Chapter

THE INFLUENCE OF ORAL ENVIRONMENT ON DIET CHOICES IN GOATS: A FOCUS ON SALIVA PROTEIN COMPOSITION

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ABSTRACT

There is ample evidence that ruminants are capable of making choices between different foods that provide a more balanced diet that would be obtained by eating at random. In the particular case of goats, they occupy a diversity of habitats and different breeds present variability of feeding behaviors resultant from adaptations to the existent plant species. In their food search activity, individuals are faced with variable amounts of plant secondary metabolites (PSMs), which may present some toxic and anti-nutritional effects depending on the individual's ability to deal with it.

The oral cavity has a key role in the recognition and decision processes of ingestion or rejection. In this chapter we will first consider how goats identify foods and behave according to the food items available. Focus will be done on the importance of taste sense in this process and the information available on the main structures involved in taste detection and perception in goats will be reviewed. In a second section we will focus on the characteristics of goat's saliva, particularly in terms of their protein composition, presenting results obtained by our research team.

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INTRODUCTION

Goats (*Capra hircus*) were domesticated around 7000 BC (Mason, 1981) and are present in different ecosystems but in higher number in the tropics, dry zones and developing countries (96% of the world goat population) (FAOSTAT, 2009). Goats are valued for the ability to exploit land of low productivity and marginal areas, as well as for their low cost and low labor management. This is an important husbandry species worldwide, which trough time has been subjected to trait selection and breed differentiation (Galal, 2005). Actually 880 million goats, belonging to 570 different breeds are distributes worldwile (Dubeuf and Boyazoglu, 2009). This high biodiversity results in high variability in feed availability and consequently in feeding strategies adopted.

Goats are characterized by their selective behavior. In normal conditions they graze or browse selectively, whereas in more stringent conditions of food availability they can be heavy browsers of trees and shrubs, and even consume foods that otherwise they would reject (Animut et al., 2005). Nitrogen content in vegetation plays a key role in nutrition and diet selection, since nitrogen is a limiting element for herbivores (Tipler et al., 2002). On the other hand, plant secondary metabolites, such as tannins, can be potentially toxic and/or anti-nutritive (being the intensity of the negative effects dependent on the defense mechanisms animals possess), resulting in avoidance of the plants presenting higher levels of these compounds (Provenza et al., 1992).

The ability to select and make the more suitable choices will depend on the capacity of goats to detect feed characteristics. The oral cavity has a key role in this process of recognition and in the decision of ingestion or rejection. On one hand, through taste receptor located in the mouth, animals may perceive some food characteristics. As such, the sensitivity for each class of taste is crucial. Basic tastes are usually associated to the level of particular food constituents and usually result in an innate response of acceptance or rejection. For example, sweet and umami taste appears to be characteristic of nutritious diets, being linked to the presence of carbohydrates and proteins, respectively. Inversely, bitter and sour tastes are associated to toxic or spoiled foods. On the other hand, saliva present in the oral cavity may also be determinant in dietary choices. This fluid characteristics influence oral medium and consequently may affect the way food is perceived. It may interact with food constituents altering their sensorial characteristics, both taste and mechanical sensations. One example of this last situation is the precipitation of polyphenolic compounds by particular salivary proteins, resulting in astringency perception.

Consequently, the particular characteristics of goats oral cavity, like in the other animal species, influence dietary habits and a comprehension of them may help to understand why these animals are able to select food that other species reject. In the present chapter we will focus on the oral characteristics of goats that may contribute to their characteristic feeding behavior, with focus on taste function and saliva. We will start for reviewing the characteristics of goats feeding behavior and after that the importance of both taste and saliva on this behavior will be critically discussed.

GRAZING BEHAVIOR AND DIETARY CHOICES

According to Hofmann classification of ungulates goats belong to the intermediate feeding type. This means they will both graze and browse depending on food quality and availability (Hofmann, 1989).

Domestic goat (*Capra hircus*) is a specie greatly found in different ecosystems and whose feed strategies usually have an impact on vegetation (Papanastasis and Peter, 1998; Perevolotsky et al., 1998). However, in contrast to their negative image, concerning the effect on plant biodiversity, goats are also considered as useful biological agents of woody plant control (O'Connor, 1996), due to their particular dietary choices.

Although goats have a high capacity to adapt to diet conditions available [i.e. they depend heavily on plant availability (Barroso et al., 1995)], one of their ingestive characteristics is their very efficient selective behavior, picking some plants or plant parts, whereas others are totally or partially rejected. This allows these animals to improve the nutritive value of total ingesta. In general, they prefer nutritious food and avoid foods with low nutrient content or high levels of toxic/antinutritive compounds (Bryant et al., 1991; Provenza et al., 1992). Goats in temperate climates, where foraging availabilities are relatively equilibrated and nutritiously uniform, may behave similarly to other domestic ruminants (e.g. sheep and cattle), having no need of special selective skills for high-quality diet. However, in harsh environments, this specie has the ability to thrive better.

The influence of plant species available on goats diet selection pattern was observed in animals living in different environments, namely in zones of high plant diversity (Hendricks et al., 2002), Mediterranean arid scrublands (Barroso et al., 1995) or semi-arid savannas (Dziba et al., 2003). In harsh environments browse is clearly a major component of the diets (Pawelek et al., 2008). In such conditions, goats are able to utilize the scanty shrubby resources, selecting the more nutritive parts and converting them in a useful product. Browse species are more important for these ruminants production during dry season when herbaceous species have a poor quality and have limited biomass (Abdulrazak et al., 2000). The plant parts usually chose as feed include leaves, tender shoots or twigs, fruits, pods and seeds (Aganga and Tshwenyane, 2003).

The grazing characteristics of goats are different from other grazing ruminants not only in the type of plant and plant parts choose, but also in the way they bite. Whereas sheep show a tendency to penetrate into the canopy to take deep bites on legumes, goats appear to graze from the top downwards. Physically it might be because goats are less able to exert the force necessary to graze lower down into swards. Sheep usually had greater bite weight and larger bite volume than goats when grazing vegetative and reproductive legume swards (Animut and Goetsch, 2008). Goats showed a greater disposition to graze all accessible components of reproductive swards, especially reproductive grasses. However, the goat ingestion profile changes seasonally, according to the type of feed available. The highest bite rates appear to be achieved during the dry season, comparatively to wet season (Yayneshet et al., 2008). It was tentatively explained to result from the low availability of forage existent during the dry season, what could result in an increase the bite sizes.

Selection by goats between diverse plant species (Dziba et al., 2003) or between individuals of the same plant species (Riddle et al., 1996) is greatly performed according to plant nutritional quality or the concentration of chemical defenses. These animals feeding behavior adapts to food physical and chemical characteristics (du Toit et al., 1991; Provenza et al., 1992; Villalba and Provenza, 2000). One of the drawbacks of browse species is their relatively high content of defense mechanisms against herbivory. Among there are structural factors, such as the presence of morphological structures (e.g. spines, thorns and prickles), which limit the access to animals, and the fiber content (e.g. cellulose, hemicellulose and lignin). Although structural factors are not associated with animal intoxication, they reduce forage intake (Shipley et al., 1998), digestibility (Edwards and Ulrey, 1999), or both, and consequently animal performance is adversely influenced. One of the goats physical characteristics that allow them to select plants and plant parts, even with these structural defense characteristics, concerns their mobile lips and precise tongue movement. This makes possible to take only the fragments of interest, leaving the unchosen ones and allows the selection of nutritious materials even from low accessible sites (Illius et al., 1999).

Besides these structural defense mechanisms, plants (and principally browse) possess a wide variety of chemicals, which function as feeding deterrents, reducing forage value by being antinutitive and/or toxic and resulting in sickness and even deaths. These plant secondary metabolites (PSMs) have a negative impact on the fundamental biochemical processes (e.g. survival and growth) and on the selective behavior of herbivores. Despite the high number of existing PSMs (e.g. alkaloids, essences, terpenes), tannins constitute one of the most important groups. Tannins are mainly found in woody species and probably have the largest influence on the nutritive value of browse as forage (Reed, 1995). Tannins are commonly divided into two groups: hydrolysable and condensed tannins (Butler et al., 1999). The antinutritive value of browse is mainly attributed to condensed tannins (Reed, 1995). The presence of these PSMs is one of the principal conditioning factor of goat feed choices, although the nutritional fractions (e.g. protein, soluble carbohydrate, fiber) are also frequently connected with palatability (Malachek and Provenza, 1993).

It was observed that goats can tolerate a relatively high intake of tannins and can, therefore, feasibly increase their nutrient intake by ingesting plants with these PSMs for limited periods of time (Provenza et al., 1990). The capacity of ingesting a diet with higher levels of tannins than grazer species has been attributed to the presence of diverse defense mechanisms. For example, the presence of tannin-resistant bacteria in goat rumen, which is capable of clearing tannin-protein complexes, was presented as one of these mechanisms (Brooker et al., 1994). Salivary proteins were also reported as a first line defense mechanism present in species for which regular diets are usually high in tannins. The binding of salivary proteins to plant chemical compounds modulates their oral perception, affecting taste and preferences. This issue will be further on detailed.

TASTE FUNCTION

Taste reception takes place in taste cells, located on papillae, distributed on the dorsal surface of the tongue, soft palate, pharynx, and the upper part of the oesophagus (Lindemann, 2001). Despite the importance of these structures in taste, the sense of smell together with oral tactile sensations (texture of food, temperature and stimulation of pain endings), greatly alter the taste experience (Ginane et al., 2011). The importance of taste lies in the fact that it allows the selection of food based on its constituents, in accord with pleasure (hedonic factors) and with the body tissues' metabolic need for specific substances (homeostatic factors) (Salles et al., 2011). So, by being the sense involved when food are swallowed, taste is fundamental for animals regulating the intake of suitable foods and rejecting the unsuitable ones.

Taste buds are mainly located in papillae. The types, numbers and distribution of papillae in the tongue vary greatly among species. The lingual mucosa of goats, as for other domestic ruminants, exhibits differentiated types of papillae that can have gustatory and mechanical functions. In the tongue of goats, five types of papillae can be found: filiform, large conical, lenticular, fungiform and vallate (Kumar et al., 1998). Among these, fungiform and vallate papillae are the ones with taste perception functions.

The filiform papillae are conical-shaped, with 3-6 pointed projections and 6-8 secondary papillae at the free tip and the base of the dorsal surface of the tongue, respectively. These papillae have only a mechanical function. The large conical papillae have a round base and a blunt tip without any projection, and are found on the torus of the tongue. The lenticular papillae are present in close relation with the vallate papillae, having a wide range of sizes. In fact, two types of lenticular papillae can be distinguished, one with blunt apex and other, more frequent, with pointed apex and pyramidal shape (Kumar et al., 1998) and are characteristic of ruminants. The fungiform papillae are smooth papillae, with a rounded surface, mainly located on the anterior and lateral anterior parts of the tongue. These papillae have a convex shape, raise above the lingual mucosa and are scattered among the filiform papillae, being smaller on the ventral surface than on the dorsal (Kumar et al., 1998). Their number is relatively high, but varying among different species. Even within species fungiform papillae number differs among different individuals. The vallate papillae are the largest tongue papillae and they are usually present in a small number. The vallate papillae are characterized by a papillary groove and an annular pad, and taste buds are present beneath the papillary epithelium. The number of vallate papillae differs among the several animal orders: a reduced number is observed in rodents and some omnivores, a slight increase in man and carnivores and a markedly higher number in herbivores (Table 1).

Table 1. Differences in the number of vallate papilla among different species

Animal specie	Feeding type	Vallate papillae (number)	Reference
Cattle (*Bos taurus*)	Herbivore Ruminant (grazer)	24-30 8-17	Davies et al.,1979 Agungpriyono et al., 1995
Sheep (*Ovis aries*)	Herbivore Ruminant (grazer)	18-24	Agungpriyono et al., 1995
Goat (*Capra hircus*)	Herbivore Ruminant (intermediate)	12-18	Agungpriyono et al., 1995
Lesser mouse deer (*Tragulus javanicus*)	Herbivore Ruminant (browser)	2-5	Agungpriyono et al., 1995
Horse (*Equus caballus*)	Herbivore Monogastric	2-3	Pfeiffer et al., 2000
Pig (*Sus scrofa domesticus*)	Omnivore	1-2	Montavon and Lindstrand, 1991
Man (*Homo sapiens*)	Omnivore	12 7-9	Kobayashi et al., 1994 Jung et al., 2004
Dog (*Canis lupus familiaris*)	Carnivore	4-6	Holland et al., 1989

Cat (*Felis catus*)	Carnivore	7-8	Robinson and Winkles, 1990

Like the other ruminants, goats tongue presents a lingual torus (lingual prominence). This appears to be a characteristic structure which has developed primarily in grass eating animals (Zheng and Kobayashi, 2006).

Taste reception occurs in the taste receptor cells located in the taste buds. Taste stimuli reach the apical end of the taste receptor cell. This interaction results in an afferent signal, which is transmitted to the central nervous system via three cranial nerves [chorda tympani (VII), glossopharyngeal nerve (IX) and vagus nerve (X)].

In terms of taste perception, goats are able to distinguish the five basic taste modalities - bitter, salt, sweet, sour and umami – through their lingual taste receptors (Ginane et al., 2011).

It is thought that taste sense has evolved to allow the recognition of food characteristics, ensuring the choice of a diet suited to body needs and the avoidance of toxic or antinutritive feed. Bitter and sour tastes are often associated to the presence of toxic and spoiled food, respectively. Sweet taste is present in carbohydrate rich foods. Salty taste is associated to the presence of sodium or salts in general. Concerning umami taste, the most common umami taste stimulus is the amino acid L-glutamate, and as such this taste is normally referred as indicating the presence of proteins.

It has been shown that taste perception differs according to animal species, which appears to be related to dietary needs. In herbivores in general, and consequently in ruminants, bitter taste has the particular importance of being associated to the presence of PSMs. Bitter taste receptors belong to the T2Rs superfamily of G protein-coupled receptors. There are diverse T2Rs genes coding for bitter taste receptors, which number is variable according to the animal species. Twelve functional genes were identified in cow versus thirty seven in rats (Shi and Zhang, 2006). This difference among species appears to relate to the variety of toxins usually found in the animal regular diet (Nei et al., 2008). It is possible that ruminants may have developed a low sensitivity (and consequently a high tolerance) for bitter compounds, since they need to accept some bitterness in order of not to limit too much the food ingested. The number of studies about ruminant taste sensitivity is limited, and most derive from behavioral experiments (e.g. Robertson et al., 2006). In general it appears that the sensitivity of ruminants to the basic tastes is in the order bitter>sour>salty>sweet (Goatcher and Church, 1970). However, the taste thresholds (concentration levels of a tastant necessary for being perceived) appear to be lower in cattle than in goats and sheep. Apart from goats having lower taste thresholds than sheep, they can tolerate higher levels of tastants than sheep. These results may be discussed in function of the feeding habits of the different species (Goatcher and Church, 1970; Glendinning, 1994). Cattle and sheep are grazers, whereas goats may behave like grazers or browsers depending on plant availability. Goats may have a diet with high levels of browse, which frequently produce bitter-tasting compounds. If goats encounter bitterness more often than grazer species, it is possible that they are more able to cope with this sensation through physiological mechanisms, among which saliva may have a primordial role.

SALIVARY GLANDS AND SALIVA PROTEOME

Saliva is the liquid that bathes oral cavity, the local of food entrance and in which taste and aroma compounds are released. Moreover, saliva presents constituents that can interact with food components, influencing their perception (Spielman, 1990). As such, it has an important role in food perception and preferences.

Saliva has a major importance for diet adjustment as it serves as physiological buffer against variations between the animal external and internal milieus. It is produced by three pairs of major salivary glands (parotid, submandibular and sublingual) and numerous minor salivary glands, being this classification in “major” and “minor” based on the amount of saliva produced. Apart from the general characteristics, salivary glands are highly diversified structures exhibiting a complex degree of heterogeneity among the different animal species, both in location, development, microstructure and function (Phillips and Tandler, 1996). The vast multiplicity of diet chemical composition can contribute to diversity in salivary glands characteristics and saliva composition. A general conclusion that emerges from the comparative studies performed by Tandler and co-workers (Tandler et al., 1986; 1997; 1998; 2001) is that in mammalian species that have specialized diets, the major salivary glands exhibit differences when compared with relatives that are dietary generalists, presenting evidences that salivary glands are intimately related to dietary characteristics.

The normal composition of ruminant saliva is quite different from the saliva of monogastric animals: it is an isotonic bicarbonate phosphate buffer secreted in large quantities and with a high pH (8,2) (McDougall, 1948). Apart from the general functions described earlier for saliva, in goats, equally to ruminants in general, it has an additional major purpose of maintaining rumen homeostasis, by avoiding high and rapid drops of pH due to ruminal fermentation (McDougall, 1948). The high content of phosphates characteristic of ruminant saliva, besides providing alkalinity, is an additional phosphorus source for rumen bacteria (Breves et al., 1987). A large fraction of whole saliva (about 50-60%) is supplied by the parotid glands. The submandibular glands secrete only about one-eight as much saliva as the parotid gland and most of this saliva is secreted during periods of feeding (Kay, 1960).

Ruminants are known to produce saliva with widely varying volumes and protein concentration, depending upon circumstances, such as if the animal is resting, eating or ruminating. This is due to the different contribution of each gland according to the conditions. Parotid saliva is maximal stimulated at the onset of eating but volume rapidly decline during meal (Carr and Titchen, 1978; Carter and Grovum, 1990; Meot et al., 1997). Eating effects on the parotid gland volume vary both according to the nature of diet consumed and the duration of a meal, inversely to what occurs for submandibular secretion. The amount of parotid saliva produced on a meal of fresh grass is higher than the one produced on a dry food meal, inversely to what occurs with submandibular saliva secretion, for which volumes are higher on dry foods (Carr and Titchen, 1978; Carr, 1984).

Similarly to other ruminants, the structure of parotid gland cells in goats is suggestive of copious secretion of saliva with a low protein concentration (Elewa et al., 2010). Parotid saliva concentrations of about 0,1 mg/mL were observed in these animals (Lamy et al., 2009). The total secretion of saliva per day, in these animals, has been estimated to be 6 to 16 liters (Elewa et al., 2010).

In previous points of this chapter the particularities of goat ingestion have been elucidated. There are a significant variability in goat breeds and habitats that also reflect variability in ingestive behavior and adaptations. Hofmann (1989) related salivary gland size, particularly parotid gland size, with ruminant feeding strategy. Accordingly, the ratio salivary glands weight (with more emphasis to parotid gland/total body weight) was thought to increase with the digestibility of the diet usually consumed, which means that concentrate selectors would have higher salivary glands weight than grazers. In this way, the size of the salivary glands would reflect a functional relationship between the mass of the glands and the composition of the diet. Based on this assumption, goats would be expected to present salivary glands sizes in the between of browsers and grazers.

One explanation for the different sizes in parotid glands is thought to be related to their function of detoxifying PSMs present in feed (Hofmann, 1989). As it was referred before, one of the most important classes of PSMs, in goats' nutrition, are tannins. Parotid glands are considered responsible for the synthesis and secretion of salivary proteins with a high affinity for tannins, being considered as a first line defense against the potential toxic and/or anti-nutritive effects produced by these PSMs. In general, it is greatly reported that animals feeding in a vegetation rich in tannins might develop the competence of producing of such tannin-binding salivary proteins (TBSPs) (Shimada, 2006).

In ruminants it has been suggested the presence of such type of salivary proteins in concentrate selectors or browsers (e.g. deer) and their absence in grazers (e.g. sheep and cattle). Moreover, changes in salivary protein profiles have been observed to be induced by high levels of tannins in diets, even in animal species which do not present TBSPs constitutively in their saliva (Lamy et al., 2011). Since goats are intermediate feeders, whose diets may present considerable levels of tannins, the presence of such a salivary defense mechanism could be a possibility. However, this issue remains controversial.

The induction of TBSPs in response to diets high in tannins, which was observed for laboratory rodents (Mehansho et al., 1985;1987) was also hypothesized for herbivores such as goats (Robbins et al., 1987). However, to our knowledge, an exact identification of such salivary proteins was not performed until now. The high ability to counteract the negative effects of PSMs in tropical tannin-rich plants, by goats, was suggested to be due to the presence of TBSPs in their saliva (Alonso-Diaz et al., 2009; Alonso-Diaz, 2010). It is hypothesized that the presence of such salivary proteins can modify the astringency and post-ingestive effects of tannin-rich plants. Also in favor of the presence of TBSPs, it was reported a relatively richness in proline (6.5%), glutamine (16.5%) and glycine (6.1%) of goat parotid saliva, and an increase in parotid saliva concentration when these animals fed a tannin-rich diet, comparatively to a diet with low levels of these PSMs (Silanikove et al., 1996). By analyzing salivary glands, Vaithiyanathan et al. (2001) also suggested the presence of TBSPs for goats.

However, in some experiments the secretion of TBSPs was not observed. Distel and Provenza (1991) did not find the most well studied type of TBSPs (the Proline-Rich Proteins – PRPs) in goat saliva. Instead, these authors argue that goats can consume amounts of tannins relatively high due to the presence of other different defense mechanisms. Recently, using proteomic techniques, PRPs were also not identified in goat parotid saliva, neither constitutively (Lamy et al., 2008; Lamy et al., 2009), neither when feeding a tannin-enriched diet (Lamy et al., 2011). Coincidently, Hanovice-Ziony et al. (2010) reported the absence of goat salivary proteins that directly bind tannins (either tannic acid or quebracho tannins).

Despite the heterogeneity in reports about salivary defense mechanisms against tannins in goats, changes in parotid salivary proteome induced by tannin ingestion were observed (Lamy et al., 2011), and as such the involvement of saliva in the consumption of tannins, by this specie, may not be discarded. Consumption of quebracho tannins (condensed tannins) resulted in the increase in expression of both the protein cytoplasmic actin 1 and the protein annexin A1. We cannot assure that these proteins act as TBSPs, and in fact they may be only the consequence of an increased salivary gland function, induced by tannins. Nevertheless the role of these salivary proteins in goats tannin ingestion deserves further elucidative studies.

Apart from TBSPs, goat, like the other animal species, present a diversity of salivary proteins (Lamy et al., 2009), and their salivary proteome needs to be deeply studied. Many of the identified proteins are also present in other animal species, but their exact function in goat saliva, and their relation to food perception is not completely elucidated. One of the already referred characteristics of goats is that they seem not reject bitter foods as intensely as other species (Church and Goatcher, 1970). Annexin A1, identified in goat parotid saliva when consuming regular diet (Lamy et al., 2009), and increased after tannin consumption (Lamy et al., 2011) was reported to be increased in human saliva after stimulation with bitter taste (Neyraud et al., 2006). Although its role in bitter taste detection had not been mentioned, it should not be discarded a potential involvement in the bitter perception of tanniniferous plants by goats.

Additionally to the mentioned salivary proteins, many others may be also involved in ingestive behavior and feed choice. For example, the salivary protein anhydrase carbonic VI [which is present in different isoforms in goat saliva (Lamy et al., 2009)], has been linked to taste sensitivity (Tatcher et al., 1998). Other salivary proteins are being studied for their involvement in food perception in humans (Dsamou et al., 2011), and it is to expect that also in animals salivary proteins can modulate food perception and condition feed preference.

In conclusion, saliva modulates the way feed is perceived. Further advances about goat saliva composition might increase the knowledge on how food is perceived by these animals. It is important to highlight that most of the divergence existing in goat saliva composition may be derived from the huge variety of breeds and habitat conditions existent. Goats which live in temperate climates may present considerable differences when compared with goats living in arid or tropical areas. These factors should be taken into consideration when conclusions about the involvement of saliva in goat food intake are to be taken.

CONCLUSION

Goats are small ruminats presenting a great biodiversity. Goats have increased very much in number not because they are more productive than other domestic ruminant species, but because they are adapted to very different conditions, allowing them to have good performances in a variety of habitats with a diversity of feed resources available. The adaptive potential of this specie results from the development of physiologic mechanisms. Among them the oral cavity has a major importance. First, through taste sensitivity and food perception, it is involved in plant selection and in the decision process of ingesting or not. Animals assign a signal value to taste, which allow them to distinguish between nutrients and antinutritive/toxic compounds. Moreover, saliva composition has a critical role in goat ingestive behavior, since it modulates feed sensorial characteristics, on one hand, and, in the other hand, some salivary proteins bind PSMs, namely tannins, impeding them to act negatively in digestive tract. In that way it would avoid post-ingestive negative effects that would result in conditioned feed avoidance.

Whereas taste function and salivary proteome studies have increased for humans and laboratory animals, studies investigating how goats perceive basic tastes and how salivary protein composition contributes to ingestion process are still few in number. Studies about goat oral cavity characteristics, namely taste function and salivary characteristics, might allow improving prediction of diet selection, and consequently improving goat production.

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