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Supplemental nutrients increase the consumption of chemically defended shrubs by free-ranging herbivores

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ABSTRACT

Large herbivores are purported to continue consuming toxin-containing forages as long as their capacity to neutralize, detoxify and excrete dietary toxins is not exceeded. This capacity depends on the availability of liver enzymes, energy and amino acid precursors. While this may explain increased intake of toxin-rich forages by herbivores supplemented with nutrients, a different effect may emerge in rangelands dominated by forages that are rich in condensed tannins which are not as degradable and readily absorbable as toxins. In a field experiment, we investigated the effects of supplementing animals with a high-energy source (yellow maize grain) and a high-protein source (soybean meal) on browse intake, foraging behaviour and diet composition of goats in a semi-arid savanna. In line with our prediction, nutrient supplementation increased the percentage time spent by goats on browsing and subsequently enhanced browse intake. Supplemented goats consumed more condensed tannins than goats that were not supplemented. Goats from supplemented groups tended to compose different diets from goats that received no supplement. Supplementation may have modified animals' requirements for nutrients in ways that influenced feeding behaviour. We contend that supplements likely replaced the nutrients that are routinely bound and rendered indigestible by condensed tannins and thus increased the intake of tannin-rich forages through delaying a negative post-ingestive feedback (aversion) from dietary tannins. In conclusion, we showed that nutrient supplementation can be used to increase defoliation of tannin-rich shrubs by mixed feeders which suggests a potential for browsers and mixed-feeders to serve as biological bush control agents. Furthermore, these results have serious implication for herbivores and the environment.

1. Introduction

With woody expansion predicted to increase globally (Hughes, 2003; O'Connor et al., 2014), it will soon not be possible to sustain animal production from the shrinking grass layer alone (Gordon and Prins, 2008; Estell et al., 2012). The increasing demand for animal protein to feed the growing human population (FAO, 2009) and the increasing ruminant populations (Rischkowsky et al., 2006) will further complicate the situation. The challenge facing farmers, managers, and ecologists alike will be to mitigate the predicted forage shortfall through enhancing the utilization of the shrubs that are starting to dominate global rangelands (Gordon and Prins, 2008; Estell et al., 2012). This need is increasingly being acknowledged, particularly in the shrub-dominated rangelands of southern Africa (Mapiye et al., 2011; O'Connor et al., 2014). Browse has been reported to provide nutrients such as protein, vitamins and minerals that are sometimes in short supply in grasslands especially during the dry seasons (Le Houérou, 1980; Prins, 1996b; Mapiye et al., 2011).

Although shrubs are known to enable browsers and mixed-feeders to survive critical periods of prolonged drought (Franzel et al., 2005), the extent to which domestic and wild herbivores consume these shrubs varies widely depending on the shrub and

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animal species among other factors (Papachristou et al., 2005). Cattle have been reported to spend 4–7% of their time browsing, while goats browse for 43–52%, and sheep are intermediate at 4–28% (Prins et al., 2000; Sanon et al., 2007). Goats are mixed-feeders with a narrow mouth, mobile lips and tongue (Solaiman, 2010), which help them to deal with plant physical defences such as thorns (Gowda, 1997; Gowda et al., 2003). Additionally, goats are known to possess proline-rich proteins in their saliva (Juntheikki et al., 1996; Shimada, 2006), which help them utilise chemically defended forages better than other domestic herbivores and many wild grazers (Hanovice-Ziony et al., 2010; Solaiman, 2010).

Although goats are anatomically and physiologically suited to thrive in shrub-dominated ecosystems, the extent to which they consume savanna shrubs (Bakare and Chimonyo, 2011; Perez et al., 2013; Hacker and Alemseged, 2014) is still largely limited by the presence of plant secondary metabolites (PSMs) (Kaitho et al., 1997; Scogings et al., 2014). Among other physiological effects, PSMs have been shown to affect both domestic and wild animals' intake, food preference, and behaviour (Mueller-Harvey, 2006; Estell, 2010; Foley et al., 1999). Consequences for consuming PSMs range from beneficial, to negligible or acutely toxic, depending on the particular PSM and the amount consumed (Villalba and Provenza, 1999). In southern Africa, browse species are well endowed with carbon-based secondary metabolites (Scogings et al., 2014), a group that includes many different phenolic compounds such as furanocoumarins, low molecular weight phenolics (Hattas et al., 2011; Hattas, 2014), condensed tannins (CTs) and hydrolysable tannins (Cooper and Owen-Smith, 1985; Owen-Smith, 1993; Scogings et al., 2004). Alkaloids have also been observed among African woody species (Scogings, 2005). Therefore, in order to increase their utilisation of savanna browse, African browsers and mixed-feeders have to counteract a complex system of plant chemical defence.

There is evidence that supplementing herbivores with nutrients does not only improve their nutrient balance (Illius and Jessop, 1996; Foley et al., 1999), but it also increases the amount of toxins that animals can consume (Provenza et al., 2003). Intake of forages that are rich in these chemicals is assumed to be controlled by nutrient-toxin interactions that increase or reduce animal's preference for food and habitat (Provenza et al., 2003; Iason, 2005). The rate at which toxin-rich foods can be eaten depends on how quickly the animal can detoxify, deactivate or eliminate ingested toxins from the body (Foley et al., 1995). The process of transforming the more toxic compounds into less toxic water soluble compounds requires nutrients, especially energy, protein and water (Illius and Jessop, 1995). This implies that nutrient deficiencies will negatively affect the efficiency of animals to detoxify and eliminate toxins from the body. Logically, supplementing animals with food sources that are high in nutrients has been reported to increase the animals' capacity to detoxify dietary toxins (Provenza et al., 2003; Marsh et al., 2006). While nutrient supplementation has been shown to increase utilization of terpene rich sagebrush by sheep in North America (Dziba et al., 2007) and chemically defended and unpalatable shrubs in the Mediterranean systems (Banner et al., 2000; Rogosic et al., 2008, 2011; Saric et al., 2013), no study has tested this prediction in the context of African savannas.

The influence of nutrient supplementation on PSM-rich forage intake depends on the kind and amount of nutrients and PSMs to which the animal is exposed (Villalba et al., 2002a). Although diverse PSMs are prevalent among the African savanna woody plants, CTs are the main chemical component affecting leaf defoliation by browsing ruminants (Owen-Smith et al., 1993; Chapman et al., 2010; Scogings et al., 2011). Unlike most PSMs that are categorised as toxins owing to their property of being easily absorbed, detoxified and eliminated from the body via the liver (Marsh et al., 2003, 2005), CTs are not toxins (Makkar, 2003). Since rumen microbes are not capable of degrading CTs (Lopez-Andres et al., 2013), CTs are structurally too big and unlikely to be absorbed and transported to liver cells (Makkar et al., 1995a, 1995b). Therefore, detoxification through activation of liver enzymes cannot explain changes in intake of CT-rich forages in response to nutrient supplementation.

Ruminants have been purported to learn about the consequences of food ingestion (Provenza, 1995) and discriminate between the post-ingestive effects of energy and protein (Villalba and Provenza, 1999). Although feeding experiments with sheep have reported supplementation with high-protein and high-energy concentrates to improve utilization of tannin-rich shrubs (Villalba et al., 2002b, 2002c), no field studies have investigated this supplementation-induced increase in tannin-rich shrubs intake. In this study, we investigated the effects of high-protein and high-energy concentrate supplementation on woody plant utilization by free-ranging goats in a South African semi-arid savanna. Semi-arid savannas are highly seasonal and forage availability is generally reduced during the dry season, when grass dries out and deciduous shrubs lose leaves (Prins and Beekman, 1989). The remaining evergreen species are usually of reduced quality and are highly defended by CTs which results in reduced defoliation (Prins, 1996a; Ganqa et al., 2005). As a result, decreases in herbivore productivity are reported mainly during the dry season (Prins, 1989; Mapiye et al., 2011; Sebata et al., 2011).

We conducted a field experiment during a dry season and predicted that supplementing animals with high-protein and high-energy concentrates would (1) increase the percentage foraging time of goats, (2) increase browse and thus (3) CT intake (g DM) and (4) increase the percentage inclusion of tannin-rich forages in the diet. Lastly, given the high prevalence of CTs in African savanna browse and the higher affinity that tannins have for dietary protein compared to other nutrients, we expected (5) goats that were supplemented with a high-protein concentrate to use browse more than the goats supplemented with a high-energy concentrate.

2. Materials and methods

We conducted a field experiment that lasted for 15 days in July 2013 at the Roodeplaat Experimental Farm of the Agricultural Research Council (ARC) in Pretoria, South Africa (25°20′–25°40′E; 28°17′–28°25′S). The climate is semi-arid with an average annual rainfall of 646 mm and daily mean temperatures ranging between 2 and 16 °C in July. The main dry season in the study area starts in May and reaches its peak in July. The vegetation is classified as savanna (Mucina and Rutherford, 2006) and the rangeland in the study area is dominated by *Vachellia karroo*, *Vachellia tortilis, Ziziphus mucronata,* and some *Euclea* species (Coates Palgrave, 2002; Kyalangalilwa et al., 2013).

2.1. Experimental design and habituation period

A camp of 1.8 ha size was fenced with a mesh wire and stocked with 15 indigenous female goats (South African veld goats) that were 12 months old and with an initial body weight of 20.6 (SD ± 2.5) kg. Goats were allocated to three treatment groups (i.e., high-energy supplement, high-protein supplement, and no supplement) of five goats each. Animals were assigned to treatments such that all groups had a similar mean body weight. They stayed in these groups for the duration of the experiment. They were subjected to a two-week habituation that was aimed at (1) establishing the correct amount of supplement to offer, (2) familiarizing the animals with presence of observers and (3)