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Diet mixing and condensed tannins help explain foraging preferences by Creole goats facing the physical and chemical diversity of native woody plants in the central Monte desert (Argentina)

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ABSTRACT

The aim of this study was to understand the benefit of diet mixing for Creole goats grazing native forage species in the central Monte desert of Argentina and the drivers of preference in the mixed diet. To achieve this goal, cafeteria-style experiments were conducted with thirty female Creole goats (2 years old; 44 ± 1.4 kg) and forage species that are typically ingested by goats in this region: Two tanniniferous (*Tricomaria usillo*, *Mimosa ephedroides*) and three non-tanniniferous shrubs (*Prosopis flexuosa*, *Capparis atamisquea, Atriplex lampa*). In Experiment 1, goats were assigned to three groups ($n = 10$); two groups were offered single tannin-containing shrubs as their basal diet (*T. usillo*; SDTU or *M. ephedroides*, SDME), whereas the third group received a combination of all five forages (Mixed diet of forages, MD). After a fifteen-day adaptation period, half the animals in each group ($n = 5$) were dosed with polyethylene glycol (PEG), a polymer that neutralizes the negative effects of tannins, whereas the other half (Control) were not dosed (CG). Daily dry matter intake (DMI), *in vivo* apparent digestibility of the diet (ADD) and nitrogen (ADN) were determined. For goats fed MD, preference was estimated based on the DMI of each of the forages offered. Jugular blood samples were collected on the first and last days of the experiment to determine concentrations of blood urea nitrogen (BUN) and serum metabolites indicative of liver damage. In experiment 2, intake rates (IR) of the five forage species were estimated. No significant differences in DMI were detected among treatments. However, goats offered a choice of forages (MD) in the CG treatment had greater diet digestibility and lower BUN than animals fed the single shrubs, showing evidence of a nutritional benefit with dietary diversity. Goats changed their foraging preferences in response to PEG supplementation. Animals in the CG treatment preferred *M. ephedroides* whereas animals in the PEGG treatment preferred *A. lampa.* There was a positive correlation between forage preference and IR of crude protein ($r = 0.65$; $P < 0.001$) in PEGG goats, and between forage preference and IR of total tannins ($r = 0.77$, $P < 0.001$) in CG goats. When PEG attenuated biological effects of condensed tannins, goats switched their preference from forages that offered the greatest IR of total tannins (i.e., *M. ephedroides*) to those that led to the greatest IR of crude protein (i.e., *A. lampa*). In summary, a mixed diet led to greater nutritional benefits than

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single diets, which contribute to explain the diverse array of food items goats typically show when browsing in the central Monte desert of Argentina. Our results also show that CP, tannins and plant structure (which offer variable intake rates) play significant roles in goats' foraging preferences in this environment.

1. Introduction

Free-range grazing herbivores face the nutritional challenge of maintaining the constancy of their internal environment (i.e., homeostasis) despite the functional heterogeneity of the forage resources offered by the grazing environments. Among domestic ruminants, goats (*Capra hircus*) stand out for their wide distribution and better productive performance in arid and semi-arid rangelands. This has been explained mostly in terms of behavioral and physiological strategies distinctive of goats, which are continually shaped by the interplay between the environment and the genome (Provenza, 2008; Silanikove, 2000). As a result of the interaction between these forces, grazing goats select a balanced diet from many species that differ in their morphological and chemical characteristics (e.g., physical and chemical defenses, nutritional characteristics). This leads to the selection of three to five food items, which typically make up the bulk of a meal (Papachristou et al., 2005; Provenza et al., 2007). Likewise, in a desert region – the central Monte of Argentina – grazing Creole goats incorporate over fifteen forage species into their diet, out of which only five represent almost 70% of the diet (Allegretti et al., 2012; Egea et al., 2014). Among these species, the shrubs *Tricomaria usillo* and *Mimosa ephedroides* stand out, not only for their significant contribution to the bulk of the diet but also for their high content of phenolic secondary compounds (Allegretti et al., 2012; Egea et al., 2014).

Originally, plant secondary compounds (PSCs) were considered as by-products of plant metabolism and means for deposition of excesses of C fixed by photosynthesis. Although it is still unknown whether these compounds are involved in the primary metabolism of plants, there is no doubt about their involvement in defense against herbivory (Iason, 2005). Plant secondary compounds have been widely studied for their aversive orosensory and toxic effects, which have a deterrent effect on herbivores. However, more recent studies indicate that the intake of adequate amounts of some of these compounds can have positive effects on nutrition, productive performance, and even on the health of domestic ruminants (Waghorn, 2008). Among phenolic secondary compounds, condensed tannins constitute a good example of this duality, since they can be either harmful or beneficial to the animals (Makkar, 2010). The biological effects of tannins in animals does not only depend on the concentration of these components in the plants' tissues, but also on their chemical structure, interaction with other PSCs and/or nutrients in the diet, plant growth stage, specie and physiological condition of the animal, among other factors (Makkar, 2003; Min et al., 2003). The dissuasive power of tannins would be mediated by their deleterious effects on palatability, intake and digestibility of forage species (Goel et al., 2005). However, tannins are not completely avoided by goats, but rather are tolerated under certain threshold (Jansen et al., 2007; Egea et al., 2014). This may be related to benefits provided by intake of small amounts of tannins. For example, by making dietary protein unavailable for ruminal digestion until it reaches the more acidic abomasum and small intestines, modest amounts of tannins improve the protein nutrition of ruminants (Barry et al., 2001; Min et al., 2005). This enhances immune responses (Niezen et al., 2002) and improves reproductive efficiency (Min et al., 2001). In addition, a reduced protein digestion in the rumen decreases the rate of ammonia production, a potentially toxic chemical detoxified in the liver (Chalupa et al., 1970) which represents a metabolic cost to the host (Parker et al., 1995). Contrariwise, in the absence of tannins or when animals are dosed with substances that inactivate tannins, such as Polyethylene glycol (PEG), ruminal microorganisms could reach their maximum protein degradation rate with the consequent production of ammonia (NH3). Ammonia concentration may exceed the capacity of rumen bacteria to incorporate it in the synthesis of bacterial protein. The ammonia not incorporated in the synthesis of bacterial protein is absorbed through the rumen wall to be used as a precursor in the hepatic urea synthesis. Urea is transported by blood to the rumen and/or excreted in urine. As a result of the urea entering into the bloodstream, the concentration of blood urea nitrogen (BUN) increases (McMahon et al., 2000).

In addition to chemical defenses, some morphological traits of plants, such as specific leaf area (SLA), specific stem density (SSD), tensile strength and spines affect and/or restrict the food ingestion-digestion process and, consequently affect the feeding behavior of herbivores (Cooper and Owen-Smith, 1986; Sebata and Ndlovu, 2010). Studies realized by Egea et al. (2014) in the study area – the desert central Monte of Argentina – showed that free-range grazing Creole goats mainly consumed the terminal ends of growing shoots (stems with leaves and/or leafless) of woody species which were markedly different in their physical traits. In the same work, food selection of Creole goats could be better explained in terms of the mechanical features of food (SLA and SSD) than in terms of chemical features. Considering that herbivores crop between 10,000 and 40,000 bites per day from different individual plants (Illius et al., 1999), dietary decisions performed by goats based on the physical characteristics of forage have important implications for nutrient and PSCs intake rate and animal performance (Illius et al., 1999; Shipley et al., 1999).

From the perspective of the nutritional challenge that physico-chemical diversity of forage resources in arid and semi-arid ecosystems offer to goats, intake of a varied diet could be viewed as a behavioral strategy. This strategy would allow goats to achieve their nutritional requirements, counteract the deleterious effects of PSCs and, in some instances, benefit