Mediterranean shrub diversity and its effect on food intake in goats

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Abstract

Mediterranean ecosystem offers a variety of shrubs that were over long periods of time involved in the evolution of complex plant-animal interactions. Biochemical components of these plants enter different metabolic pathways after digestion and absorption, resulting in development of dietary preferences in browsing animals. Herbivores in general were found to perform better when grazing in a mixed plant community composed of diverse species, and show preferential feeding behaviours for mixed vs single species diet. Our findings demonstrate an asymptotic relationship among Mediterranean shrubs species diversity and their voluntary intake by goats. Shrub biomass intake showed linear increase when number of different shrubs in diet increased from one to three. However, goats did not further increase intake when the number of shrub species increased from four to eight. As the number of shrub species offered increased, goats exhibited more preferential feeding behaviour for Quercus pubescens, Praxinus ornus, Rubus heteromorphus and Arbutus unedo and decreased the intake of Hedera helix, Juniperus oxycedrus and Helichrysum italicum. This asymptotic relationship indicates that the maintenance of plant species richness in Mediterranean shrublands can overall benefit domestic goat farming, goat’s productive performance, and the conservation of plant biodiversity.

Introduction

Plant and animal ecologists have been striving for decades to understand the mechanisms by which herbivores interact with plant resources and adapt their foraging behaviours. Herbivores have more opportunities to choose the palatable plants and optimise nutrient intake when plant species diversity is higher. Simultaneously, a greater variety of plant species makes it more difficult for them to determine and select which foods best meet their nutritional needs, due to more choices and greater biochemical complexity. The domestic goats (Capra hircus L) in extensive and intensive farming operations along the Mediterranean basin represent one of the most important biological factors determining the structure and species composition of the Mediterranean maquis plant community (Rogosic, 2000). Several studies show that small ruminants and herbivores in general show better performance when consuming a mixture of different plant species (Burritt and Provenza, 2000; Marsh et al., 2006; Rogosic et al., 2006b). Small ruminants were also found to consume more shrub biomass when foraging in a plant community of higher species diversity and richness (Rogosic et al., 2006a, 2007). Furthermore, a steady increase in food intake was observed as the number of plant species offered to sheep and goats increased. Ruminants show tendency for a selective feeding behaviour within a mixture of plant species to better meet their needs for nutrient supply and to avoid toxicity (Provenza, 1995, 1996). Proposed are several different hypotheses that play a role in this phenomenon. The nutrient balance hypothesis proposes that dietary diversity allows individuals to balance intake of different nutrients. The detoxification limitation hypothesis predicts that the amount of food that an herbivore can safely ingest directly correlates with the detoxification rate of plant secondary metabolites contained in the food (Freland and Janzen, 1974). The satiety hypothesis suggests that satiety can be achieved faster when herbivores eat a mixed and rich diet due to interactions among primary and secondary compounds within their gastrointestinal tract. Satiety in that aspect causes transient food aversions that result in preferential feeding behaviours: animals are seeking variety of foods and forage in a wider range, which has an indirect positive effect on their health and performance (Provenza, 1996; Provenza et al., 2003).

The objectives of this study were to determine: i) the hypothesis of an asymptotic relationship between Mediterranean shrub species diversity and food intake by goats; ii) whether introduction of a new shrub in the goats’ mixed diet reduces the intake of previously offered shrubs; and iii) whether goats’ preference changes for the same shrub if offered individually or simultaneously with other shrubs in a mixed diet.

Materials and methods

Study site and test animals

The study was conducted at the Ecological Center Zemunik Donji, located at University of Zadar, Croatia. Research protocols for this study were approved by the Ministry of Agriculture, Agency for Animal Care and Use Committee; No. UP/I-322-01/11-01/118, Republic of Croatia. The experimental goats (4 months of age) were cross-breeds of domestic goats with Saanen and Alpine breeds. These cross-breeds are recognised for their favourable milk production and excellent foraging capabilities on shrub ranges in the coastal Adriatic region. All experimental animals were raised on the same farm and were fed shrubs of the Mediterranean maquis. Eighteen goats of both sexes, with the mean
body weight (BW) of 13.4 kg, were kept outdoors, in individual, roof-covered adjacent pens measuring 2.0 m×2.5 m. Throughout all the experiments, all animals had free access to trace mineral blocks and fresh water. The study was conducted from June to August 2011.

Mediterranean maquis and study shrubs

This study included 8 dominant shrub species of the Mediterranean pubescent oak maquis plant community: downy oak or pubescent oak, Quercus pubescens Willd (Fagaceae); English ivy, Hedera helix L. (Araliaceae); prickly juniper, Juniperus oxycedrus L. (Cupressaceae); South European flowering ash, Fraxinus ornus L. (Oleaceae); curry plant, Helichrysum italicum (Roth) G. Don (Asteraceae); blackberry, Rubus heteromorphus Ripart ex Genev. (Rosaceae); strawberry thorn, Rubus heteromorphus L. (Rosaceae); blackberry, Rubus heteromorphus L. (Rosaceae); strawberry thorn, Rubus heteromorphus L. (Rosaceae); and mastic tree, Pistacia lentiscus L. (Anacardiaceae). Together they constitute about 70% of the shrubby vegetation from a total of 30 to 35 commonly browsed species within the Ostryo-Quercetum pubescentis maquis plant community (Rogosic, 2000). All of these species represent important dietary components for farmed sheep and goats in the coastal region of Eastern Adriatic (Rogosic et al., 2006b). All shrubs were hand-harvested each week within 3 km of the research station. Leaves and 1-yr-old twigs (about 10 cm in length) were clipped and placed in paper bags. Within 1 h the plant material was ground to 1 cm in length with a chipper, mixed for uniformity, placed in woven polyethylene bags and refrigerated at +4°C. During the experiment, new bags of shrubs were removed from the cold storage each morning and offered to animals.

Experimental protocol

Prior to the experiment, baseline intake of alfalfa pellets was determined for each animal for 5 days. After establishing the baseline, all animals entered a 5-day preconditioning period and were fed ad libitum a mixture of 8 Mediterranean shrubs that would be used in the study to reduce neophobia. After this precondition period, 18 goats were randomly assigned to 3 groups (6 animals per group). The length of the experiments was 5 days and treatment groups remained the same during the experiments. Throughout the duration of the experiment, each goat received 100 g of barley at 08:00-08:30 h and the serving of 200 g of each shrub species offered simultaneously in separate feeders at 09:00 and left until 15:00 h. Animals and food boxes were inspected every 30 min and additional feedstuff was added as needed. At 15:00 h, refusals and leftover feed were collected, measured, the total daily intake was determined and no other food was offered until the next morning. The same procedure was carried out for each experiment. Among the experiments, alfalfa pellets and barley were fed at maintenance level for 3 days.

Statistical analyses

The experimental design for the shrubs fed individually to goats was randomised. The model included 3 groups (Table 1) and shrub species (in different experimental groups). The total daily shrub intake in each experiment was used as the dependent variable in the analysis. A one-way ANOVA was used for all analyses and means of the groups were compared among groups through using Tukey’s test. The significance level was set at P<0.05. Statistical dependence between number of shrubs and total daily shrub intake by animals in group 1 was calculated by Spearman rank correlation. All analyses on shrub intake were adjusted for body weight (g/kg BW) and performed with the SAS 8 statistical package (SAS, 1999).

Results

In experiment 1, there was not a significant difference among 3 groups of goats fed with Q. pubescens (19.78±1.91 vs 21.73±1.49 vs 20.09±1.67 g/kg BW; P=0.68; Figure 1).

Table 1. Shrub species offered to goats during 8 consecutive experiments.

| Experiment | Group 1 | Group 2 | Group 3 |
|------------|---------|---------|---------|
| 1          | Quercus pubescens | Quercus pubescens | Quercus pubescens |
| 2          | Quercus pubescens; Hedera helix | Quercus pubescens; Hedera helix | Quercus pubescens; Hedera helix |
| 3          | Quercus pubescens; Hedera helix | Quercus pubescens; Juniperus oxycedrus | Quercus pubescens; Juniperus oxycedrus |
| 4          | Quercus pubescens; Hedera helix; Juniperus oxycedrus; Fraxinus ornus | Fraxinus ornus | Quercus pubescens |
| 5          | Quercus pubescens; Hedera helix; Juniperus oxycedrus; Fraxinus ornus; Helichrysum italicum | Helichrysum italicum | Quercus pubescens |
| 6          | Quercus pubescens; Hedera helix; Juniperus oxycedrus; Helichrysum italicum; Rubus heteromorphus | R. heteromorphus | Quercus pubescens |
| 7          | Quercus pubescens; Hedera helix; Juniperus oxycedrus; Fraxinus ornus; Helichrysum italicum; Rubus heteromorphus; Arbatus unedo | Arbatus unedo | Quercus pubescens |
| 8          | Quercus pubescens; Hedera helix; Juniperus oxycedrus; Fraxinus ornus; Helichrysum italicum; Rubus heteromorphus; Arbatus unedo; Pistacia lentiscus | Pistacia lentiscus | Quercus pubescens |
Goats in group 1 of the experiment 2 ate equal amounts of *Q. pubescens* and *H. helix* (Table 2), and they ate more of that combination of shrubs than did goats in group 3 that were fed only *Q. pubescens*, but not more than goats in group 2 fed only *H. helix* (Figure 1).

In the experiment 3, goats in group 1 ate more of a combination of *Q. pubescens*, *H. helix*, and *J. oxycedrus* than did goats in group 2 fed only *J. oxycedrus* or in group 3 fed only *Q. pubescens* (Figure 1). Goats in group 1 ate more *Q. pubescens* and *H. helix* than *J. oxycedrus* (Table 2).

In experiment 4, goats in group 1 ate more of a combination of *Q. pubescens*, *H. helix*, *J. oxycedrus*, and *F. ornus* than did goats in group 2 fed only *F. ornus* or in group 3 fed only *Q. pubescens* (Figure 1). Within the group 1, goats ate more *Q. pubescens* and *H. helix* than *J. oxycedrus* and *F. ornus* (Table 2).

Goats in group 1 of experiment 5 ate much more of a combination of *Q. pubescens*, *H. helix*, *J. oxycedrus*, *F. ornus*, and *H. italicum* compared with goats in group 2 fed only *H. italicum* or in group 3 fed only *Q. pubescens* (Figure 1). Goats in group 1 ate more *Q. pubescens* than any of the other shrubs; they ate similar amounts of *H. helix*, *J. oxycedrus*, and *F. ornus*, but very little *H. italicum* (Table 2).

Goats in group 1 of experiment 6 ate much more of a combination of *Q. pubescens*, *H. helix*, *J. oxycedrus*, *F. ornus*, *H. italicum*, and *R. heteromorphus* compared with goats in group 2 fed only *R. heteromorphus* or in group 3 fed only *Q. pubescens* (Figure 1). Goats in group 1 ate more *Q. pubescens* than any of the other shrubs; they ate similar amounts of *H. helix*, *J. oxycedrus*, and *F. ornus*, but very little *H. italicum* or *R. heteromorphus* (Table 2).

Goats in group 1 of experiment 7 ate much more of a combination of *Q. pubescens*, *H. helix*, *J. oxycedrus*, *F. ornus*, *H. italicum*, *R. heteromorphus*, and *A. unedo* compared with goats in group 2 fed only *A. unedo* or in group 3 fed only *Q. pubescens* (Figure 1). Goats in group 1 ate more *Q. pubescens* than any of the other shrubs; they ate similar amounts of *H. helix*, *J. oxycedrus*, *F. ornus*, and *A. unedo*, but very little *H. italicum* or *R. heteromorphus* (Table 2).

Goats in group 1 of experiment 8 ate more of a combination of *Q. pubescens*, *H. helix*, *J. oxycedrus*, *F. ornus*, *H. italicum*, *R. heteromorphus*, *A. unedo*, and *P. lenticus* compared with goats in group 2 fed only *P. lenticus* or in group 3 fed only *Q. pubescens* (Figure 1). Goats in group 1 ate more *Q. pubescens* than any of the other shrubs; they ate similar amounts of *H. helix*, *J. oxycedrus*, *F. ornus*, and *A. unedo*, but very little *H. italicum*, *R. heteromorphus*, or *P. lenticus* (Table 2).

The relationship between the increase of the number of Mediterranean shrubs in a mixed shrub diet and the voluntary shrub biomass intake by goats in 8 consecutive experiments is presented in Figure 2.

**Discussion**

The present study has established an asymptotic relationship between the increase.
of the number of different Mediterranean shrubs in a mixed shrub diet and the voluntary shrub biomass intake by goats in 8 consecutive experiments in the group 1 (Figure 2). This can be explained by the development of preferential feeding attitude of goats to satisfy their nutritional needs and regulate intake of secondary compounds when given the opportunity for voluntary selection among variety of shrub species (Provenza, 1996). Goats in group 1 increased the overall shrub biomass consumption when number of shrubs increased from 1 to 2 (P<0.001) and from 2 to 3 (P=0.015). However, this trend was not observed when the number of shrubs increased from 4 to 8. After the fourth shrub was offered to goats, the asymptotic curve had a horizontal trend suggesting that the diversity and richness of Mediterranean shrubs increases the biomass intake to a certain level, after which the intake of shrubs shows only a minimal variation around the peak value.

Average daily intake of shrubs by goats in group 1 showed an increasing trend throughout the entire research period (Figure 2), indicating a strong correlation between number of shrub species offered and the total intake of Mediterranean shrubs (t=0.78; P<0.001). The largest increase in shrub biomass intake was recorded when the number of shrubs increased from 1 to 2 (Exp. 2; P<0.001) and from 2 to 3 (Exp. 3; P=0.015). Thereafter, consumption of shrubs progressively increased, but did not show a statistically significant difference.

Goats in group 2 showed great variability in average daily intake among different experiments, depending of the species offered (Figure 2). The highly consumed shrubs in group 2 were: *Hedera helix*, *Juniperus oxycedrus*, *Juniperus oxycedrus*, *Arbutus unedo*, and *Helichrysum italicum*. However, when we offered all 8 shrubs together to goats in group 1 (Exp. 8), intake was different than when shrubs were offered individually. As the variety of shrubs offered in the diet increased, goats showed a preferential feeding pattern and decreased the intake of *Hedera helix*, *Juniperus oxycedrus* and *Helichrysum italicum*, but not of *Quercus pubescens*, *Fraxinus ornus*, *Rhamnus heteromorphus* and *Arbutus unedo*.

Intake of *Quercus pubescens* in group 3 did not change throughout all experiments (Figure 2), and ranged between 20.5 and 25.8 g/kg BW from the first to the last experiment.

Although previous studies have shown that generalist herbivores, especially ruminants, perform better when eating a mixture of plant species (Bernays et al., 1994; Burritt and Provenza, 2000; Marsh et al., 2006), this is the first study to show that goats will not show a constant linear increase in biomass intake as the number of shrubs in their diet increases. The generalist herbivores were found to consume greater quantities when grazing a plant community of higher species diversity, but these studies only considered the effects of mixed diets by comparing the two extremes: single vs mixed species (Burritt and Provenza, 2000; Marsh et al., 2006). The possible expla-

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**Table 2. Average shrub intake by goats (g/kg BW±SEM) in Group 1 (n=6) in all eight experiments.**

| Shrubs          | Experiment 1 | Experiment 2 | Experiment 3 | Experiment 4 | Experiment 5 | Experiment 6 | Experiment 7 | Experiment 8 |
|-----------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| *Quercus pubescens* | 19.78±1.91   | 19.2±1.94    | 19.6±1.76    | 19.5±2.26    | 20.7±1.60    | 21.9±1.57    | 21.0±1.46    | 20.9±1.56    |
| *Hedera helix*   | 19.9±3.29a   | 17.0±1.96ab  | 13.1±1.66bc  | 9.8±1.48a    | 7.1±0.80c    | 7.0±0.33c    | 7.5±1.37c    | 7.4±0.65c    |
| *Juniperus oxycedrus* | 10.9±0.50a  | 7.0±0.53a    | 7.9±0.69b    | 8.1±0.69c    | 10.0±0.94a   | 10.2±1.14c   | 10.4±1.14c   | 10.4±1.14c   |
| *Fraxinus ornus*  | 8.3±1.23     | 8.3±0.69     | 10.0±0.94    | 10.2±1.14c   | 10.2±1.14c   | 10.4±1.14c   | 10.4±1.14c   | 10.4±1.14c   |
| *Helichrysum italicum* | 1.4±0.14a | 0.2±0.05b    | 0.3±0.04c    | 0.3±0.04c    | 0.3±0.04c    | 0.3±0.04c    | 0.3±0.04c    | 0.3±0.04c    |
| *Rubus heteromorphus* | 1.9±0.38     | 2.5±0.65     | 1.9±0.38     | 1.9±0.38     | 2.5±0.65     | 1.9±0.38     | 1.9±0.38     | 1.9±0.38     |
| *Arbutus unedo*   | 5.5±1.00     | 5.5±1.00     | 5.5±1.00     | 5.5±1.00     | 5.5±1.00     | 5.5±1.00     | 5.5±1.00     | 5.5±1.00     |

*aDifferent letters indicate the statistically significant differences within each shrub species (P<0.05).*

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**Figure 2. Total shrub intake in 3 groups of experimental goats (n=6 per group) fed ad libitum.** In group 1 the number of shrubs offered to goats increased gradually from 1 to 8 over the experiments. In group 2, goats were fed exclusively the same new shrub that was added to the diet of group 1. In group 3, *Quercus pubescens* was offered to goats throughout all eight experiments. Different letters indicate statistically significant differences (P<0.05) among experiments within the same group.

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nation for this phenomenon includes monotonous flavour, nutrient or toxin composition, and biochemical capacities for toxin neutralisation and elimination (Provenza, 1996; Provenza et al., 2003). Within Mediterranean shrublands, which are generally low in nutritional quality (Rogosic et al., 2006a), the increases in shrub species diversity and richness in goats diet led to an increase in food intake that will presumably result in the increased daily nutrient intake with an overall positive effect on their nutritional status and production performance. The asymptotic relationship indicates that the maintenance of plant species diversity in Mediterranean maquis ecosystem will benefit both domestic herbivore production and the conservation of plant biodiversity.

The Mediterranean maquis consists of numerous shrubs species (Rogosic, 2000) with different growth patterns and concentrations of nutrients and secondary compounds. They also come in a variety and various intensities of flavours that contribute to the differences in their palatability for browsing goats (Rogosic et al., 2006b). The level of palatability of plants also depends on other types of food present in a mixed diet (Rogosic et al., 2006a). From the aspect of the plant defense mechanisms, none of these can guarantee a reduced consumption; their efficacy is multifactorial and depends of the biochemical characteristics of plant itself, but it also involves availability and characteristics of other plants in the herbivore diet and their interactions within the animal’s body. Consequently, some plant defense mechanisms will be effective in a given environment, but not in others, making generalisation about its efficacy conditional (Offü and Ritchie, 1998). We suggest that the reason for the difference in overall intake and dietary preferences of investigated shrubs in goats was not its poor nutritional quality (Rogosic et al., 2006b), but rather a composition of different classes and concentrations of secondary compounds as the plant’s defense mechanisms (Burritt and Provenza, 2000). This can be supported by findings that high concentrations of tannins in Quercus calliprinos reduce preference of that shrub by sheep and goats (Perevolotsky et al., 1993). Tannins were also found to limit intake of strawberry trees (Arbutus unedo) and holly oak (Quercus ilex), dominant shrubs in Mediterranean maquis vegetation (Rogosic et al., 2006a, 2006b). Thus, as most Mediterranean shrubs contain secondary compounds, consumption of a variety of plants and their parts by herbivores results in the intake of different types and concentrations of secondary compounds (Rogosic et al., 2007). With respect to this, toxic compounds compel herbivores to select a variety of plants to meet their nutritional needs because pathways of detoxification are saturable (Freeland and Janzen, 1974). Thus, as animals meet detoxification capacities for particular toxins, they must find alternative forage sources with complementary nutrients and toxins (Rogosic et al., 2006a; Burritt and Provenza, 2000). While herbivores have evolved mechanisms to deal with phytochemicals to a certain extent, practical management methods to safely increase shrub intake by livestock are warranted. A variety of management practices and diet additives have been already investigated to allow the increase in the intake of secondary metabolites (Provenza et al., 2000). One approach involves supplementation of various nutrients that will counteract negative effects on nutrient absorption in the intestinal tract and/or enhance clearance of secondary compounds post-absorption. In addition to nutritional manipulation, a variety of treatments and dietary additives that enhance detoxification, reduce absorption, or otherwise counteract limitations of secondary compounds on intake have been investigated (Provenza et al., 2000; Rogosic et al., 2006c, 2008, 2009). Increased dietary diversity (increased number of shrub species consumed) and complementarity of shrubs containing different classes of secondary compounds have also been considered in sheep (Rogosic et al., 2007).

Goats browsing on Mediterranean shrublands select plants that are richer in nutrients and have lower concentrations of toxins than the average levels present in the surrounding vegetation (Rogosic et al., 2006b). One of the mechanisms involved is the association of the sensory properties of food plants with their postingestive consequences and adjust their diet selection appropriately, it is not clear how relevant such mechanisms are to the complex diets generally consumed by free-ranging herbivores. In these animals, anyone feeding bout might include a number of different plant species, and the possibilities for associating postingestive consequences with particular species appear remote. The ability of goats to associate toxic effects with the sensory properties of food plants containing the toxic compounds is thought to be an important means by which they can learn to avoid toxic plants (Provenza, 1995).

Conclusions

Mediterranean maquis plant communities usually consist of 20 to 25 shrubby species which are generally high in secondary compounds and low in nutritional quality. The shrub species diversity has a positive effect on goats’ food intake and nutrition. Goats browsing in diverse maquis plant communities encounter a wide array of biochemical compounds (nutritious, toxic, and beneficial) that create a multidimensional feeding environment. Our experiments demonstrate an asymptotic relationship between shrubs species diversity and their voluntary intake by goats. Shrub biomass intake showed a linear increase when number of shrubs is increased from 1 to 3, but not when number of shrubs is further increased from 4 to 8. The asymptotic relationship indicates that the maintenance of plant species richness in Mediterranean shrublands will benefit both domestic goat (and possibly other herbivores) and the conservation of biodiversity.

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