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Rate of Passage of Digesta in Ruminants; Are Goats Different?

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Additional information is available at the end of the chapter

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Abstract

Fluid passage rates through the rumen influence digestion of soluble food nutrients, amount of short-chain fatty acids absorbed in the rumen and that pass out of the rumen, the amount of by-pass protein of dietary origin and the amount of microbial protein available to the host as a protein source, making modelling of passage imperative. Current research on passage rate should seek to incorporate various factors that affect rumen fill, and solid and liquid passage rates to develop intake and passage rate prediction models. The aim of this paper was to discuss factors that affect rates of passage of digesta and rumen digesta load. Ambient temperature, animal physiological status and reproductive status, fermentation and diet quality are major factors affecting digesta passage rates. The animal physiology also influences digesta passage rate. Computation of animal production level to account for all the physiological processes that affect passage rate is vital. Discrepancies on how ambient temperature and particle density (buoyancy) affect the passage rate of digesta in the rumen may cause uncertainty in calibration of temperature and buoyancy in prediction models. Corrected for diet properties, goats have similar passage rates to other ruminants.

Keywords: diet selection, feeding behaviour, intermediate feeder, prediction model, ruminant

1. Introduction

Goats have become one of the most important livestock for resource-limited farmers around the world because they can survive in harsh climatic conditions from cold temperate regions (in the Siberia) to hot arid deserts (in the Kalahari). Key to their ability to survive in diverse climatic regions is their ability to walk through tight, narrow places and their capability of efficiently utilising vast plant feed resources. Goats are important as a source of protein (milk and meat) and wealth. Given the increasing importance of goats among resource-limited farmers in tropical

and subtropical regions around the world, research on the physiological aspects of goat nutrition is vital for improved goat production. Feed availability and quality are the major factors affecting yields for and quality of chevon and milk in rural goat production systems. Enhanced milk and chevon productivity is largely dependent on their selective feeding behaviour supported by improved nutritional status through supplementation of poor-quality roughages with feeds of high nutritional value (e.g., protein and energy concentrates). Concentrates are generally expensive for resource-limited farmers in rural communities around the world, especially in Africa and Asia. Hence, cost-effective usage of these feeds is vital. Fundamental to cost-effective concentrate supplementation for improved productivity of goat farming systems in the tropics relies on accurate and precise prediction of roughage intake. Accurate prediction of roughage intake would enable farmers to calculate precise quantities of concentrates to be fed to achieve a cost-effective level of production of good-quality meat and milk.

One of the major challenges in developing sustainable and cost-effective feeding strategies for goats in rural production systems in Africa, Asia, and other parts of the world is the inability to accurately predict roughage intake in goats. This is partly due to limited information on the critical factors that affect intake, passage rates of digesta and rumen fill for goats. Nsahlai and Apaloo [1] examined the appropriateness of model in [2] to predict the intake in ruminants grazing on poor quality roughages in tropical regions and showed that the model, though structurally adequate, underestimated roughage intake, partly due to poor estimates of gut fill and rate of passage. Similarly, the authors [3–5] showed that the model of Illius and Gordon [2] overestimated retention time in browsing ruminants for particle sizes less than 2 mm. Nsahlai and Apaloo [1] pointed out that the model of Illius and Gordon [2] erroneously estimates rumen fill levels and passage rates as a function of body weight alone.

Given the role of fluid passage rates through the rumen in affecting by-pass proteins and fatty acids that are assimilated in the hindgut, passage of fluid would have a significant influence on milk protein and butterfat composition in dairy goats. This makes the study and modelling of digesta passage rate relatively important. Modelling of passage rates would necessitate prediction of roughage intake, microbial protein yield and milk composition in goats. Before any passage rate modelling exercise can be effectively carried out, factors that affect passage rates need to be reviewed and used to predict digesta passage rates.

Given the abundant literature on passage rates for cattle and sheep, and other ruminant feeding types, and limited data on goats, the chapter (i) identifies the major factors that affect passage rates in ruminants, (ii) explains the fundamental mechanisms by which each identified factor possibly affected rates of digesta passage from the rumen, (iii) gives suggestions of the major factors that can be considered as critical input factors for developing passage rate prediction models distinguishing studies on goats and (iv) determines whether goats are different with respect to other ruminants in terms of passage rates.

2. Rumen fill, gut capacity and its estimation

Gut fill is referred to as rumen fill with respect to ruminants based on the facts that the rumen is the only site in the gastrointestinal tract where distension has an effect of restricting digesta

flow to a great extent [6]. Maximal rumen load for dry matter is determined by allometric procedures as a function of body weight [1, 2]. However, a ruminant's fill capacity also depends on the volume of digesta that causes rumen distension and on rate of flow of digesta from and rates of degradation of digesta in the rumen [6, 7]. As a result, criticism on determination of rumen fill based on body weight alone has been raised giving better models for rumen load based on body weight, mature body weight and dietary crude protein [1]. This fill capacity may also be determined practically by manually emptying the rumen at a time when full gut capacity is reached and weighing out digesta at that time [8] or slaughtering animals upon meal termination [9]. Rumen fill varies greatly with body weight and feeding habit. Rumen fill is approximated to be about 9 and 13% of body weight for browsers and grazers, respectively [8]. Interestingly, there is no apparent approximation of rumen fill based on body weight for intermediate feeders such as goats, although it may be assumed to fall within the range of 9–13% when grazers and browsers are regarded as extremes.

Carrying out rumen evacuations to determine maximal rumen digesta load is not an easy task. It is assumed that the only or best way to know when an animal has reached its maximal gut capacity is when it stops or terminates feeding [10]. This theory is supported by Boudon et al. [11], where termination of short-term feed intake was attributed to signalling from the rumen wall as a result of rumen fill. Taweel et al. [12] and Williams et al. [13] reported scenarios whereby maximal rumen fill was greater after termination of late afternoon feeding bouts just around sunset than bouts from other parts of the day. According to these results, measuring maximal rumen fill after termination of morning feeding maybe misleading. However, Baumont et al. [14] reported rumen fill to reach its first maximum after the main morning meals, with a daily maximal rumen fill being reached after the evening meal. Similar results were obtained by Thomson et al. [15], where maximal rumen fill was observed after termination of first morning meal and late evening meal at 0900 h and 2000 h, respectively, in grazing sheep. Assuming that at meal termination, ruminants would have reached maximal rumen capacity is misleading as well. This assumption is supported by Taweel et al. [12] and Chilbroste et al. [16] who reported findings where maximal rumen capacity had not been reached when grazing dairy cows terminated feeding bouts. Greenhalgh and Reid [17] reported similar results where sheep fed on hay and straw-terminated feed intake way before maximal gut capacity was reached. These and other experimental results therefore suggest the existence of different sets of rumen fill levels which are time dependent, either before or after feeding bouts. These fill levels may be a function of the rate of emptying of rumen digesta after eating has stopped. At any given time, rumen fill levels are a function of the rate of feed intake, rates of digestion and particle breakdown, and rates of outflow [13]. As such, rumen fill levels or values are dynamic and thus should not be regarded as constants and times in which rumen capacity is measured should be taken into account as well.

Based on rates of passage and digestion, estimation of rumen capacity using mathematical procedures gives variable but useable results. Estimated rumen pool size based on passage and degradation rates at the point of meal termination gave values which were even twice as large when compared to average observed values obtained from the literature (Nsahlai, unpublished data). Failure of mathematical procedures to achieve tenable outcomes suggests that something uncertain takes place during the period after meal termination before evacuation.

3. Factors that affect rumen fill levels and rates of passage through the rumen

3.1. Animal species and feeding types

Ruminant livestock has different feeding habits [4] with cattle, buffalo and sheep classified as grazers and goats as browsers or intermediate feeders [18]. Differences in type of diets and processes associated with feeding behaviour between these classes of animals may have an effect on rates of passage of liquid and solid phases in the rumen [19] and their rumen fill.

Sheep had lower mean retention times of solid in the rumen than cattle (58 vs. 65 h) [20]. Lechner-Doll et al. [21] added that selective retention of particles is more pronounced in cattle than in sheep suggesting that the passage rate of large particles is greater in sheep than in cattle. Outflow rates of fine solid material are normally estimated by allometric procedures as an inverse function of body weight, which infers erroneously that the rate of passage in smaller ruminants is always greater than that in larger ruminants [1]. Parra [22] showed higher passage rates for smaller herbivores than larger herbivores with diet quality held constant. Differences between cattle and sheep with respect to solid retention times depend on chewing activities of these species. Average chewing rates are higher in sheep (80–100 chews per minute) than in cattle (40–60 chews per minute), indicating different efficiencies in these ruminants. Consequently, cattle have developed pronounced selective retention mechanisms for large particles in the floating fibre mat found in the dorsal rumen to improve particle size reduction and perhaps nutrient extraction; hence, retain particles for longer periods compared to sheep [23, 24].

Oshita et al. [25] reported differences in passage rates and rumen fill levels among cattle as a result of different grazing strategies. Rumen fluid dilution rates were higher for rotational grazed cattle (12.2%/h) compared to cattle fed pasture in confinement (9.9%/h). Similarly, rumen volume was lower for rotationally grazed cattle (79.9 l) compared to cattle fed in confinement (110 l). Williams et al. [13] showed no variations in rumen pool sizes with pasture allowance and time of day. Lack of differences in rumen fill levels with increasing pasture allowance is due to great variations in outflow rates.

Great variation in passage rates between animals of the same class of ruminants may occur as a result of differences in feeding habits. Although very little or no evidence for this phenomena has been documented, it is highly likely to occur. Dorper sheep are less selective of feed, consumed more shrubs and bushes than Merino sheep during grazing in the Noorsveld Karoo, South Africa [26]. Dorpers would be expected to have slightly faster passage rates than Merinos because they consume more browse. Hence, it would be expected that Dorpers spend less-time re-chewing twigs than Merinos resulting in more-intense rumen contractions that forced digesta out of the rumen quickly. Goats have a much similar feeding habit to these Dorper sheep as they utilise both graze and browse and are more selective of high-quality browse. It can be concluded that passage rate in ruminants is affected by interactions between diet, ruminant species and their climatic environment.

Molina-Alcaide et al. [27] observed no differences in particle passage rates in goats (intermediate feeder) and sheep (grazer) fed on various diets with average rates of 0.030 and 0.025/h, respectively. However, Clauss et al. [28] suggested that smaller browsing species had much greater solid and fluid passage rates through the rumen than grazers of a much similar size. A much different trend exists in larger individuals of each feeding habit. Larger grazers tend to show higher solid and fluid passage rates through the rumen than browsers of similar size [28, 29]. Surprisingly, intermediate feeders (such as goats) were not included in this comparison. Processes that occur in the rumen when different diets are fed coupled with the anatomy of the fore stomach associated with each ruminant feeding type are implicated in these differences. Fluid and solid passage out of the rumen occur through an opening between the reticulorumen and the omasum called the reticulo-omasal orifice [30]. Positioning and size of the reticulo-omasal orifice may shed insight on the flow of liquid and solid digesta from the rumen. Hofmann [18] showed that the size of the reticulo-omasal orifice was greater in browsers than in grazers. It may be hypothesised that due to the larger reticulo-omasal orifice in browsers, a much greater volume of solid and fluid passes through the rumen per unit time than in grazers. This may cause browsers to have higher fluid passage rates than grazers in smaller animals [30].

With respect to the larger groups of animals, grazers possess larger omasum than browsers [18]. One of the functions of the omasum is to absorb water [31], thus it may be logical to assume that there is a much greater water pulling effect (cohesion and capillary movement) of the grazers larger omasum than that of browsers. This could result in higher passage rates of fluids out of the rumen of grazers. Due to a greater receptive space of the omasum, the pressure difference between the rumen and omasum [30] is larger in grazers than in browsers. Hence, greater rates of passage of fluid observed in grazers may be due to a larger pressure difference. This may not apply to small grazing and browsing animals. Hence, a gap in knowledge on the relative sizes of the omasum in smaller grazers, intermediate feeders and browsers exists.

Indirect evidence suggests that browsing ruminants have shorter mean retention times for liquid and solid digesta in the rumen compare to grazers. These include postruminal absence of glucose transport mechanisms (GLUT transporters) in grazers which are present in browsers [4, 32, 33], deposition of large quantities of polyunsaturated fatty acids in browser carcasses compared to grazers [4, 34], lower efficiency of fermentation [4, 35] and total tract digestibility [36] in browsers than grazers and presence of large amounts of particles that are greater than 1 mm in faecal samples from browsers compared to grazers [3, 18, 37, 38]. These differences are partly a result of faster fractional passage rates of fluid and solid through the rumen of browsers compared to grazers.

Differences in viscosity of rumen fluid and saliva between grazers and browsers exist [39]. Browsers have more viscous rumen fluid [29] and saliva [18] than grazers. The thicker and stickier the fluid digesta may have an effect of reduced movement of the fluid through the rumen due to increased attachment of water molecules to feed particles. Hence, fluid is less likely to escape from the rumen thus resulting in reduced fractional passage rate

of fluid in the rumen of browsing animals. However, Silanikove et al. [40] obtained conflicting results to [29], where polyphenolic compounds increased the rate of fluid passage through the rumen. Polyphenolic compounds cause fluid digesta to be thick and sticky as a result of more viscous saliva production, which is a case in browsers [39]. Hence, viscosity of rumen fluid increases due to the presence of polyphenolic compounds. The expected outcome is decreased fluid outflow rate. Contrary to that, increased viscosity due to polyphenolic compounds may increase the rate of passage of fluid. Fluid from the interstitial spaces may be drawn into the rumen in an attempt to wash off these polyphenols [40] as a physiological response by the animal against them. This occurrence may then result to increased rates of fluid passage through the rumen.

Due to observed differences in passage rates among ruminant species, possible differences in rumen fill may be expected given that the passage rate is related to the amount of digesta in the rumen at any given time. Molina-Alcaide et al. [27] showed that rumen fill and amount of rumen contents are larger for goats compared to sheep. It was concluded that goats possessed a unique characteristic of being able to maintain larger rumen fill levels without noticeable rumen distension than sheep when fed medium-quality diets. These results were not expected taking into account observations by Clauss et al. [28] showing that smaller browsing species had much greater fluid and solid passage rates through the rumen than grazers of a much similar size, suggesting that goats should have lower rumen fills than sheep. Cattle are expected to have a much larger gut capacity than sheep and goats when scaled to body weight. Parra [22] showed that metabolic rate increased as a fractional power of mass (W^x) suggesting that small ruminants have smaller rumen capacity per unit metabolic need. Hence, as a result, cattle would be expected to have a greater rumen capacity than sheep and goats. Due to the above-mentioned theories, small bodied ruminants with smaller gut capacity must compensate for this constraint by increasing passage rate to ensure they maintain adequate feed intakes to meet metabolic needs [41]. This may help explain why sheep had higher passage rates compared to cattle [20]. Body weight cannot be convincingly classified as a factor that affects mean retention time [42]. At body masses less than 100 kg, Wenninger and Shipley [43] showed in cattle that there was no relationship between the body weight and mean retention time.

Differences in passage rates among ruminants exist as a result of differences in habitats in which they live and are adapted, which is dependent on the type of diet available. Silanikove et al. [44] showed that average fractional flow rates tended to be lower for desert goats (0.084/h) than non-desert goats (0.099/h). This translated to +39% higher fluid passage rate in non-desert goats per unit body weight. Again, mean retention time of solid particles was 10 h greater for desert goats with intake being predominantly limited by high levels of rumen fill [44]. These findings indicated that desert ('tropical' or hot climate) goats may possess greater digestive capacity than other breeds of goats as a result of adaptation to feed and climatic conditions in the desert. Passage rate and rumen fill data for goats adapted to subtropical and tropical climates in sub-Saharan African are limited, thus necessitating data on how climatic adaptation influences passage rates and rumen fill.

Rumen capacity and fill levels at any given time vary according to breeds as well. Breeds better adapted to low-quality forages tend to possess increased rumen capacity for both

digesta phases. Weyreter and Engelhardt [45] found that Heidschnucken sheep (well adapted to high fibre roughages) were better able to consume large amounts of fibrous diets compared to Merino sheep (less adapted to high fibre roughages). This suggested that Heidschnucken sheep have greater potentials in expanding their rumen capacity compared to Merino sheep. Black head sheep (cold climate or temperate breed) are unable to make such an adaptation relative to Heidschnucken sheep [45].

A new theory on passage rate is beginning to unfold based on anatomical features of the rumen in different ruminant feeding type. Clauss et al. [46] suggested that digesta passage patterns are correlated to and influenced by intraruminal papillation patterns. Differentiation between grazers and browsers using papillation patterns characterised grazers as having long, thick papillae and deep reticular crests and ridges. Browsers characteristically have short and much thinner papillae and shallower reticular crests compared to grazers. Presence of deep reticulorumenal papillae and crests caused entrapment of small particles in ridges of grazing ruminants than in browsers, causing longer retention times in grazers [42].

3.2. Level of nutrition and feed intake

Plane of nutrition may be referred to as the level of feeding and animal production level. Level of feeding is defined as the amount of feed the animal consumes relative to its level of feeding to meet maintenance requirements [8]. Cases of hyperphagia increase demands for expanded rumen capacity so as to accommodate much greater digesta load [47]. Quantities of feed ingested by ruminants depend on animal species, and the variability in intake levels occurs between breeds and/or individual within a breed [48].

Haaland and Tyrrell [49] observed that the rates of passage of fluid through the rumen increased by 13% when animals were fed at two times maintenance from feeding at maintenance level. The authors [50–53] observed that an increase in dry matter intake was associated with linear increases in fluid passage rate. As an animal eats more dry matter, solid material entering the rumen accumulates, and there is a possibility of dry matter taking up space occupied by the fluid in the rumen thus exerting pressure on the rumen contents. With dry matter being more bulky [54] than liquid, there is a possibility of the bulk forcing liquid out of the rumen at a much faster rate as the pressure builds up in the rumen compared to low intake levels. In muskoxen, Barboza et al. [47] showed that elevation of feed intake by 74% increased gut fill by 31–34%. Hyperphagia increases gut fill, and gut fill is usually a result of reduced passage rate of solid material. On the other hand, this observation is inconsistent with studies where increased feed intake has been shown to increase passage rates. Although Lindberg [51] showed a strong relationship between liquid passage rate and feed intake in dairy goats, no correlation was reported between dry matter intake and mean retention time in addax [54]. This suggests that high dry matter intakes may not necessarily influence passage rates through the rumen. Long mean retention times for particulate matter at high dry matter intakes in addax may have been due to a high reserve capacity of the reticulorumen. Accurate determination of the extent to which rumen capacity may expand to accommodate various types of forage diets in different ruminants would be important. This elicits determination of maximal rumen fill levels in ruminants. Body weight had high positive

correlation to rumen capacity [55]. Distension of abdominal cavities during the projected increases in rumen capacity have not yet been quantified and documented in any species [56]. Estimates to which ruminant gastrointestinal tracts stretch to accommodate a given diet range roughly lies between 10 and 17% of the body mass in ruminants, with an upper limit of 20% for cattle. Goats and sheep reach this upper limit more frequently and easily than cattle [57]. Body weight alone is not a good indicator of maximal rumen fill; Purser and Moir [58] reporting variation in gut capacity among animals of similar body weight. Tulloh and Hughes [59] reported larger rumen volumes in lactating cows than dry cows. Hence, rumen fill or volume is more a function of various physiological states.

3.3. Forage-to-concentrate ratio in the diet

Supplementation of predominantly roughage-based diets has become a major practice in ruminant nutrition. Protein concentrate supplementation of ruminants grazed on pasture increases the nutritional status of ruminants [60]. Levels of concentrates added to predominantly roughage feed would affect the rate of passage of liquid and solid through the rumen. High roughage to concentrate ratio in the diet would lead to greater fluid and particulate passage rates from the rumen (**Table 1**). Passage rate is affected by roughage quality and the rate at which rumen digesta disappeared from the rumen is positively related to diet quality [1].

Bartocci et al. [20] reported an increase in passage rates of fluid and particulate matter from the rumen with an increase in the proportion of dietary fibre in diets fed to buffalo, cattle and sheep. All authors [61–65] reported that high proportions of concentrate in diets decreased the rates of fluid dilution and turnover in the rumen.

Although similar trends on the effects of forage-to-concentrate ratio on fluid dilution rate and fractional passage of solid were observed, a number of suggestions have been given toward explaining these observations. Forage-to-concentrate ratios can alter a number of processes in ruminants, and these processes have been implicated to changes in fluid and solid outflow rates from the rumen. These processes include the amount of saliva produced and the degree of stratification of rumen contents.

Froetschel [66] showed that cattle produced an average of 100–200 l of saliva in a single day when fed high-fibre diets. Saliva is mainly used as a buffering agent and lubricant as roughage digestion produces large amounts of short-chain fatty acids that may lower rumen pH.

Phase	Diet	F:C = 87.5:12.5	F:C = 75:25	F:C = 62.5:37.5	F:C = 50:50
	Parameter				
Liquid	OFR (l/h)	3.47	3.16	2.76	2.41
Liquid	RF (l)	49.10	46.10	43.60	40.00
Solid	k_1 (%/h)	3.15	2.71	2.71	2.48

F:C, forage-to-concentrate ratio; OFR, outflow rate; RF, rumen fill; k_1 , fractional passage rate. Adapted from Ref. [20].

Table 1. Effect of forage-to-concentrate ratio in diet on rate of solid and fluid passage through the rumen.

Increased amount of saliva forces ruminal wall contractions to escalate [66]. An increase in these contractions may be stimulated by increased distension and tactile stimulation of the rumen wall due to filling by saliva. Distension of the rumen wall results to contractions, emptying the rumen fluid and solid digesta to prevent it filling. These contractions squeeze solid and fluid digesta out of the rumen at an increased rate increasing the efficiency of microbial protein synthesis. Bartocci et al. [20] observed decreased amounts of saliva production in animals fed high-concentrate diets that constituted 50% of the diet. Hence, reduced salivation may be responsible for lower passage rates in high-concentrate fed animals due to reduced rumen contractions. Another possibility is that occurrence of these increased contractions might be due to mineral ions present in saliva.

Due to the bulky nature of forage, high roughage diets may occupy a large space in the rumen. Bulky forage may force liquid out of the rumen at a much faster rate as competition for space increases. Tactile stimulation of the rumen wall by the roughage is a likely facilitator. Because of a much greater degree of tactile stimulation, rumen wall contractions may occur, thus forcing rumen fluid to pass through the rumen at a much faster rate. Okine and Mathison [67] showed that an increase in duration and amplitude of reticulorumen contractions resulted in an increase in passage rate of both solid and liquid matter out of the rumen. Due to less bulk, concentrates would occupy far much less space in the rumen than forages; thus, high-concentrate diets would induce low-amplitude rumen contractions due to reduced tactile stimulation of the rumen wall. Low power of contractions would force less fluid out of the rumen per unit time compared to roughages leading to lower fluid and solid passage rates. Rumen fill was reported to be greater in diets that had higher proportion of roughage because roughages contribute to rumen fill more than concentrates in view of longer retention times in the rumen and selective retention in the fibre mat. Lui et al. [68] observed reduced clearance rates of solid digesta in the rumen of animals fed bulky high fibre crop residues. Lui et al. [68] gave clear evidence of enhanced rumen fill levels as a result of high fibre/roughage content in ruminant diets. Concentrate particles are small and the chance of being trapped in the floating mat is minimal; thus, it passes out of the rumen at a much faster rate than roughage particles.

In the rumen, stratification occurs (**Figure 1**). Stratification involves separation of liquid and solid components into distinct layers according to density [69]. Stratification is evident when a mat-like layer forms and floats on the liquid phase. Fibre promotes the formation of the floating mat [70] in roughage more than concentrate diets because concentrate particles are smaller forming more homogenous mixtures in the rumen. Formation and presence of a floating mat in the rumen stimulates ruminal wall contraction [57], possibly due to tactile stimulation of the rumen wall. These contractions may lead to a rapid outflow of liquid

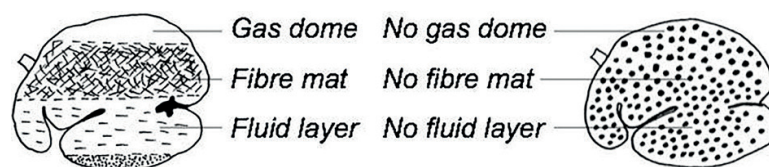


Figure 1. Proposed degree of stratification in rumen due to roughage (left) and concentrate (right). Adapted from Ref. [69].

and fine-solid digesta through the rumen. Faichney [71] showed that entrapment of large solid particles in the filter bed of the rumen restricted their outflow. Entrapment increases retention time of large particles; hence, fibre-mat formation may be a factor labelled as affecting rate of passage of solid through the rumen.

However, the theory of stratification may be challenged. Moore et al. [70] showed that cottonseed hull diets, even though fibrous and elicit a faster rate of liquid flow through the rumen, do not promote stratification. Hulls are smaller and denser and form a more homogenous-like mixture in the rumen [57]. Moore et al. [70] concluded that rates of fluid flow through the rumen increased because of increased intake of the hull diet. Contrary to that, Owens and Goetsch [72] reported that cottonseed hulls resulted in decreased passage rates of fluid in the rumen, thus supporting the theory of stratification. Further studies on the effect of cottonseed hulls on the rate of passage need to be done. The theory of stratification that supports increased flow rate of fluid through the rumen may be applied to higher passage rates in grazers than in browsers due to differences in diet. Grazers are mainly roughage eaters, and browsers are concentrate feeders [18]. Hence, higher rates of passage of fluid are seen in grazers than browsers.

Stage of development of forage may also have an effect on the fluid dilution rate and solid passage rate [55]. When a plant is young, it contains a higher proportion of water than old plants, with older plants tending to have a larger proportion of lignin. With older plants having large proportions of lignin than younger plants, it is expected that forages at a late stage of development may induce higher liquid passage rate. However, ruminants that graze on grass that is at an earlier stage of development have high fluid passage rates through the rumen than those grazing on mature pasture. Work by Adams et al. [55], Estell and Galyean [73] and McCollum and Galyean [74] showed that animals grazed on young pastures have higher dilution rates (18.3%/h) than animals grazed on mature pastures (9%/h). The presence of high mineral and water content in young forage may lead to increased osmotic pressure in the rumen causing the relaxation of the reticulo-omasal orifice thus increasing fractional rates of passage of fluid through the rumen. Lignin and hemicellulose contents of forages may have a substantial effect on passage rates of both solid and liquid matter in the rumen. Mature forage contains a higher proportion of hemicellulose than young forages [75]. Hemicellulose has hydrophilic properties [76] and capabilities of absorbing and holding water in the rumen are high. Due to hydrophilic properties of hemicellulose, fractional rate of passage of fluid through the rumen decreases because hemicellulose absorbs a greater proportion of fluid and reduces fluid outflow rate. This phenomenon is most likely to occur when high roughage diets are fed.

Van Weyenburg et al. [76] observed higher fluid passage rates in Lucerne hay than in grass hay. Analysis of the hemicellulose content in both feeds showed higher hemicellulose content in grass hay than in lucerne hay. The water holding capacity of the hemicellulose is approximately 260 g water/kg DM for grass hay and 59 g water/kg DM for lucerne hay [76]. This suggests that the greater the hemicellulose content of forages, the greater the amount of water that forage can hold. The greater the quantity of water held by the forage then the lesser the proportion that leaves the rumen, resulting in a decrease in the fractional rate of fluid passing through the rumen. Seemingly, Froetschel and Amos [77] found no correlation between water

holding capacity of digesta and fluid outflow rate, but a positive correlation between water holding capacity and ruminal fluid volume. More evidence of this subject is needed.

Dietary roughage quality affects rates of passage of solid material through the rumen [1]. Rinne et al. [78] found out that clearance of digestible plant cell wall fractions of particulate matter was slower than indigestible fraction of matter. This is perhaps due to sorting of particles in the rumen by stratification [79] and entrapment of digestible material in the floating fibre mat. Within a feed particle, digestible portions of feed retain for longer periods in the rumen and degrade slowly to a high extent, whereas indigestible portions clear from the rumen through passage quickly because of their size and density. Plant particles undergoing fermentation produce gas, hence float and get entrapped in the floating fibre mat restricting their passage out of the rumen. As a result, fractional clearance rate of indigestible part of fibre such as lignin is more rapid than that of digestible fractions such as hemicellulose [80] and may reduce rumen fill [6]. Contrary to this view, Baumont et al. [81] suggested that increases in lignin content of roughage would make it stay much longer in the rumen before being cleared through passage out of the rumen, increasing rumen fill as a result. Baumont et al. [81] was of the view that retention time in the reticulorumen depended on the rate of degradation of the degradable fraction and on the proportion of non-degradable fraction. This suggests that increased proportions of non-degradable fractions slowed down the rate of degradation of the degradable fractions, with overall effects of slowing down passage rate and increasing rumen fill. For microbes to get access to the digestible fractions of fibre, microbes must etch into and remove lignin so as to access these digestible fractions. Hence, as a result of high-lignin content, the rate of degradation is greatly reduced, thus increasing retention time in the reticulorumen. Grasses tend to contain high contents of neutral detergent fibre compared to browse leaves and legumes. Browse leaves are shown to contain much more lignin compared to grasses [82]. Panjaitan et al. [83] reported mean retention times of lignin fraction that were three times greater than those of neutral detergent fibre fraction across four grass species.

Rumen fill is at times described based on fibre (neutral detergent fibre, NDF) fraction [84] on the basis that fermentation and passage rate of neutral detergent fibre through the rumen are slower than of any other dietary constituent. Fibre exerts a greater filling effect in the rumen [6]. Indirect evidence on the effects of NDF content on rumen fill exists. Using sheep fed on alfalfa hay and orchard grass hay, Baumont et al. [85] observed higher dry matter intakes in sheep fed alfalfa hay relative to orchard grass hay, which was attributed to lower NDF content in alfalfa hay. Due to lower NDF content in alfalfa hay than in orchard grass hay, alfalfa had a lower filling effect on the rumen due to rapid rates of fermentation and passage through the rumen [86]. In conclusion, low NDF content is associated with low rumen fill levels, suggesting a positive linear relationship between NDF content (x-axis) and rumen fill (y-axis), which reaches a plateau when rumen capacity cannot increase further with additional increase in NDF content.

Grazing herbivores have an ability to gradually modify rumen volume and increase passage rates in accordance with a reduction in roughage quality [87]. Due to slower passage rates of the digestible fraction, ruminants fed on highly digestible feed may experience maximal rumen fill. Boudon et al. [11] stated that attainment of maximal rumen fill would limit feed

intake in dairy cows grazed on highly digestible rye grass. Also, rumen fill in grazing animals varies greatly from the beginning to the end of a feeding session [11]. On the contrary, Dove [88] suggested a relationship, whereby rumen fill played a major role in regulation of feed intake with decreasing digestibility of a feed. Digestibility is negatively related to lignin content and high lignin content caused slow passage rate in the rumen [78, 88]. This actually suggests that passage rate of solid material was slower for low digestible feeds. Slower passage rates increased rumen fill because feed stays for a much longer time in the rumen. Faverdin et al. [89] demonstrated a more or less similar phenomenon where the overall effect of indigestible feed components resulted in increased rumen fill of approximately 1 kg DM which resulted to a corresponding depression in feed intake of 0.6 kg DM/day. The most probable explanation for this would be a reduction in the rates of clearance of digesta from the rumen, mainly by passage.

3.4. Ambient temperature

As ambient temperature fluctuate during the course of the year due to seasonal changes, or as the day progresses from sunrise to sunset; animals respond to these changes in varied ways and to different extents. Temperatures that might lead to severely altered physiological processes would result in changes in rates of passage of fluid and solid through the rumen. These include temperature ranges above and below the thermo-neutral zone for ruminants [50].

Warm-blooded animals mainly respond to high environmental temperatures by panting, sweating or licking own body, which loses heat from body fluid via evaporation. Increasing plasma volume to increase heat dissipation [90] possibly via radiation may occur. Under extremely high temperatures, animals become reluctant to eat thus reducing dry matter intake [30] to cut down on heat production and heat increment due to feeding. In response to rather low environmental temperatures, warm-blooded animals shiver increasing movements of body parts to generate heat energy internally and generally tend to increase dry matter intake [30].

Low ambient temperatures generally lead to increased rates of fluid and solid passage through the rumen. Kennedy [91] reported a 21% decrease in mean retention time of solid digesta in the rumen as ambient temperature decreased from 21 to 0°C. This increase in the rate of passage may be attributed to occurrence of shivering and increased movements of various body parts [30]. Contraction and expansion of muscles and organs in close association with the rumen may exert pressure on the rumen wall causing it to contract and decrease in size momentarily. Thus, exertion of some pressure on the rumen and its contents may force out rumen fluid and solid from the rumen at a much faster rate. Extents to which such an occurrence affect rates of passage of fluid through the rumen is virtually undocumented and may require further study. Increased rumen movement has been documented at low ambient temperatures [30], probably as a result of movement of organs in close proximity to the rumen. Such movements of the rumen are accompanied by increased power of ruminal wall contraction [30], which may squeeze rumen digesta resulting in it escaping from the rumen at a more rapid rate. Increased dry matter intake on exposure of animals to low ambient temperature [92] is also assumed to have an effect of increasing passage rate of fluid through the rumen due to a push effect.

In extremely high ambient temperatures, slower rates of fluid passage through the rumen are due to a decrease in the pushing effect on the ruminal fluid as a result of low intake. Contrary to that, Chaiyabutr et al. [90] observed that higher ambient temperatures resulted in an increase in the rate of fluid passage through the rumen even when a decrease in feed intake occurred.

Rates of passage of fluid from the rumen increased by almost double from an ambient temperature that is within the thermo-neutral zone of cattle to a temperature slightly above the thermo-neutral zone (**Table 2**). The observed increase in blood and plasma volumes indicated that animals responded to heat stress dissipating heat via evaporation and radiation through the skin thus cooling their bodies using blood water as a medium. Water has a high specific heat capacity with reference to biological systems and hence may be used to dissipate heat [93] in most animals.

The rumen acts as a water reservoir [8]. Water that contributed to an increase in plasma levels may have been from two sources, water intake and rumen, or both. Water may either enter blood through flowing across the ruminal wall [90]; however, proportions that go through this route are minute [94] or diffusion into the blood stream through the intestines [95]. Assuming that water was rapidly mobilised from the intestines into the blood, the capability of the intestines to provide large amounts of water is unlikely. Since the rumen acts as a fluid reserve, it is likely that water would pass from the rumen into the intestines for absorption into the blood. As water from the intestines is lost into the blood, a high water concentration gradient between the rumen and the intestines is created. Suction power for water from the intestines would become high resulting in an increased flow of fluid through the rumen into the intestines [90]. Most studies have reported contradictory results to those of Chaiyabutr et al. [90] on the effect of high temperature on fluid passage rates, thus making this appear as a special adaptation strategy of Swamp buffalo (*Bubalus bubalis*). Further research is needed to prove this theory.

Warren et al. [96] observed increased levels of water intake with increasing ambient temperature. A study by Waybright and Varga [97] showed increased fluid passage rates of up to 64% in water-infused rumen. Tactile stimulation of the distended rumen wall triggers relaxation of the reticulo-omasal orifice and contraction of the rumen wall resulting in rapid flow and passage of fluid and particulate matter through the rumen [98]. Studies by Warren et al.

Environmental temperature	26°C	41°C
Rate of flow (l/h)	1.82	3.12
Rumen retention time (h)	18.7	13.5
k_1 (per hour)	0.06	0.086
Blood volume (ml/kg)	63.95	68.08
Plasma volume (ml/kg)	47.45	50.83

k_1 , fractional passage rate. Adapted from Ref. [90].

Table 2. Effect of heat stress on blood volume, plasma volume and fluid passage rate through the rumen of Swamp buffalo.

[96] stated that mean retention time was directly related to or affected by ambient temperature rather than feed intake as influenced by temperature. Desert species are expected to have faster rates of passage compared to species of similar rumen physiology from temperate regions [28]. The study by Warren et al. [96] used Holstein cattle which are adapted to temperate climates; hence, it is expected that a temperate breed would respond to high ambient temperatures of above 32°C to a great extent. Ruminants that are well adapted to high ambient temperatures in tropical and sub-tropical climates may respond to temperatures of 32°C and above in a different way and probably to a lesser extent when compared to temperate breeds. A change in passage rate as a result of fluctuations in ambient temperature is very high, and the direction of change is unpredictable necessitating more research on the subject. Research needs to focus on the effects of differences in thermal resistance and/or thermal tolerance levels on passage rates in ruminant animals in the tropical regions. These suggest that studies need to consider season and place of study to index ambient temperature when modelling liquid passage rate to take into account the future effects of global warming on digesta passage kinetics. The research needs to consider accounting for the effect of ambient temperature on passage rate.

3.5. Stage of reproductive cycle and physiological state

The reproductive cycle can be subdivided into the lactational and non-lactational period, pregnancy stage, non-pregnancy stage and the number of days in gestation. During the productive cycle, animals undergo structural and functional changes during gestation and lactation [99]. Behavioural changes like loss or gain of appetite and increased or decreased water intake may be observed during these stages [100]. Rate of passage of liquid and solid material through the rumen may be altered by these changes. Gunter et al. [101] showed that rates of particulate and liquid passage through the rumen were higher for pregnant than non-pregnant animals, higher in lactating animals than their non-lactating counterparts, but lower during the late than the early stages in gestation (**Tables 3 and 4**). Helander et al. [102] suggested that different fractional solid and liquid passage rates should be used when formulating diets for pregnant and lactating ruminants.

During pregnancy, nutrient requirements for pregnant animals are higher than for non-pregnant animals [30]. This is due to high demand for protein and energy used for foetal growth [103] and development. Rumen fluid contains dissolved protein [104], short-chain fatty acids [105] and microbial protein. Because of increased demand for the above mentioned nutrients, an increase in rates of passage of fluid through the rumen is observed as a physiological response to meet the increased demand for nutrients in pregnant animals [100].

During the lactation period, there is high demand for water [101, 106], minerals and soluble protein for the process of milk production [30, 106]. All nutrients for milk synthesis are absorbed across foregut walls and small intestines into the blood stream for transportation to the mammary gland. Rumen fluid serves as a water reservoir in ruminants and contains dissolved minerals and soluble proteins [8]. High demand for water in the lower intestines may result in mobilisation of water stored in the rumen. Hence, ruminal fluid passes out of the rumen at a faster rate to meet animal's requirements for water and minerals for milk

Phase	Parameter	Lactating	Non-lactating	Non-pregnant	Pregnant
Liquid	Outflow rate (l/h)	0.7	0.5	0.4	0.5
Liquid	Rate of passage (%/h)	11.1	8.1	10.9	13.9
Liquid	Turnover (h)	9.3	12.7	9.5	7.5
Liquid	Rumen volume (l/kg BW)	0.07	0.08	0.05	0.04
Solid	Rate of passage (%/h)	4.6	4.3	4.9	6.8
Solid	Gut fill (g/kg BW)	5.7	7.7	6.8	4.8
Solid	Mean retention time (h)	26.6	27.9	24.4	18.1

Adapted from Ref. [101].

Table 3. Gut fill levels, and rumen liquid and solid passage rates in pregnant, non-pregnant, lactating, and non-lactating ewes.

	Parameter	Phase	d 102 gestation	d 118 gestation	d 132 gestation
Non-pregnant	Gut fill (g/kg BW)	Solid	5.6	3.8	5.0
Pregnant	Gut fill (g/kg BW)	Solid	6.1	6.6	7.7
	Outflow rate (l/h)	Liquid	0.6	0.4	0.5

Adapted from Ref. [101].

Table 4. Influence of gestation stage on rumen fill levels and fluid outflow rate in ewes.

production. When an animal is non-lactating, there is no demand in water for milk production; thus, the rate of passage of liquid through the rumen is much lower than in lactation. This is in accordance to Chaiyabutr et al.'s [90] theory that increased water demand in the lower gut might result in increased movement of water out of the rumen to meet demand in the lower tract (see Section 3.4). Consequently, the authors [102, 107] observed increases in dry matter intakes of about 20–30% from pregnancy to early lactation, which explains higher rates of liquid and solid passage through the rumen during lactation than during pregnancy [101, 108]. Work on sheep revealed increased rumen fluid volume of 15% during lactation compared to fluid volume at pregnancy [109] supporting the theory of increased water demand during lactation. Contrary to these findings, Hartnell and Satter [110] showed 10%/h higher fluid dilution rates for grazing non-lactating than lactating cows fed silage, suggesting the necessity of more data on the subject. Hence, investigations of effects of interaction between lactation and/or non-lactation period and diet type on dilution rate need to be done.

The rumen and pregnant uterus are in close proximity in the abdominal cavity [109]. It is therefore common sense to assume that as a foetus increases in size there is likelihood that it exerts a pressure on the ruminal wall [76, 99]. This pressure may at least squeeze the rumen thus forcing out some liquid and solid particles with a much greater rate than prior to pregnancy. Increased occupation of abdominal cavity space by growing foetus in pregnant ruminants may have an overall effect depressing total rumen volume. Rumen fill would

be expected to decrease exponentially in pregnant cows as pregnancy progresses. Dairy cows in early lactation have shown increased incapability of consuming enough feed to meet daily requirements for energy. To a certain extent, diminished rumen volume as a result of squeezing from growing foetus causes a reduction in available space for the rumen to expand in anticipation of increased feed intake. Hence, reduction of rumen fill is a result of pregnancy, due to a decrease in rumen volume. Forbes [111] reported an approximate decrease of 0.39 l/l in volume of ruminal contents as pregnancy progressed in sheep fed on hay. However, Kaske and Groth [109] observed increased rumen fill levels from mid pregnancy (60–80 days post conception) to lactation (35–55 days postpartum) with fill levels of 0.946 and 1.444 kg DM, respectively, in ewes. Percentage dry matter content of digesta increased modestly, mean retention times of liquid and small solid digesta reduced by 20–30% at late pregnancy compared to mid pregnancy, with fluid passage rates being approximately three times faster than small solids in sheep [109]. Fluid outflow rate through the rumen increased by 20–36% between late pregnancy and lactation [109]. Generally, rumen fill levels are expected to decrease with an increase in passage rates of solid and liquid digesta. Progressive increments in rumen fill levels in the course from mid pregnancy to lactation were suggested to be due to a gradual reduction in sensitivity of mechanoreceptors on the rumen wall [112]. Such findings may suggest that reticulorumen volumes during various stages of the reproductive cycle may not depend on availability of space in the abdominal cavity alone. They may depend on numerous factors such as diet quality and nervous system response.

Time spent eating and the number of eating sessions were higher during pregnancy than lactation in ewes [102]. Similarly, Kaske and Groth [109] showed a 19% increase in chewing frequency from mid-pregnancy to lactation in sheep. Duration of eating periods and perhaps increase in chewing times may have some effect on rates of liquid and solid passage through the rumen. Oshita et al. [25] showed higher fractional rates of liquid passage through the rumen in non-lactating cows grazed on rangeland (13.95%/h) than those fed fodder ad libitum in stalls (9.4%/h). Animals that graze on rangelands spend more time chewing and eating than those confined to pens [25, 53]. Cows have a greater frequency of rumen contractions during eating than during both rumination and rest [67]. Processes of chewing and rumination stimulated rapid movement of material from the rumen into the reticulum [79] compared to resting. Typical values for frequency of rumen contractions are 1.4/min at rest, 2.3/min during ruminating and 2.8/min during grazing [113] for cattle. It is therefore assumed that frequency of rumen contractions in goats and sheep is not documented. The greater the number of ruminal contractions the greater the fractional rate of liquid and solid passage through the rumen [67]. Thus, animals that spend more time grazing on rangelands have faster fluid and particulate passage rates through the rumen than stall-fed animals. Okine and Mathison [67] concluded that the major determinant of digesta flow through the rumen is a result of reticular contractions. Distension of reticulorumen wall would stimulate an increase in rumen contractions. Fractional passage rate of NDF out of the rumen increased by about 34% as a result of increased rumen contractions [114]. One may tend to wonder the true effect of NDF on rumen fill. Earlier discussions pointed out that high NDF content is associated with increased rumen fill levels.

From an angle associated with reticulorumen contractions, fibre or NDF is a major contributor to increased tactile stimulation of the rumen wall. It may be argued that high levels of NDF

in the rumen would increase the intensity and frequency of rumen contractions through tactile stimulation of the rumen wall. This would result to increased passage of digesta out of the rumen with an overall effect of reducing rumen fill.

So far, a general trend in results showed higher fluid and solid passage rates in lactating than non-lactating ruminants. However, contrary effects have been reported. Oshita et al. [25] observed 10%/h higher fractional passage rates for fluids in non-lactating than lactating cows when fed off silage. These results raise a question on effects of diet and lactation and diet and non-lactation interactions on rates of passage. Further research is needed to cover the gap in knowledge on these observations.

3.6. Particle size and functional specific gravity

Particulate matter is discriminated from moving out of the rumen at two major points in the gut, which are at the dorsal rumen and at the reticulo-omasal orifice [79] because of particle size and functional specific gravity. The likelihood of particles escaping from the rumen is strongly determined by particle size and density [21]. These two factors are inversely related when fermentation has not occurred [115], but in the course of fermentation, Lirette and Milligan [116] observed a negative curvilinear relationship between functional specific gravity and particle size. Various work on effects of particle size and FSG on passage rate have reported similar findings. Allen and Mertens [117] suggested the passage of particulate matter depended on how much particles were present near the reticulo-omasal orifice during the second contraction of the rumen, suggesting that passage rate of solids depended on density. Functional specific gravity of a particle is defined as a physical measure of the weight of a given volume of a particle in the rumen relative to the same volume of fluid in the rumen [8]. The functional specific gravity is determined mainly from the chemical makeup of the lignocellulosic matrix [118]. Lechner-Doll et al. [21] showed a negative correlation between particle density and mean retention time in the rumen. Before fermentation occurs, a solid particle is intact and tends to be heavy (high functional specific gravity) enough to sink to the bottom of the rumen, close to the ventral part of the rumen where its chances of moving out of the rumen through the reticulorumen orifice is increased. So, at this point, movement is only prevented by particle size. Hence, particles tend to have differential passage rate, where it tends to be higher for unfermented particles.

In the course of fermentation after the lag phase (colonisation of feed particles by bacteria), gas is produced from and stays within feed particles [79]. Gas production within particles increases buoyancy of large particles, and as a result, particles tend to float and become entrapped in the floating fibre mat. Probability that these trapped particles are cleared from the rumen through passage is reduced as they would remain trapped until fermentation is completed. Thus, the rate of passage is slow for particles undergoing fermentation. Overall, high fermentation rate may depress the functional specific gravity through increased buoyancy thus reducing the rates of passage. Smith et al. [119] showed that grasses containing higher levels of fermentable organic matter than legumes had much higher retention times in the rumen as a result of increased susceptibility of being trapped in the floating fibre mat. This supports a phenomenon whereby slower passage rates are associated with high

fermentation rates and proportion of degradable matter. Thus, Rinne et al. [78] found that clearance of digestible plant cell wall fractions of particulate matter was slower than indigestible matter. Bayat et al. [120] also showed faster passage rates for indigestible neutral detergent fibre compared to that of potentially degradable neutral detergent fibre of a smaller particle size (**Table 5**).

Although increased reticulorumen contractions have been shown to increase passage rates of both solid and liquid through the rumen, this may directly apply to fermenting solid material because of variable functional specific gravity. The authors [98, 118] suggested that increasing the intensity of rumen contractions actually decreases the rate of passage of particles with low specific gravity from the rumen because contractions propel particles further away from the exit point, the reticulorumen orifice, before it even opens. Inferences on the effect of reticulorumen contractions on passage rate should be specific on which fraction of solid matter and on the value of specific gravity.

Particle size	Parameter	Grass		Red clover	
		Early	Late	Early	Late
Rumen digesta (kg)					
Large	iNDF	0.88	0.97	1.59	2.36
Large	pdNDF	3.20	3.37	1.83	1.68
Small	iNDF	1.16	1.41	1.36	2.41
Small	pdNDF	2.34	2.61	1.36	1.46
Mean retention time (h)					
Large	iNDF	28.7	24.3	49.8	37.6
Large	pdNDF	13.9	14.8	13.4	11.0
Small	iNDF	23.8	24.6	29.0	29.8
Small	pdNDF	15.2	14.9	17.9	16.2
Potentially degradable NDF					
Large	k_p	0.0034	0.0038	0.0041	0.0039
Small	k_p	0.0280	0.0271	0.0242	0.0252
Indigestible NDF					
Large	k_p	0.0050	0.0062	0.0046	0.0049
Small	k_p	0.0428	0.0424	0.0356	0.0343

iNDF, indigestible neutral detergent fibre; pdNDF, potentially degradable neutral detergent fibre; k_p , fractional passage rate of particulate matter. Adapted from Ref. [120].

Table 5. Effects of particle size and digestibility on mean retention time, rumen fill levels and rates of passage in the rumen.

The theory of the ability of particles to sink (sedimentation) and/or float (stratification) in the rumen resulting in passage out and/or entrapment in the rumen may be true for species of ruminants (grazers) where stratification occurs. There is overwhelming evidence that stratification does not occur in the rumen of browsing ruminants [3]. Passage of particles out of the rumen in browsers is by mass flow, determined by abundance of digesta in the rumen and is normally a function of the occurrence of reticulorumen contractions [4]. Reticulorumen contractions are one of the most important factors that lead to passage of digesta out of the rumen. More studies have to be done to clarify why browsers characterised by lower occurrences of rumen contractions may have faster passage rates of digesta compared to grazers. The authors [21, 121] suggested that lack of stratification was responsible and strongly linked to reduced particle retention times in the rumen of browsing ruminants. It is suggested that particulate matter in browsing ruminants flows out of the rumen at a rate that is proportional to fluid flow rate. It thus remains to be determined how and to what extent passage rates of fluid affect passage of small solids and vice-versa. Thus far, the selectivity factor (SF) is the only proposed measure of the relationship between mean retention times (passage rates) of solid and liquid particles in the rumen ($SF = MRT \text{ particles} \div MRT \text{ liquid}$). SF quotient values are used to describe ruminant ecological differences and find application in classification of ruminants into different feeding types [4]. Given that rumen retention time is a function of roughage quality, SF may be used to describe physiological differences in the degree of adaptation of ruminants to different roughage qualities. Nsahlai et al. [122] proposed a relationship that took the form: $kl = (k_p - 0.0018) \div 0.360$. Both these relationships are mathematical in nature and do not give the clear biological relationships between passage rates of the two phases of rumen digesta. Given that both liquid and solid digesta phases exist intermingled together in the rumen, studies need to consider developing passage rate models that can be used to predict passage rates for both phases using one model.

Reduction in size of large particles of feed is a prerequisite for particulate flow out of the rumen via the reticulo-omasal orifice and may be an important determinant of rumen fills [6]. Particle size reduction occurs during rumination or rechewing of previously swallowed feed [91]. The authors [123, 124] showed that resistance to particulate flow through the rumen increases with an increase in particle size. The rate of passage of particulate matter is inversely related to particle size [79]. There is, therefore, a critical size that particle should reach for them to pass out of the rumen via the reticulo-omasal orifice [21]. There are suggestions that critical particle size ranges from 1 to 4 mm [21, 123]. Small dense particles tend to fall into the ventral rumen just close to the reticulorumen orifice [125].

These small particles are capable of passing out of the rumen at the occurrence of the reticular contractions [126] because they would have reached a size that permits passage. Large particles that have a high density are prevented from passing out of the rumen [127] because of sedimentation of these particles at the bottom of the rumen [128]. These particles would still be large and hence are unlikely to pass out of the rumen. The theory of critical particle size as a prerequisite for particulate passage out of the rumen may be questionable because larger particles than this are prevalent in faeces. The authors [129, 130] showed that reticulorumen contractions were accompanied by drastic increases in outflow of solid particles termed

to be large particles (particles greater than 5 mm). McBride et al. [131] argued on how the so-called large particles are prevented from leaving the rumen yet the diameter of the reticulo-rumen orifice opening of 35 mm [132] is sevenfold greater than the critical particle size. Kaske et al. [128] revealed that when sedimentation was prevented in the rumen of sheep, outflow of 10-mm-sized particles was 40% of the outflow of 1-mm-sized particle, which shows that a great fraction of large particles do leave the rumen. An argument that can be raised is whether or not particle size is an important factor that leads to increased mean retention times in the rumen or it is the effectiveness of the floating mat in entrapment and sedimentation of large particles that determine passage rates to a greater extent than particle size.

Rates and extents to which solid particle size may be reduced depend on fragility of particles. Now, inclusion of particle fragility as a factor that influences passage rate and ultimately rumen fill opens a new dimension to the current discussion. As noted earlier, high chewing frequencies have an overall effect of increasing passage rates through stimulation of reticular contractions. Chewing also reduces time for particle size reduction ensuring that particles reach a critical size that allows them to pass through the reticulo-omasal orifice swiftly. It can be hypothesised that highly fragile particles pass out of the rumen much faster than less brittle particles. This may be supported by the fact that brittle particles take a much shorter time to undergo particle size reduction, and thus would have a shorter retention time in the floating mat than less fragile particles. This gives more fragile particles a faster passage rate than less fragile particles. Egan and Doyle [80] explained a faster passage rate of indigestible fibre components such as lignin using this phenomenon. Taking a closer look at possible causes of particle fragility, a contrary effect of fragility on passage rate is developed. Increased fragility of plant fibre is caused by high lignin content. As a result, degradation rate of high lignin containing particles is reduced, hence more time is required by microbes to colonise and ferment digestible components of fibre. This would result in increased retention times of high lignin particles in the rumen for efficient fermentation. Hence, these particles are likely to be retained for a much longer time in the floating raft. This phenomenon may be aggravated when there are large-sized particles with high lignin content, whereby particles would be restricted by size from flowing out through reticulo-omasal orifice, resulting to reduced passage rates.

4. Are goats different in passage rates compared to other ruminants?

4.1. Background discussion

Generally, rates of passage of solid digesta are greatly dependent on the quality of diets ruminants consume. Botanical and nutritional compositional preference of plant feed sources in ruminants varies greatly. Although goats are classified as intermediate feeders [18], they are selective feeders. Goats demonstrate their botanical wisdom through a mastery of selecting high-quality leafy parts on shrubs, trees and grass stalks that are of higher protein and lower cellulose contents compared to sheep and cattle. This wisdom allows goats to specifically select diets that are able to provide enough net energy and protein to meet their requirements for maintenance for which sheep seem to fail to achieve [133]. This implies that total

tract digestibility and degradation rates of diets eaten by goats should be higher than diets eaten by sheep [36]. Degradation rates of diets consumed by goats were higher than diets consumed by sheep [133], ensuring that goats maintain high intake levels to meet energy requirements (**Table 6**). Goats will spend more time eating per unit lucerne hay compared to sheep, due to their selective feeding behaviour [134]. This mastery in the art of selection of high quality feeds is well documented in goats [36, 134–136] and is proposed to be one of the major reasons why goats have faster digesta passage rates than sheep and cattle. The art of botanical feed selection and preference differs between ruminants, with implications in differential passage rates in ruminants. Consequently, browsing ruminants have shorter mean retention times for liquid and solid digesta in the rumen compared to grazers largely because of increased diet quality.

Feed residues obtained from troughs used for feeding goats had high crude protein and low NDF content compared to those obtained from sheep [36, 134, 137]. These results may be interpreted in two ways. Firstly, it may be that goats select for low crude protein content and high NDF in feeds compared to sheep. However, sheep select plant feed materials of high cell wall content when compared to goats on pasture [133]. Goat selection for diets with low crude protein seems to be a phenomenon common to trough-fed goats. Secondly, the use of residues left behind after feeding and trough feeding of goats and sheep do not give clear results on diet and/or feed selection in these two ruminant species. Differential feeding behaviours occur in trough-fed goats and sheep. When fed from troughs, goats eat feed from top to bottom, whereas sheep eat from bottom to top. High crude protein and low NDF feed particles are finer than low crude protein and high NDF feed particles and are found at the bottom of feed troughs [36]. This implies that goats fed using feed troughs are more likely to consume low crude protein and high NDF diets. Differences in diet selection between goats and sheep fed through feeding troughs warrant more research.

	Proportions (%)					
	I		II		III	
	Goats	Sheep	Goats	Sheep	Goats	Sheep
Grass	78	80.5	76.5	76.5	80.5	78.5
Shrubs	8	8.5	23.5	23.5	17	19.5
Trees	14	11	0	0	2.5	2
c (per h)	0.038	0.038	0.089	0.068	0.063	0.053
	NDF consumed (g NDF/kg DM)		Digestibility of DM		Digestibility of NDF	
L	662	658	0.495	0.524	0.471	0.521
M	677	671	0.475	0.522	0.466	0.533
S	660	656	0.480	0.493	0.446	0.475

I, April to May; II, May to June; III, June to July; L, long staple length; M, medium staple length; S, short staple length. Adapted from Refs. [36, 133].

Table 6. Botanical and chemical compositional characterisation of diets consumed by goat and sheep.

Botanical variation in diets consumed by goats and other ruminants are wide (Tables 6 and 7) and dependent on seasonal availability of different classes and types of feeds in each climatic region. Although predominantly grazers, cattle consumed diets that contained 84 and 48% woody plants in the late wet season and early dry season [139]. Number of plants selected by goats and sheep (25 plants) grazing in a semiarid thornbush savannah were similar, but lower in cattle (10 plants). While total eating time was evenly shared between monocotyledonous and dicotyledonous plants in sheep across all seasons, cattle tend to select monocotyledonous plants (90% of total eating time) and goats consistently selected dicotyledonous plants (82% of total eating time) [136]. Sheep diets contained lower lignin levels in the wet season compared to goats due to selection against browse by sheep [138].

The question on whether goats have faster passage rates than sheep, cattle and other ruminants by virtue that they select less of fibrous plant material is debatable. Generally, goats had faster passage rate than sheep (0.069 vs. 0.033/h when fed as a group; 0.054 vs. 0.029/h when fed individually) when fed formulated diets meeting requirements for maintenance and lactation [140]. Other workers have reported faster passage rates of solid digesta [36, 133, 140–142], slower passage rates [143] and similar passage rates [27] in goats compared to sheep fed on the same diets. Schlecht et al. [142] observed faster passage rates in goats than cattle fed on the same diet (0.042 vs. 0.033/h when fed on bush hay; 0.053 vs. 0.042/h when fed on green feed).

Discussions on differences in passage rates between ruminant feeding types and species that do not consider effects of factors influencing digesta passage rates highlighted here lack descriptive and explanatory power. Given the large number of factors implicated in differential passage rates among goats and other ruminants, a digesta passage rate modelling exercise was used to test the null hypothesis that passage rates in goats are not different from other ruminants (grazers: cattle, sheep, buffalo, antelopes, mouflons, muskoxen, nilgai, blackbucks; browsers: moose, okapi, deer's, dik-dik, duikers; intermediate feeders: goats, anoa, reindeer, gazelles and ibex).

4.2. Methodology

Data were collected from studies that reported at least average values or ranges for body weights of animals used, measured fractional passage rates and/or mean retention times in the reticulo-rumen. A dataset was created bearing passage rates from wild and domesticated ruminants. Factors that affect passage rates were identified in each of these studies and included animal and feed factors. Quantification of factors that affected passage rates are described in [144]. Process models developed as part of this study have been deposited into the Repository of Intelligent Models (REDIM) with accession number PRDA001762 and PRCN001814 for the estimation of solid and liquid passage rate, respectively, as indicated at <http://www.redim.org.za/?search=PRDA001762> and <http://www.redim.org.za/?search=PRCN001814>.

	Crude protein consumed (g/kg DM)				Proportions (%)	
	Cattle	Sheep	Goats		Goats	Sheep
DS	45 ± 5	100 ± 10	125 ± 15	Grass	5.3	14.2
INT	70 ± 10	115 ± 15	125 ± 15	Browse	45.3	40.2
GS	110 ± 10	175 ± 25	195 ± 15	Forbes	44.1	41.5

DS, dry season; INT, intermediate season; GS, green season. Adapted from Refs. [136, 138].

Table 7. Botanical and crude protein of diets consumed by cattle, sheep and goats in different seasons.

4.3. Results

After correcting for variation in 17 (liquid passage) and 23 (solid passage) factors that affect passage rates in the model, predicted solid and liquid passage rates for goats lay near the ideal prediction line and generally embedded with other ruminant feeding types (Figures 2 and 3).

This sparse distribution and entanglement of passage rates for goats within that of other ruminants strengthen the view that goats cannot be easily distinguished from other ruminants based on digesta passage rates; so, differences between goats and other ruminants are largely due to variation in diet quality.

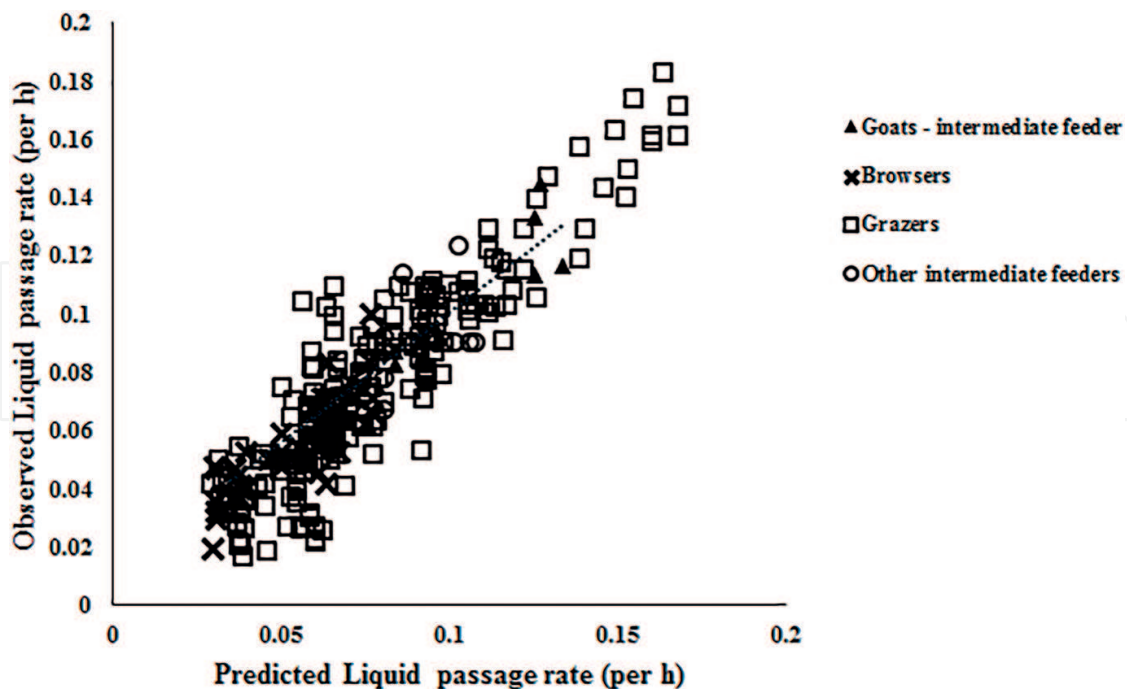


Figure 2. Relationship between observed and predicted liquid passage rates for goats and other ruminant feeding types.

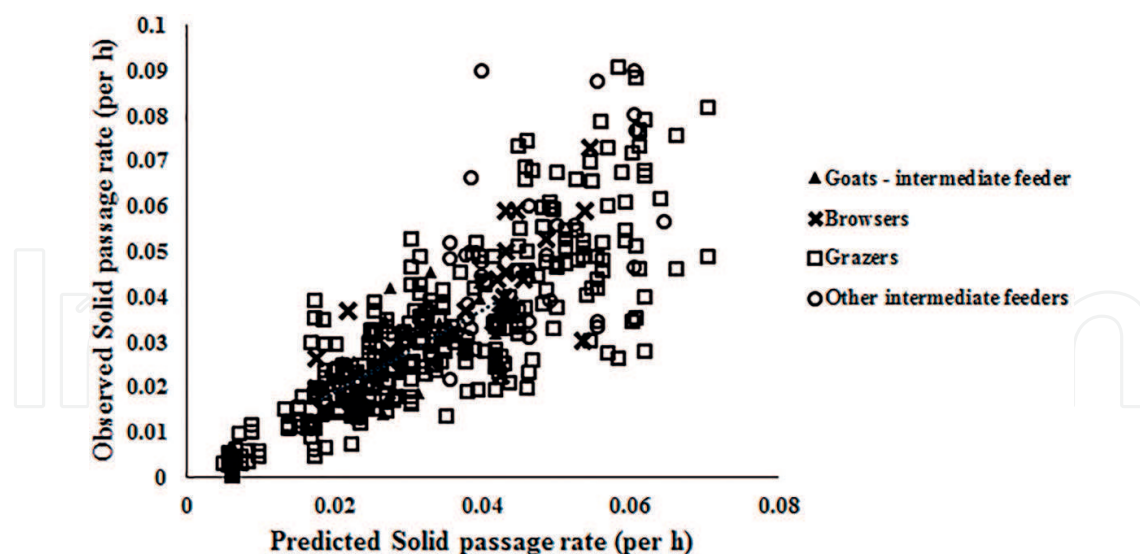


Figure 3. Relationship between observed and predicted solid passage rates for goats and other ruminant feeding types.

5. Summary

Countless factors influence passage rates. Research has not considered effects of various combinations of factors on rates of passage of solid and fluid through the rumen. Mathematical models that seek to accurately predict passage rates, rumen fill levels and ultimately roughage intake should increase understanding of why part of the variation is not explained.

Animal and feed compositional attributes are the major factors to be included into passage rate prediction models. The role of animal physiology in influencing digesta passage rate is critical. Accounting for the influence of various physiological changes in ruminants, feeding level, stage of pregnancy and lactation, and growth in passage rate models can be done by computation of the feeding level based on total net energy requirements relative to net energy requirement for maintenance (animal production level, APL). It is evident that there are still discrepancies on how ambient temperature and particle density (buoyancy) affect the passage rate of digesta in the rumen. Indexing for buoyancy in solid passage rate, prediction models would likely involve determination of the extent of degradability of a particle taking into account the time available for digestion.

6. Conclusion

After correcting for variation in factors that affect solid and liquid passage rates, goats are not different from other ruminants with respect to passage rates suggesting differences between goats and other ruminants are largely due to dietary quality. More studies should be carried to ascertain the dynamics of digesta kinetics after meal termination in goats.

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