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Review article

Foraging ecology of goats and sheep on wooded rangelands[☆]

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Abstract

Wooded rangelands are a vast grazing land resource globally, including shrublands, savannas and forested ranges. They generally provide forage year-round for small ruminants and they are vitally important for livestock production, especially goats. While the productivity of wooded rangelands is low to moderate, their importance to small ruminant production is considerable. In this paper, we begin by discussing some anti-quality characteristics (mechanical and chemical defences) of woody vegetation that reduce their forage value, deter foraging, and reduce performance and productivity of small ruminants. We then present examples of grazing studies that illustrate how small ruminants select their diets on wooded rangelands. We conclude by discussing why small ruminants select the diets they do within the evolutionary processes of plant–herbivore interactions. Finally, we discuss how this knowledge can be integrated into approaches for sustainable management of wooded rangelands for small ruminant production. Plant defences are abundant in wooded rangelands but they are not a complete barrier to small ruminants as they often use woody plants as part of their diets. Indeed plants with such defences may represent a significant forage resource enabling small ruminants to survive on wooded rangelands with a prolonged dry period when more preferred defenceless species are absent. Future research in plant–herbivore interactions should include investigating how plant biochemical diversity influences herbivore preference for various plant communities, and integrating this information to develop recommendations for managing wooded rangelands.

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1. Introduction

Ruminants use 3.3 billion hectares of grazing lands and the production from about one-quarter of the

world's croplands (FAO, 1998). Small ruminants – sheep and goats – are critical components of production systems throughout the world and they are essential in agricultural systems. Most sheep and goats exist in natural environments such as rangelands and forestlands and agricultural ecosystems such as pasturelands. Through grazing small ruminants convert an otherwise unused natural resource into animal protein of high biological value. However, grazing is applied in most regions of the world without established principles of

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proper utilization. Consequently, rangeland productivity has deteriorated, as has the productivity of other forage resources such as forestlands. Grazing animals, especially goats, are considered despoilers of rangelands. However, with good management small ruminants can make a positive contribution to the natural resource base by enhancing soil quality and increasing plant and animal biodiversity (El Aich and Waterhouse, 1999).

Lands dominated by woody species, namely shrublands, savannas and forested ranges, are a substantial portion of the world's rangelands (Stoddart et al., 1975). They play an important role in areas with a long dry period and harsh environmental conditions (e.g. Mediterranean regions, tropical, arid and semi-arid areas), because they provide green forage for grazing animals throughout the year (evergreen species) or at specific critical periods of the year (deciduous species). Goat husbandry, and to some extent sheep husbandry, both depend on browse and herbage produced by wooded rangelands during certain times of the year. An appropriate grazing management of such wooded rangelands ensures not only forage but also water for off-site use, wildlife habitat, soil protection from erosion and wood production (e.g., firewood, fence posts). However, achieving good grazing management of wooded rangelands presupposes knowledge of how goats and sheep interact with the vegetation.

In this paper, we review complex interactions between wooded rangelands and small ruminants. We also discuss behavioural challenges small ruminants face when foraging and management approaches for sustaining small ruminant production.

2. Constraints of browse as animal food

The dominant vegetation in wooded rangelands is shrubs and trees. Goats and sheep can utilize the browse of numerous woody species to satisfy their needs for nutrients (Wilson, 1969; Holechek, 1984; Ramirez et al., 1991; Nastis, 1993; Papachristou, 1997a,b; Papachristou et al., 1999). However, woody plants possess a wide variety of chemical and physical properties that reduce forage value and serve as grazing deterrents (Cooper and Owen-Smith, 1986; Bryant et al., 1991; Van Soest, 1994; Allen and Segarra, 2001; Laca et al., 2001). These anti-quality attributes reduce the

digestibility of forage nutrients, produce toxic effects, and can cause illness (Launchbaugh et al., 2001). It is important to understand how anti-quality factors affect grazing animals in order to create livestock management strategies for wooded rangelands.

2.1. Mechanical defences

Spines and thorns are common in numerous woody species and influence browsing rate by reducing bite mass and decreasing biting and chewing rates (Cooper and Owen-Smith, 1986; Haschick and Kerley, 1997; Dziba et al., 2003). They make it difficult for animals to strip leaves off stems, which forces animals to crop individual leaves (Belovsky and Schmitz, 1991, 1994; Belovsky et al., 1999; Laca et al., 2001). Spines also slow chewing rate by requiring herbivores to carefully manipulate plants in their mouths to avoid pain and injury (Cooper and Owen-Smith, 1986). However, the influence of spines and thorns on ingestion depends on the mouth size of the foraging animal (Spalinger and Hobbs, 1992; Gordon and Illius, 1988; Perez-Barberia and Gordon, 2001). Most browsing animals have lips and tongues that are very agile and can more easily select leaves and avoid thorns (Gordon and Illius, 1988). Goats, for instance, with their mobile and narrow muzzle, can manoeuvre their mouths more easily among thorns to pluck small leaves, such that thorns may be less effective in reducing cropping rates (Shipley et al., 1998, 1999; Cooper and Owen-Smith, 1986; Illius and Gordon, 1987). This partially explains why goats can be more effective browsers than sheep.

Plant morphology, which is affected by browsing (Meuret, 1997), also, influences browsing rates and daily food intake (Shipley et al., 1999; Laca et al., 2001). Whereas plants whose leaves grow on old shoots tend to result in high bite rates and reduced food intake rates, plants with leaves that grow on young edible shoots allow bigger bite sizes and relatively high intake rates (Dziba et al., 2003). Because bite size plays a major role in influencing intake rates (Spalinger and Hobbs, 1992; Illius et al., 2002), plants and plant parts that afford animals bigger bite sizes are likely to be preferred. Animals select plants from which they can harvest bigger bite sizes, which increase instantaneous intake rates and daily food intake (Ungar, 1996). However, instantaneous intake rates might not explain longer-term daily food intake because they vary with

the hunger status of the animal and with forage availability. As animals satiate on particular food items, they are more likely to select a different food item not only on the basis of the amount of biomass an animal can harvest but due to a need to meet other nutritional requirements or to avoid excesses of nutrients and toxins (Provenza et al., 2003). As animals continue to feed in a patch, browse availability declines over time and so does the rate of food intake because bite sizes decline while bite rates increase (Spalinger and Hobbs, 1992; Shipley et al., 1999). However, bite rates cannot compensate adequately for smaller bites when forage availability has declined significantly. Other factors such as plant phenology may influence availability of leaf material for small ruminants during the dry season and reduce intakes rates and daily food intake. Plants that loose their leaves during the dry season (deciduous plants) provide less forage material during these periods compared to evergreen species whose browse material is available throughout the year (Scogings et al., 2004). Small ruminants foraging in wooded rangelands combining herbaceous and browse material select food particles from both green and dead plant material (Meuret, 1997). Moreover, the heterogeneous forage environment of wooded rangelands offers conditions that may favour a very fast intake for small ruminants that discriminate between forage materials while at the same time maintaining an intake rate higher than that observed during their meal.

2.2. Chemical defences

Browse of woody species also contains compounds that reduce forage quality because they are nearly indigestible (e.g. lignin), affect the digestibility of other plant compounds (e.g. tannins), and have post-ingestive and post-absorption effects on animals. Aversive post-ingestive feedback causes herbivores to decrease intake of foods containing toxins such as condensed tannins in blackbrush (*Coleogyne ramosissima*), terpenes in big sagebrush (*Artemisia tridentata*) and juniper (*Juniperus* spp.) and oxalates in greasewood (*Sarcobatus vermiculatus*) (Provenza, 1995). Herein, we do not review all woody plant phytotoxins that deter browsing ability of small ruminants but we will give some examples.

Condensed tannins are a major group of secondary compounds found in a wide range of woody plants commonly consumed by ruminants. Condensed tannins

affect both the nutritive value of plant forage (Zucker, 1983) and diet selection (Provenza and Malechek, 1984; Provenza et al., 1990). For the most part, they do not appear to be absorbed from the digestive tract of ruminants and act by forming complexes with dietary protein and digestive enzymes (Terrill et al., 1994), thereby reducing the apparent digestibility of protein (Robbins et al., 1987a,b) by increasing nitrogen excretion in faeces (Kumar and Vaithyanathan, 1990). Condensed tannins in forages, also, have positive effects on nutritive value (Reed et al., 1990), since they prevent bloat and increase the flow of non-ammonia nitrogen and essential amino acids from the rumen (Barry and Manley, 1984; McNabb et al., 1993). Also, ruminants grazing on forages that contain condensed tannins reduced their parasite burden compared to those grazing on similar quality forages that does not contain condensed tannins (Athanasiadou et al., 2001). The effects of condensed tannins have been regarded as indirect effects through enhanced immunity and/or direct anthelmintic effects on the nematodes (Coop and Kyriazakis, 2001). It has been reported that the optimal balance between positive and negative effects of condensed tannins was achieved in sheep when their dietary concentration was 3–4% (Barry et al., 1986). However, neutralization of tannins in diets of goats fed Mediterranean browse species (*Quercus calliprinos*, *Pistacia lentiscus* and *Ceratonia siliqua*) using polyethylene glycol resulted in increased food intake, increased digestibility, and improved energy balance (Silanikove et al., 1996; Landou et al., 2002).

Forage digestibility and intake of browse species are also affected by lignin and fibre contents (Wilson, 1977; Nastis and Malechek, 1981; Nastis, 1993; Van Soest, 1994). High content of indigestible compounds decreases the digestive benefits of browse species by tying up nutrients, and thereby reducing preference and intake (Jung and Allen, 1995; Moore and Jung, 2001). However, the nutritive value of browse is reduced more by high tannin than by fibre content (Makkar et al., 1993). Nastis and Malechek (1988) reported that a diet containing 80% oak browse with an ADF content of 32% and a tannin content of 7% was 17% less digestible in vitro than an alfalfa diet containing 40% ADF and 1% tannin. This general rule, sometimes, is contradicted. For example, Papachristou (1997a) studied two browse species (*Carpinus orientalis* and *Fraxinus ornus*) with a similar CP content, but *Carpinus*

had a higher content than *Fraxinus* of ADL (9% versus 7% DM), phenolics (69 versus 57 mg/g DM), and tannins (49 versus 19 mg/g DM). For the same species, Khazaal et al. (1993) investigated gas production and DM degradation and suggested that the nutritive value of *Fraxinus* was higher than that of *Carpinus*. However, goats and sheep consumed more *Carpinus* than *Fraxinus* (Papachristou, 1997a). Digestibility results indicate that an accurate assessment of the true forage value of woody species, especially when they contain high levels of phenolics and tannins, can only be made from feeding and digestion trials.

Oxalic acid is also found at high concentrations in many plants consumed by small ruminants. For instance, greasewood, which provides fair forage for livestock and big game during the winter and early spring, contains oxalates in the leaves and may cause mortality in sheep. Oxalic acid forms calcium oxalate crystals in blood capillaries, causing direct cellular damage as well as reducing the systemic availability of calcium (Vonburg, 1994). Although rumen microbes can degrade oxalic acid (Allison et al., 1977), non-adapted animals may absorb significant amounts of oxalic acid with potentially toxic consequences (James and Butcher, 1972).

There is an ongoing debate about the influence of terpenes on preference and intake of shrubs, especially sagebrush. Earlier studies suggested that terpenes kill microbes in the digestive system, thereby reducing forage digestibility (Nagy and Tengerdy, 1968; Oh et al., 1968). Although recent studies support these earlier findings (Ngugi et al., 1995), the greatest criticism has been that all these studies have been conducted in vitro (Cluff et al., 1982; Welch et al., 1983; White et al., 1982). According to Welch et al. (1983), terpenes are volatile organic compounds that are expelled quickly, and thus have little effect on rumen microbes and digestibility. However, Foley et al. (1987) found detectable traces of terpenes in the stomach of marsupials suggesting that terpenes can affect rumen microbes. Pharmacokinetic studies with sheep show significant amounts of monoterpenes are absorbed from the rumen and have considerable influence on the feeding behaviour of animals (Dziba et al., 2005a). A robust evaluation of the effects of terpenes is still necessary to advance knowledge that will form a basis for mitigating deterrent effects of terpenes to herbivory.

Clearly, there is a huge range of plant defences in wooded rangelands and this variation occurs among and within plant species. For example, trees regularly stripped of their bark by herbivores contain higher concentrations of tannins than trees not stripped of their bark (Gill, 1992), and browsed shrubs produce a greater density of longer thorns than unbrowsed ones (Milewski et al., 1991). In Greece, for the same browse species (*Quercus coccifera*) five rangeland types were identified (Liacos and Mouloupoulos, 1967) of varying morphology (e.g. in the size, shape and colour of adult leaves and in the size of leaf spines) and chemistry (Papachristou et al., 2003), which is probably a response to herbivory. Small ruminants are thus always interacting with plant defences of one type or another in a very dynamic way. The significant issue is to better understand interactions between anti-quality factors and grazing animals.

3. Diet selection by small ruminants

3.1. How small ruminants select their diets

Over the past decades, considerable information has appeared in the literature on the small ruminants' dietary selection in wooded rangelands (Malechek and Provenza, 1981; Pfister and Malechek, 1986a,b; Lu, 1988; Kirmse et al., 1987a,b,c; Schacht and Malechek, 1989, 1990; Papachristou and Nastis, 1993a,b, 1996; Papachristou, 1997b; Kronberg and Malechek, 1997; Kababya et al., 1998; Provenza et al., 2003). These studies and others (see Hughes, 1993; Forbes, 1995; Holecheck et al., 2000) indicate that small ruminant diet selection is influenced by many factors. Among them are the available woody and herbaceous species, forage availability and availability of nutritious alternatives, period of grazing, stocking rate, and whether goats and sheep forage as sole rangeland users or together with other animal species. An important finding, however, is that browse is an important forage source for goats throughout the year and for sheep during the dry periods when herbage was limited. For example, Papachristou and Nastis (1993a) studied, on a yearly basis, the goats' diets in Mediterranean shrublands dominated by woody species including *Quercus coccifera*, *Cistus incanus*, *Rubus* spp., and herbaceous undergrowth consisting of *Festuca* spp.,

Dactylis glomerata, *Trifolium* spp., *Medicago* spp. and *Vicia* spp. The herbaceous component contributed more than 50% of the goat diets during spring when herbs were green, although browse was of high quality during this period. On the other hand, *Vicia* spp., although of high availability and CP content, were not preferred by goats during spring when their tannin content was 20 mg CE/g DM, but they were preferred in the remaining periods when their tannin content declined to 8 mg CE/g DM (Papachristou and Nastis, 1993c). During the rest of the year, goats selected huge amounts of browse (>60%). Leaves of all forage species contributed more than 70% during in all periods, while twigs of shrubs and stems from herbaceous species were low but constant throughout the year.

In semi-arid subtropical savannas, the diet selected by goats varies with season. For example, during the wet season, goats select a more mixed diet of browse, grasses and forbs (Raats et al., 1996). However, during the dry season goats spend more time browsing because many species of browse are evergreens that provide good quality forage during the dry season. There are significant variations among individuals that allow them to browse more or graze more. Defining feeding behaviour along a continuum, rather than categorizing different species of herbivores as grazers, mixed feeders and browsers, is preferred (Perez-Barberia et al., 2004), because most animals graze or browse opportunistically.

The availability of woody and herbaceous vegetation also affects the diet selected by goats. Goats selected a diet higher in CP content and more digestible in shrubland with 35% kermes oak, 18% other woody species and 31% herbaceous species compared to shrubland with 63% kermes oak, 4% other woody species and 11% herbaceous species (Papachristou and Nastis, 1993b). Studies in tropical woodlands in Brazil (Pfister and Malechek, 1986a,b; Kronberg and Malechek, 1997) indicated that goats also consumed large amounts of browse in the dry and wet periods of the year but sheep only consumed large amounts of browse during the dry season when tree leaf litter was a major component of available forage. However, during the dry season browse CP content did not meet animal requirements. These studies suggested additional CP is needed during the dry season to enable both animal species to conserve energy by spending less time foraging and to prevent body weight loss.

The proportion of woody and herbaceous vegetation and seasonal changes in wooded rangelands affect the diet selection of goats and sheep, and dense wooded rangelands provide limited amounts of usable forage because they are difficult to penetrate compared to more open wooded rangelands preferred for grazing. Consequently, people often suggest a reduction of woody cover (Liacos et al., 1980; Kirmse et al., 1987a,b; Schacht and Malechek, 1989, 1990; Papachristou et al., 1997) with appropriate range management techniques (Valentine, 1990). This reduction aims to create a heterogeneous landscape, which increases and diversifies forage production, increases livestock production (Liacos et al., 1980; Kirmse et al., 1987b; Tsiouvaras, 1987; Schacht and Malechek, 1989; Papachristou et al., 1997), limits the risk of uncontrolled fires, and ensures other services such as wildlife habitat or aesthetic landscapes (Liacos, 1982).

Experimental work on diet selection on such improved wooded rangelands was done in Greece (Mediterranean shrublands) and in Brazil (tropical deciduous woodlands) in the 1980s and 1990s. For example, Papachristou (1997b) and Papachristou et al. (1997) assessed the effects of clear cutting and slashing followed by seeding with grasses and legumes and compared them with untreated shrublands of medium density (56% shrub cover). Clearing and slashing resulted in higher amounts of available herbaceous forage and useable browse. Herbaceous biomass was generally 2–3 times higher in the treated shrublands than in the control at least for 3 years after vegetation improvement, and while browse biomass was slightly less (1078 versus 1533 kg/ha), the forage was easily accessible because of the open structure and the lower height of the sprouting shrubs. Forage selected by animals grazing on treated, as opposed to untreated, shrublands was higher in crude protein, more digestible and lower in NDF and lignin. Similarly, Kirmse et al. (1987a,b) and Schacht and Malechek (1989, 1990) found that clearing and thinning of tropical woodland vegetation optimized forage and wood production. Forage conditions and animal performance were improved by the increased amount and diversity of forage. Based on these studies, we suggest that the woody component of rangelands should to be maintained at less than 50% of the total land cover as this produces the best overall foraging conditions and animal performance due to enhanced plant diversity. A further improvement by augmenting

woodlands with evergreen or deciduous fodder shrubs and tree species can be achieved (see Papachristou et al., 1999; Papanastasis, 1999).

3.2. Why small ruminants select the diets they do

Research over the past 30 years and examples described above provide useful information concerning the desired percentages of woody plant cover, the preferred mosaic of rangeland vegetation and the diets small ruminants select under certain conditions. However, why ruminants select particular plants and avoid others is complex and multi-faceted, ever challenging researchers to understand the complexities of wooded rangelands. The consequences for managing such ecosystems are significant because the gap in understanding plant–herbivore interactions restricts potential implementation of approaches for sustainable management of small ruminants in woody plant communities.

Doubtless, in recent decades a considerable amount of work done with animals in controlled conditions has helped us to better understand how animals might forage under certain grazing conditions. Emmans (1991) argued that when an animal has to choose between two or more homogenous foods it would select a diet close to its nutritional requirements. However, in the grazing systems animals confront foods from numerous plant species that differ in their structure and contain different levels of nutrients and toxins. Laca et al. (2001) reviewed the structural anti-quality characteristics of rangeland plants based on publications of the previous 30 years. This work shows that either at low or high levels of plant biomass, rates of nutrient intake are reduced. Intake is influenced by three factors: bite size, bite rate, and grazing time ($\text{intake} = \text{bite size} \times \text{bite rate} \times \text{grazing time}$). Intake rate is most sensitive to bite size – too little or too much plant biomass diminishes bite size, and either increases (too little forage) or decreases (too much forage) with bite rate and grazing time, all of which can diminish animal performance.

These findings caused researchers to conclude that, all things being equal, herbivores should prefer plants that encourage high rates of intake. Papachristou et al. (2003) hypothesized that when goats have to make simple choices between plants with and without high levels of plant defences, all else being equal, they choose to

consume the ones with lower levels. The tested plants were two rangeland types of kermes oak, II and V, which have a similar nutritional value, in terms of primary nutrients, but type V has greater physical (spines) and chemical (phenolics) defences. Intake rate of type II was higher than type V; however, type V was still selected at an average level of 37%. This latter indicates that complete avoidance is not feasible in the grazing systems because all plants have defences against herbivory (Provenza, 1996; Provenza et al., 2003). Therefore, herbivores often consume plant species and parts that do not maximize rates of intake (Illius and Hodgson, 1996).

In wooded rangelands, small ruminants often face choices among plants with different nutritive value, and between different types and levels of defence. The question is, then, how do they make these choices and learn to mix their diets from an array of biochemically diverse plants? Possible explanations to this question, to a degree, were given from research dealt with botanical and chemical composition of the diets of goats and sheep grazing in different grazing conditions. These studies showed that small ruminants eat a diverse array of plant species – as many as 100 species have been recorded in studies of small ruminant diets – but the bulk of their meal normally contains less than 10 species. For example, in Mediterranean shrublands, goats sampled from almost all present plant species but the bulk of their diet consisted of few woody and herbaceous species, depending on grazing period (Papachristou and Nastis, 1993a). Moreover, goats selected diets significantly higher in crude protein and IVOMD and lower in NDF, ADF and ADL than forage samples collected by hand plucking mimicking goats' foraging (Papachristou, 1993). From such studies, it was also concluded that a high intake of nutrients was the dominant driving force for selection of a particular vegetation fraction but it was not clear why some plant species or plant parts were avoided even though they contained high proportions of nutrients. Goats, for instance, prefer older growth from the shrub blackbrush, even though current season's growth is much more nutritious than older growth (Provenza and Malecheck, 1984). Similarly, goats (Papachristou and Papanastasis, 1994; Papachristou et al., 1999) and sheep (Dupraz, 1999) rejected the browse of *Amorpha fruticosa*, a leguminous woody species, which is considered to be of high nutritive value and it was proposed

for the Mediterranean grazing systems, and consumed great amounts of other less nutritious woody species. Also, goats tend to select components of their diet such that the condensed tannin concentration in the total diet remains relatively constant throughout the year. This way they may not select the best quality diet available but may avoid wide variations in nutrient content of their diets throughout the year (Kababya et al., 1998).

Late in 1970s, it was discovered that so-called secondary plant metabolites play key roles in the diet selection of herbivores (Freeland and Janzen, 1974; Rosenthal and Janzen, 1979). This realization added another dimension to plant–herbivore interactions. Results of this work showed that environmental factors (e.g. soil nutrients, water, light) influence the evolution and phenotypic expression of secondary plant metabolites (Bryant et al., 1983; Coley et al., 1985), and that herbivory also affects the production of plant defences against grazing (e.g. secondary compounds, morphological characteristics; Milewski et al., 1991; Gill, 1992), which affect the diet selection of herbivores (Launchbaugh et al., 2001; Laca et al., 2001).

According to Provenza (2003), plants that produce secondary compounds have a great resistance to grazing and a better chance of surviving. This happens because plant secondary metabolites limit the potential intake of a specific plant and cause animals to search for other plants (Provenza, 1996). Moreover, the degree to which a plant will be consumed by animals is affected by the kind and abundance of their neighbours (Bryant et al., 1991), in other words from the rangeland plant composition. The fact that all rangeland plants contain some levels of secondary metabolites that at too high doses serve as toxins and limit intake raises the question: How are animals aware of how much to eat of a particular plant and still avoid poisoning?

Recent research (see Launchbaugh et al., 2001; Provenza et al., 2003) suggests there are several adaptive strategies herbivores use to limit ingestion of toxins and increase intake of nutrients. These include the ability to detoxify or tolerate consumed toxins. In addition, the amount of toxins an animal can ingest depends on the kinds and amounts of nutrients and toxins in the available forages. Nutrients and toxins both cause animals to satiate and excesses of nutrients, nutrient imbalances and toxins all limit food intake (Provenza, 1995). Therefore, animals can better meet their needs for nutrients and regulate their intake of toxins when

offered a variety of plants that differ in nutrients and toxins than when constrained to a single plant, even if that is considered the ideal food. This has a significant implication in wooded rangelands, where there is often a dominant species in the overstorey and the rest of the other plants in the understorey (Papachristou and Nastis, 1993a).

How much an animal can eat of a toxin-containing forage depends also on the way a specific toxin is detoxified and eliminated from the body (Foley et al., 1999). The rumen environment with its neutral pH helps in the detoxification either with plant toxin modification or with toxin dilution in the large volume of the rumen (Launchbaugh et al., 2001). Of great significance for ingesting toxic plants is the massive number of rumen microbes that transform most plant toxins into inert or less-detrimental compounds, thereby reducing the toxic effects of plant compounds; however, the degree of detoxification varies across and within animal species. Sheep, for instance, can tolerate and detoxify more of some alkaloids than cattle (Launchbaugh et al., 2001; Pfister et al., 2001). Detoxification of toxic compounds requires adequate availability of nutrients (Freeland and Janzen, 1974; Illius and Jessop, 1997; Provenza et al., 2003). Detoxification processes might compete for protein and energy, which would otherwise be available for animal maintenance and production (Freeland and Janzen, 1974). In pens, supplemental energy and protein allowed goats and sheep to consume more terpene-containing diet and more sagebrush compared to their unsupplemented counterparts (Banner et al., 2000; Villalba et al., 2002a,b,c). Field studies also indicated that supplemental nutrients increased the amount of time supplemented ewes spent feeding on sagebrush, a terpene-containing shrub, compared to unsupplemented ewes (Dziba et al., 2005b). Therefore, supplemental energy and protein enable animals to consume more of foods that contain plant toxins such as terpenes, tannins and saponins (Provenza et al., 2003). Conversely, low levels of sodium in the diet restrict the amount of toxins an animal can ingest, and the sodium-depleting effects of many toxins may deter herbivores from eating plants low in sodium (Freeland et al., 1985). In conclusion, supplemental nutrients help animals cope with toxins by raising toxin-satiation thresholds and reducing the time required to adapt to toxins.

Food intake and preference also depend on differences in how individual animals are reared and acquired

morphological and physiological characteristics, and even closely related animals express differences in the need for nutrients and ability to cope with toxins (Provenza et al., 2003). This individuality has significant implications for managing rangelands and has to be considered in grazing management.

Preference for certain plant species depends on gustatory and olfactory tastes and post-ingestive feedback mechanisms that enable animals to learn the value of different food items (Provenza and Balph, 1987; Provenza, 1995). Learning plays a key role in an animal's propensity to eat foods that differ in amounts of nutrients and toxins (Provenza, 1995; Provenza et al., 2003). When a grazing animal smells and tastes a plant, the flavour is either pleasing or distasteful depending on the animal's previous grazing experiences. Following ingestion, feedback during digestion can be either positive (improved nutrient or energy status of the animal) or negative (illness due to over-ingestion of toxins or nutrients), thereafter the plant flavour becomes more desirable or aversive. These flavour–consequence relationships form the basis for dietary likes and dislikes. The resulting behaviour patterns generally lead to increased consumption of nutritious foods and limited consumption of toxic or low quality plants. However, low quality plants or toxin-containing plants are not always avoided. If animals have been trained and positive consequences are paired with ingesting low quality or toxin-containing plants, then they may consume more of these plants than when they have no positive experience (Villalba et al., 2004).

Also, herbivores learn to mix diets as a function of their experiences eating a variety of foods that contain different kinds of plant toxins and available nutritious alternatives (Provenza et al., 2003). Villalba et al. (2004) showed that sheep learnt to eat different combinations of foods exhibited greater dietary breadth than animals familiar with only a few foods and concluded that this experience enhanced diet breadth and may promote greater use of all plants in a rangeland ecosystem. Nevertheless, herbivores may not learn about such complementarities when familiar and more palatable alternatives are available. Grazing management practices that encourage animals to use all plants of a rangeland favour them to mix a variety of nutrients and toxins, which will likely help them to avoid toxicity. This learning can be transferred to offspring (Thorhallsdotir et al., 1987). Small rumi-

nants live in multi-generational flocks in which dietary information can be passed easily from experienced to inexperienced animals. Learning through imitation is very effective during the weaning stage and thereafter animals can learn by continually sampling and evaluating the usefulness of various food sources (Provenza and Balph, 1987). Importantly, animals associate the aversive effects of excess nutrients or toxins with unfamiliar foods when offered meals that contain novel and familiar foods. Young livestock, therefore, do not require perfect and complete dietary information at birth. However, as animals grow older, they are more influenced by their own dietary experiences than by their mother or other social models.

4. Integration of plant–herbivore interaction knowledge into wooded rangeland management

By understanding plant–herbivore interactions rangeland managers may be able to achieve better ecological and economic returns. Successful grazing management on rangelands and sustainable management of natural resources is a challenge for land managers. Sustainable management of wooded rangelands must aim at ensuring provision of various products and services such as forage, wood production, landscape and recreation, soil protection, and water yield. Grazing animals affect vegetation community dynamics and the responses of associated fauna, and on the other hand, rangeland characteristics such as plant composition, forage availability and distribution within the grazing environment affect the foraging behaviour and nutrition of individual herbivores. In the complex grazing environment of wooded rangelands, small ruminants must consume a mixed diet from different plants that contain various levels of nutrients and toxins and whose quality varies from season to season. Small ruminants face foraging decisions between the benefits of nutrient intake and the costs of toxin ingestion, and the challenge of plant morphological characteristics (e.g. leave spines, thorns) that decrease rates of food intake and may cause injury.

The Mediterranean shrublands dominated by kermes oak are a good example of how to integrate growing understanding of plant–herbivore interactions. Since the early 1970s rangeland managers started to apply management techniques on densely wooded

shrublands to increase and diversify forage production, as well to create a heterogeneous landscape. This management had as its goal reducing the woody species such as kermes oak, which is less useful in terms of maximizing animal performance than the herbaceous species, but at the same time ensuring green forage for animals during the dry period of the year when herbs are not available. Thus a percentage of 50% woody cover had to be left and rangeland managers must then accept the lower returns associated with animals consuming well-defended forages to ensure animal survival.

The first step in this management regime is opening up the shrub canopy via prescribed burning, manual thinning or mechanical means. However, opening up shrublands raises a number of questions. Will woody vegetation be removed until the desired percentage of shrub cover is achieved or should the removal of non-preferred woody species also be considered? For example, in Greek shrublands, kermes oak appears in five rangeland types (I–V) that differ in leaf morphology and acceptance to goats. Thus, the eradication of the III and V kermes oak types, which are considered to be of low acceptability, would be a necessary management tool to improve forage conditions. However, maintaining acceptable kermes oak types I, II and IV in shrublands is a costly and recurring problem for land management agencies. In the wet months, goats consume the largely defenceless undergrowth of herbaceous species, whereas in the dry months when herbs are dry or no longer available they are left with only the kermes oak with its physical and chemical defences (Papachristou and Nastis, 1993a). Thus, in the dry months, goats rely on kermes oak because it is the only forage left and consume it in great amounts while they avoid it in wet months. Moreover, goats survive on kermes oak, which means that plant defences are not a complete barrier (Papachristou et al., 2003). Rather, defences just place the plant further down the preference list. The fact that plant defences are so widespread and often herbivores have no choice but to consume plants with defences, suggests that they are well aware of the consequences of eating most plant species (Provenza, 1996). This latter in combination with the growing knowledge on the role of learning and experience of animals gives reasons to think that sheep and goats have significant knowledge of the plant species and their defences in their home rangeland. In relation to plant defences, animals avoid defences

where possible and if not possible select the plant with the least effective defence. This may be simple and indeed obvious but it enables animals to react quickly to changes in habitat composition across seasons.

Based on experimental findings (see Provenza, 1995, 1996; Burritt and Provenza, 2000; Provenza et al., 2003), we suggest that an alternative approach to managing wooded rangelands in a sustainable way could be based on the small ruminant's natural abilities to deal with anti-quality attributes, instead of modifying the vegetation. This can be partially achieved with the creation of animal flocks including individuals that can overcome mechanical and chemical plant defences. For example, in sagebrush ecosystems, selecting or shaping animals with a superior ability to digest and detoxify terpenes contained in sagebrush forage could greatly increase the amount of available forage. Another simple approach, also tied to the animal, is selection of appropriate animal species that can utilize plants or plant parts of low quality or mechanically and chemically defended. For example, goats can graze kermes oak shrublands more safely than sheep because they are less sensitive to the mechanical and chemical defences in kermes oak (Papachristou, 1997b; Papachristou et al., 2003). This simple concept is often difficult for livestock raisers to enact because changing livestock species generally requires substantial changes in their facilities, management skills, knowledge, and philosophy.

Liacos (1982) argued that any effort to control woody vegetation has to be followed by an appropriate grazing management scheme otherwise it will fail. In the Mediterranean region a series of such grazing management schemes were applied by modifying the seasonal growth pattern of the dominant woody species in Mediterranean shrublands (i.e. kermes oak), which produces new growth in spring and again in autumn with the first rains after the dry summer. Tsiouvaras (1984) found that clipping current growth every 15 days in summer, when soil water was limited, stimulated new growth that favoured high nutritive value. In grazing conditions, this can be achieved with rotational grazing that stimulates the production of new browse growth. Such rotational grazing will minimize the production of specific kermes oak types with increased defences against grazing (e.g. spines; Papachristou et al., 2003). In semi-arid savannas, a combination of grazing with goats and controlled burning enhanced

forage production (Teague and Trollope, 1981). Varying stocking rates and stocking density modifies the impact of goats to achieve desired management goals. For instance, when the goal is to produce more herbaceous understorey, the stocking rates of goats can be increased compared to when the goal is to produce browse biomass on a sustainable basis.

Stocking density has a substantial impact on the way animals learn about different plants (Provenza et al., 2003). Low to moderate animal densities encourage selective foraging, which may prevent learning about complementarities among less palatable plants because animals can simply “eat the best and leave the rest.” Conversely, high animal densities likely encourage animals to learn to “mix the best with the rest” during a meal. When animals “eat the best first, then eat the rest” they dissociate in time high and low-quality foods, which depending on when and how foods are replenished could have a long-term influence on foraging behaviour (Villalba et al., 2004).

Grazing management schemes also have to exploit the differences in foraging behaviour of sheep and goats (Pfister et al., 1988; Papachristou, 1997b). Goats use the forage in the vertical stratum (browse) thereby allowing herbaceous species to be consumed by sheep in wooded rangelands. In addition, where forage is sparse and varied, as in semi-arid areas, small ruminants are expected to perform better than cattle. Evolutionary bulk eaters such as cattle tend to be fixed in their foraging strategy, in part due to the large amount of food they must consume daily, while the more versatile feeding behaviour of small ruminants allows more scope for selection of preferred fractions. Based on studies of diet selection of cattle, goats and sheep grazing in semi-arid heterogeneous vegetation, Nolan and Connolly (1992) concluded that small ruminants had greater ability to extend the range of plants consumed during the dry season when overall vegetation availability was sparse. Similarly, Papachristou et al. (2005, see present issue) found that cattle diets comprised mostly herbage (97%) in oak woodlands throughout the year while goats’ diets consisted of a mixture of browse (67%), and herbaceous species (33%). Mixed grazing can serve as a management tool on wooded rangelands by limiting the stocking rate of any one animal species to the level which will make optimum use of its preferred vegetation categories and to make up the remainder required to achieve overall efficient use

of vegetation with animal species with preferences for the remaining vegetation categories.

Finally, herders have to use understanding of biochemical diversity to stimulate food intake and more fully use the range of plants available by herding in grazing circuits (Meuret, 1997). A such circuit includes a moderation phase, which provides animals access to plants that are abundant but not highly preferred to calm a hungry flock; the next phase is a main course for the bulk of the meal with plants of moderate abundance and preference; then comes a booster phase of highly preferred plants for added diversity; and finally a dessert phase of palatable plants that complement previously eaten forages (Baumont et al., 2000). Daily grazing circuits are perfect for wooded rangelands with heterogeneous forage conditions and aim to stimulate and satisfy an animal’s appetite for different nutrients, and they enable animals to maximize intake of nutrients and regulate intake of different toxins (Provenza, 2003).

5. Future research and challenges: perspectives for grazing management and maintenance of landscape biodiversity

Nowadays, the greatest challenge is conserving natural resources and maintaining landscape biodiversity while simultaneously producing enough food to satisfy the demands of a growing human population. There is evidence that the state of natural resources is generally deteriorating, particularly in the developing regions of the world. Grazing animals such as goats are often considered as destroyers of natural resources and some people advocate their exclusion despite the fact that most of these systems evolved with grazing. Ecologists agree that grazing animals are a part of natural ecosystems and the harmonious coexistence of natural resources and herbivores is feasible with appropriate grazing management. This requires thoughtful use and conservation of rangeland resources – plants, animals, soil, and water – to meet the needs of current and future generations.

Enhancing and maintaining biodiversity is an integral part of conservation and herbivory affects biodiversity by influencing the structure and dynamics of plant and animal communities. Although herbivory has the potential to either increase or decrease species diversity or abundance, little is known about how patterns

of preference are modified by biochemical diversity in ways that may in turn alter biodiversity of landscapes. Biochemical diversity refers to a variety of complex ways by which plant secondary compounds and nutrients interact (Provenza et al., 2003). All plants contain toxins, which influence how herbivores select among a variety of plants that contain different kinds of toxins. However, isolated effects of toxins or nutrients do not adequately predict diet selection (Villalba et al., 2002a,b,c). Rather, complex interactions between nutrients and toxins in plants influence herbivore foraging behaviour. These non-linear interactions may be complementary, antagonistic or simply additive. Hence a plant with toxins will not always be avoided by herbivores nor will a highly nutritious plant always be preferred (Burritt and Provenza, 2000; Provenza et al., 2003). Assuming animals have experience with all nutrients and toxins in an ecosystem, will they forage in areas of maximum biochemical diversity where nutrient–toxins interactions mitigate toxin effects and enhance nutrient intake (Provenza et al., 2002)?

Traditional functional response theory explains herbivory based on constraints set by plant physical characteristics and predicts intake solely on the basis of plant biomass (Spalinger and Hobbs, 1992; Ungar, 1996). Yet, plant biochemical diversity is a critical facet of plant community dynamics and plant–herbivore interactions (Pastor and Cohen, 1997; Provenza et al., 2002, 2003). Nutrient–toxin interactions set the asymptote that defines satiation as the maximum detoxification capacity of an herbivore. Above this critical threshold, herbivory will favour domination by a plant chemotype; below it, local extinction is more likely as a species becomes less abundant (Bryant et al., 1991). While plants that are chemically defended tend to be unpalatable and avoided (Palo and Robbins, 1991), when chemically defended plants are rare and occur with nutritious neighbours they may be persistently used (Augner, 1995; Palmer et al., 2003). Toxic plants are used relentlessly as long as their toxicity does not exceed the detoxification capacity of herbivores (Freeland and Janzen, 1974). Supplements can enhance the capacity for detoxification and effectively create a unique opportunity to use livestock as a tool to enhance biodiversity. This is another area that deserves more research attention.

An integrated understanding of how plant biochemical diversity influences foraging by large mammalian

herbivores at the landscape-level and what bearing this, in turn, has on plant community dynamics will have profound implications for enhancing biodiversity of landscapes. Knowledge of foraging behaviour can markedly improve the efficiency and profitability of rangeland ecosystems, the quality of life for land and livestock managers, and the integrity of the environment. In the end, there are thresholds of plant biochemical diversity above which diversity begets diversity and below which a lack of diversity leads inexorably to less diversity (Kauffman, 1995, 2000).

Agent-based models integrate the functioning of the whole system and its influence on the behaviour of individuals (DeAngelis and Gross, 1992; Grimm, 1999) and might be used in concert with in-field studies for anticipating long-term effects of herbivory on plant communities. Agent-based models are good at illustrating the long-term dynamics of herbivory and can be used to assess potential plant community changes given different levels of plant biochemical diversity (Basset et al., 1997; Grimm, 1999). These models assess how complex non-linear dynamic systems function and are useful for investigating concurrent, distributed systems in which autonomous agents interact in a dynamically changing environment (Minar et al., 1996).

6. Conclusions

Foraging on wooded rangelands poses several significant challenges to small ruminants that must utilize both browse and herbaceous species to overcome starvation, meet nutritional needs, gain weight, and produce while avoiding mechanical and chemical defences that are integral components of wooded rangeland vegetation. Small ruminant management in such situations can be challenging. Developing grazing management plans to minimize the impacts of plant defences requires an understanding of the behavioural and physiological mechanisms small ruminants possess to extract nutrients from low quality or mechanically and chemically defended plants.

Although, plant defences are abundant they are not a complete barrier to small ruminants as they often use woody plants as part of their diets. Whereas controlled experiments might show a strong rejection of plants with defences when given as a choice with defenceless species, it does not necessarily follow that the species

with defences do not appear in herbivore diets in natural systems. Indeed plants with such defences may represent a significant forage resource enabling small ruminants to survive on wooded rangelands with a prolonged dry period when more preferred defenceless species are absent. New frontiers in forage and grazing management therefore lie in understanding the basics of small ruminant foraging ecology in relation to anti-quality characteristics.

Key objectives for future research in plant–herbivore interactions should include investigating how plant biochemical diversity influences herbivore preference for various plant communities, modelling how herbivore selectivity at various levels of plant biochemical diversity influences plant community dynamics, and integrating this information to develop recommendations for managing in ways that enhance and maintain biodiversity.

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