary greatly. More primitive animals worked around the problem while more adapted animals have evolve complex systems to maximize energy extraction. Animals can also consume large amounts of these low caloric-dense foods, dedicated much of their time on actually foraging. Continual themes in all the animals are the trade-off of digestion time versus consumption quantity. Fermentation and batch reactors slow up the system, and the animal, therefore, cannot take in additional food in the meantime. Yet, if the system is continually flushed and food quickly moves through, less absorption is taking place. The animal has, therefore, to find a medium that is suitable to its diet, defining its strategy.

Adaptations vary, and many of the adaptations seen in the more primitive animals focus on pre-consumption activities. These included selectivity in food choice and specific diet niches. If not choosing the best of what exists within that selective niche, animals can choose foods low in fiber all together. Animals often will avoid more indigestible choices or the indigestible components--such as seeds. Humans, unable to utilize fibrous foods, depend on high protein and fat foods for a large amount of their energy requirements. The cooked and processed natures of our more caloric dense foods liberates us from dedicating our time towards food gathering.

Morphological adaptations begin in the oral cavity with the grinding properties of the teeth or, in the case of the anteater, the tongue. The digestive strategy then was either a forgut fermentor or a hindgut fermentor. Special strategies included coprophagy and rumentation that allowed the undigested fiber to have a second chance at digestion. In conclusion, these adaptations occurred with the extremely high fiber foods; therefore, interacting digestive strategies have evolved corresponding to the nature of the animal's dietary niche.

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