



Condensed tannins reduce browsing and increase grazing time of free-ranging goats in semi-arid savannas



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ABSTRACT

Tannin concentrations fluctuate spatially and temporally within and among plant species, with consequences for forage quality of herbivores. The extent to which these fluctuations influence foraging activities of goats is not fully understood. While accounting for the effects of the time of the day and season, we tested the hypothesis that goats exposed to high levels of condensed tannins (i) spend less of their foraging time browsing, (ii) spend more time grazing, and (iii) reduce their total foraging time, especially during the dry season when grasses dry out and deciduous trees lose leaves. We orally dosed 15 goats with (i) 20 g of condensed tannins extract dissolved in 50 ml of water (high tannin exposure), another 15 goats (ii) with 20 g of polyethylene glycol dissolved in 50 ml of water, which neutralizes the effects of tannins (low tannin exposure), and the last group of 15 goats (iii) with 50 ml of water (control). We recorded the time spent on grazing, browsing and these two activities together (i.e., foraging) for 30 days in the dry and wet season. As expected, dosing goats with condensed tannins reduced their browsing time and increased the time spent grazing. Goats dosed with polyethylene glycol increased their browsing time and lowered their time spent grazing. Animals dosed with polyethylene glycol foraged for longer than other treatment groups in the dry season, whereas the goats dosed with condensed tannins increased their foraging time in the wet season. Overall, all treatment groups spent a similar amount of time foraging, indicating an instinctive drive by goats to maintain high total foraging time while avoiding over ingestion of tannin-rich forages. We concluded that tannins do not suppress total foraging time for free-ranging goats. Instead, they increase the amount of time animals spend on grazing on herbaceous plants and decrease the amount of time animals spend browsing on woody plants. Comparing time spent on different foraging activities by goats is a first step towards understanding how goats utilize feed resources and how tannins influence resource utilization patterns.

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1. Introduction

Browsing herbivores have been in a co-evolutionary arms race with their woody food resources for a long time (van Soest, 1994; du Toit and Olf, 2014), and consequently woody plants evolved an array of physical and chemical defences against herbivore attack (Gordon and Prins, 2008; du Toit and Olf, 2014). In Southern Africa,

condensed tannins are known to be the main chemical components affecting the nutritional value and acceptability of browse (Cooper and Owen-Smith, 1985; Owen-Smith, 1993; Basha et al., 2012). Numerous studies in the region have reported negative relationships between tannin concentrations and selection of browse by African antelopes (Cooper and Owen-Smith, 1985), and giraffe (Furstenburg and van Hoven, 1994). Similar patterns have been reported in several feeding experiments with intermediate feeders such as domestic goats (*Capra hircus*) (Dziba et al., 2003; Scogings et al., 2004; Shrader et al., 2008). However, the concentration of tannins in plants is a highly variable trait, varying with plant species (Hattas and Julkunen-Tiitto, 2012), plant part (Furstenburg and van Hoven, 1994), season (Cooper et al., 1988; Scogings et al., 2013),

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tissue developmental stage (Hattas et al., 2011), environmental conditions, and exposure to defoliation (Scogings, 2005; Wessels et al., 2007; Kohi et al., 2011). While variations in the plants' tannin concentrations may induce alterations in the activity patterns and foraging behaviour of browsing herbivores, we know of no studies that have elucidated these alterations under natural conditions.

Although the effects of biotic factors such as forage quantity, nutrient and plant secondary metabolites (PSMs) on foraging behaviour are generally understood (especially in grazing mammals), there is limited insight on the effects of condensed tannins on foraging behaviour under field conditions. Moreover, few studies have considered the variety of intertwined mechanisms used by intermediate-feeders to circumvent the negative effects of tannins (Estell, 2010). These mechanisms range from the physiological secretion of proline-rich salivary proteins (Hanovice-Ziony et al., 2010; Canon et al., 2013) to the behavioural strategies such as avoidance, regulation of intake below a certain thresholds, cautious sampling, altering sizes and patterns of feeding bouts, diet switching, or consuming diverse/complementary diets (Provenza et al., 2003; Marsh et al., 2006; Jansen et al., 2007; Estell, 2010).

Free-ranging herbivores are known to have daily and seasonal activity patterns (Shi et al., 2003) that optimize their nutrient intake (Shrestha et al., 2014). Considering that tannins are among the constraints, it is of importance to know the extent to which herbivores mitigate their negative effects. Tannins are regarded as digestibility reducers (Dearing et al., 2005) and thus reduce the nutritive value of browse forages. The resultant low nutrient concentrations in forage may mean that herbivores foraging on tannin-rich forages must either harvest and process larger volumes of food to meet their nutrient requirements (Dearing et al., 2005) or they must feed selectively to avoid over-ingesting tannins (Iason, 2005). Either way, this likely imposes a change in foraging times as a way to counter the negative effect of tannins on the nutritional value of the food.

The main objective of this study was to determine the effects of condensed tannins on foraging activity time budgets by goats in a semi-arid savanna. While accounting for the effects of time of day and season, we used yearling female goats to test the hypothesis that goats exposed to high levels of condensed tannins (i) reduce their time spent browsing, (ii) increase time spent grazing, and thereby (iii) reducing the total foraging time especially during the dry season. We hypothesized that this is a strategy used by intermediate-feeders to cope with tannin-rich foraging environments in a natural foraging context. This is based on the idea that herbivores must minimize tannin intake while maximizing nutrient intake (Freeland and Janzen, 1974; Jansen et al., 2007). We thus, expected goats exposed to low tannin levels to spend more time browsing (Landau et al., 2002) and less time grazing. Forage availability for both herbaceous and woody vegetation declines in the dry season due to drying out of grasses and leaf loss by deciduous woody species in semi-arid savannas. Given that evergreen species, which retain their forage throughout the year, are highly chemically defended, we expected goats exposed to high levels of tannins to forage for even less time during the dry season. In our experiment we dosed goats with either tannins, or polyethylene glycol (PEG), which binds tannins irreversibly over a wide range of conditions. PEG reduces the formation of protein-tannin complexes (Gilboa et al., 2000), improving browse intake by goats. For example, Silanikove et al. (1996) showed that supplementing goats with PEG increased intake of Mediterranean native woody species. Even though we used goats as model organisms, this work is of importance to understanding other intermediate feeders, such as impala or steenbok or even eland (McNaughton and Georgiadis, 1986; Hofmann, 1989).

2. Methods and materials

2.1. Study area

This study was conducted at Roodeplaat Experimental Farm of the Agricultural Research Council located in northern Gauteng, South Africa (25°20'–25°40'E; 28°17'–28°25'S). The climate in the study area is semi-arid with a mean annual rainfall of 646 mm and means daily maximum temperatures between 20 and 29°C in January and means minimum temperatures ranging between 2 and 16°C in July. The main growing season starts from November to April, and the dormant season starts in May and reaches its peak in July. The natural vegetation of the farm used for livestock production and game covers 2100 ha. The vegetation of Roodeplaat falls within the savanna biome classified as Marikana Thornveld (Mucina and Rutherford, 2006). The rangeland is dominated by *Acacia karroo*, *Acacia tortilis*, *Ziziphus mucronata*, and some *Euclea* species. The herbs found in the study sites include *Lippia rehmannii* and *Tarconanthus camphoratus*. The dwarf shrub *Aloe greatheadii* var. *davyana* is also abundant in the farm. For nomenclature of plants we followed Coates Palgrave (2002).

2.2. Study design

We used 45 yearling female goats ranging from 8 to 12 months old with an initial body weight of 14.9 (SD ± 3.7) kg. All animals were weighed one day before the experiment and were allocated to 3 treatment groups of equal number ($N = 15$) and a similar mean body weight. Every morning between 07:00 and 08:00, 15 animals were orally dosed with 20 g of polyethylene glycol (PEG 6000) dissolved in 50 ml of water, while another 15 were dosed with 50 ml of water plus 20 g of condensed tannins (extracted from mimosa bark) and the last 15 received 50 ml of water (control). To orally dose the animals, a 80 ml syringe attached to tube (30 cm long) was used. The mimosa extract was obtained from the bark of Black Wattle (*Acacia mearnsii*) tree and contained a minimum of 66% condensed tannin (<http://www.mimosa-sa.com>). These treatment groups were maintained throughout the experiment. Three grazing camps/paddocks of similar size (±1.7 ha) were fenced and stocked with fifteen animals (i.e., 5 from each treatment group) daily from 08:00 until 16:00. All animals were treated for internal and external parasites before the experiment and had ad libitum access to water throughout the experiment. From 08:00 all animals were allowed to forage freely in the field until 16:00 when they were kraaled to avoid predation. All experimental procedures were approved by the Animal Ethics Committee of the ARC under permit number: APIE11/039.

2.3. Data collection

Feeding behaviour of goats in three paddocks were monitored for 30 days during the dry (between June and August 2012) and for 30 days during wet (between January and March 2013) seasons. All study animals were marked with paint on the flanks to facilitate identification during observations. The goats were conditioned for a period of two weeks before the actual observations, to habituate them to the presence of observers and to allow close monitoring of behaviour.

On each day, nine goats (3 from each treatment group) were randomly selected and observed. The three goats observed per treatment group would be foraging in different paddocks. Of the nine goats observed each day, three (one from each treatment group) were observed in the early morning (08:00 to 10:30), three (one from each treatment group) observed in the late morning (10:30 to 12:00) and the other three (one from each treatment group) observed in the afternoon (12:00 to 15:30). Each goat

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