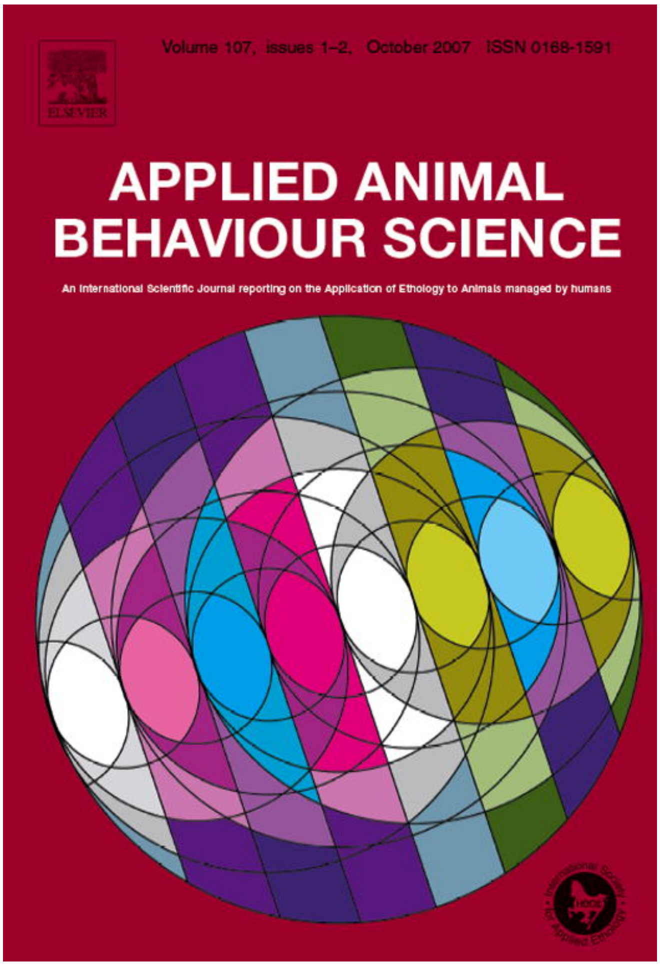
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Influence of secondary compound complementarity and species diversity on consumption of Mediterranean shrubs by sheep

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Abstract

Generalist herbivores foraging in chemically diverse grazing ecosystems like the Mediterranean maquis increase intake on mixed diets, suggesting they are more able to meet nutritional needs and avoid toxicosis. Thus, our objectives were to determine how shrub species diversity and complementary interactions between tannins and saponins influence intake of Mediterranean shrubs by sheep. We conducted four experiments (10 days each) comparing intake of mixtures of Mediterranean shrubs varying in number of species and/or principal class of secondary compound (tannins or saponins) by sheep ($n = 12$). Sheep consumed more total foliage ($P < 0.01$) when offered a high-tannin shrub (*Pistacia lentiscus*; Exp. 1), two high-tannin shrubs (*P. lentiscus* and *Arbutus unedo*; Exp. 2), or three high-tannin shrubs (*P. lentiscus*, *A. unedo*, and *Quercus ilex*; Exp. 3) when fed in conjunction with a high-saponin shrub (*Hedera helix*) than with an equal number of high-tannin shrubs (20.9 g/kg BW versus 16.3 g/kg BW; 28.8 g/kg BW versus 20.8 g/kg BW; and 35.3 g/kg BW versus 26.9 g/kg BW). Likewise, sheep ate more foliage ($P < 0.01$) of each additional individual shrub (*P. lentiscus*, *A. unedo*, and *Q. ilex*) in the mixture when fed with *H. helix* than with an equal number of high-tannin shrubs (8.2 g/kg BW versus 5.0 g/kg BW; 13.3 g/kg BW versus 10.7 g/kg BW; and 7.6 g/kg BW versus 5.2 g/kg BW; Exps. 1–3, respectively), suggesting a complementary interaction between tannins and saponins may have occurred. Sheep also appeared to increase total shrub intake as number of shrub species on offer increased, regardless of number of classes of compounds present.

Our findings suggest that secondary compounds in Mediterranean shrubs (tannins and saponins) are complementary. Species diversity also plays an important role in diet selection, as plant species with

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different types and amounts of nutrients and phytotoxins may affect forage intake and animal production. This knowledge will help livestock producers to capitalize on phytochemical interactions to enhance intake, optimize forage utilization, and ultimately improve performance of browsing ruminant herbivores.

Keywords: Biodiversity; Complementarity; Mediterranean maquis; Saponins; Secondary compounds; Sheep; Shrubs; Tannins

1. Introduction

Herbivores have major effects on Mediterranean maquis ecosystems and their effects vary across time and space (Rogosic et al., in press-a). Plant and animal ecologists are interested in understanding the mechanisms by which herbivores interact with forage resources and adjust foraging behavior. Typically, herbivores exhibit partial preferences such that a plant may be ingested or ignored (Wilmshurst et al., 1995). Partial preferences for certain plant species have been attributed to the inability of herbivores to discriminate among different plant species (Illius et al., 1999), limited perception (Berec and Krivan, 2000), attempts to meet nutritional needs (Westoby, 1978), or reducing intake of phytotoxins (Freeland and Janzen, 1974). The emerging evidence which integrates biochemical interplay between plant species and animal learning suggests that varied diets result from the interaction of experience with flavor, nutrients, and phytotoxins (Provenza, 1995; Provenza et al., 2003). Herbivores integrate the postingestive effects of nutrients and phytotoxins with sensory experience that results in flavor–nutrient–phytotoxin interactions, which are manifested as different degrees of preference for a certain plant species. Nutrients and phytotoxins do not act in isolation once a plant is ingested (Villalba et al., 2002). Phytotoxins interact with nutrients because detoxification processes impose nutritional costs to herbivores and nutrient intake affects the limit of tolerance to absorption of phytotoxins (Illius and Jessop, 1995). Phytotoxins interact with other phytotoxins to influence the total amount of food ingested (Burritt and Provenza, 2000; Rogosic et al., 2003). Animals may be able to consume more foods with different classes of phytotoxins if they produce different effects in the body and are detoxified by different mechanisms (Freeland and Janzen, 1974). These interactions may lead to complementary relationships such that eating a combination of foods exceeds the benefit of consuming any single food in isolation (Tilman, 1982).

Tannins and saponins are among the more common classes of phytochemicals in Mediterranean shrubs used as defences and can be expected to influence herbivore feeding behavior. Freeland et al. (1985) suggested that herbivores might be able to overcome the toxic effects of tannins and saponins by simultaneously consuming both classes of chemicals. In this study, we fed Mediterranean shrubs containing tannins and saponins to sheep in order to determine whether ingestion of condensed tannins in conjunction with saponins resulted in reduced toxic effects, manifested as increased shrub intake. Our objective was to determine whether increasing number of shrub species fed or number of classes of secondary chemicals present in the mixture increased intake of Mediterranean shrubs by sheep.

2. Materials and methods

Four experiments were conducted at a research station in the village of Postire on the island of Brac (Central Dalmatia), 5 km from the Croatian coastal city of Split (43°22′N; 16°38′E) during spring (May–July 2005). We examined five dominant shrubs of the Mediterranean holly oak maquis vegetation (Rogosic, 2000) on the island of Brac: *Quercus ilex* L. (Fagaceae), *Q. pubescens* L. (Fagaceae), *Arbutus unedo* L. (Ericaceae), *Pistacia lentiscus* L. (Anacardiaceae), and *Hedera helix* L. (Araliaceae). Shrubs were analyzed for tannins using colorimetric methods described by Waterman and Mole (1994). Tannin concentrations are expressed as a relative tannin index. *P. lentiscus* had the highest tannin index (1.50), followed by *A. unedo* (1.26), *Q. pubescens* (1.05), and *Q. ilex* (0.96). Other secondary compounds in these shrubs include a cyclic diterpene alcohol and quinic acid (*Quercus* genus), arbutoside and ethyl gallate (i.e., ethyl-3,4,5-trihydroxy benzoate) (*A. unedo*), and terpenes (e.g., α-pinene, β-pinene, camphene, trans-caryophyllene, and cadinene) and fatty acids (*P. lentiscus*) (Rogosic and Clausen, unpublished data). *H. helix* contains a mixture of pentacylic terpenoids (Burrows and Tyrl, 2001) classified as genins, monodesmosides (α-hederin and β-hederin), and bidesmosides (hederacosides B and C). This complex mixture is often referred to as saponins.

All shrubs were hand-harvested each week within 2 km of the research station. Leaves and 1-year-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. Each morning during studies, bags of shrubs to be fed that day were removed from cold storage and offered immediately to animals. The sheep ($n = 12$, 6 months of age, mean weight = 27.2 kg) were a local breed that is a cross between the Croatian breeds ‘‘Pramenka’’ and ‘‘Wunterberg’’. All experimental animals were raised on the same farm, with experience grazing on Mediterranean maquis vegetation.

2.1. Experimental protocol

Four experiments (10 days each) were conducted. Animals were housed individually (1.5 × 2 m pens) in covered stalls with wire mesh sides, and had free access to trace mineral blocks and fresh water. Prior to experiments, baseline intake of alfalfa pellets was determined for each animal on days 1–5. After baseline intake was established, sheep were offered all five shrubs from 09:00 to 13:00 h for 5 days. Shrub intake of each animal was monitored, and sheep were stratified into two treatment groups ($n = 6$ per treatment) based on total shrub intake. Between experiments, alfalfa pellets and barley were fed at maintenance level for 3 days.

During experiments, sheep received 100 g of barley each morning at 08:00 h. From 09:00 to 15:00 h each day, all animals were fed 200 g (as fed) of each shrub used in that study in separate food containers. Containers were monitored every 30 min and additional shrub material was placed in empty boxes. At 15:00 h, orts were weighed and shrub consumption (g/kg BW) was calculated, and sheep were fed 550 g of alfalfa pellets. The four experiments were designed using different combinations of high-tannin and high-saponin shrubs. Combining shrubs that contain tannins with *H. helix* (high-saponin content) may enhance shrub intake because tannins and saponins chelate in the intestinal tract, thereby reducing the aversive effects of both compounds (Freeland et al., 1985; Rogosic et al., 2003).

In Exp. 1, intake of two shrubs differing in major phytotoxin class (*P. lentiscus* and *H. helix*) was compared to intake of two tannin-containing shrubs (*P. lentiscus* and *A. unedo*). In Exp. 2, intake of two tannin-containing shrubs (*P. lentiscus* and *A. unedo*) plus *H. helix* was compared to intake of three tannin-containing shrubs (*Q. ilex*, *P. lentiscus*, and *A. unedo*). Intake of three high-tannin shrubs (*P. lentiscus*, *A. unedo*, and *Q. ilex*) plus *H. helix* was compared to intake of four high-tannin shrubs (*P. lentiscus*, *A. unedo*, *Q. ilex*, and *Q. pubescens*) in Exp. 3. Intake of *P. lentiscus*, *A. unedo*, *Q. ilex*, and *H. helix* was compared to intake of three high-tannin shrubs (*P. lentiscus*, *A. unedo*, and *Q. ilex*) in Exp. 4.

2.2. Statistical analyses

Total daily shrub consumption was used as the dependent variable in the analysis. The experimental design for the different combinations of Mediterranean shrubs was a completely random design. Animals were a random factor in the mixed model analysis (SAS, 2000). The model included high-tannin shrubs with (group 1) or without the high-saponin shrub *H. helix* (group 2) (group 1 versus group 2) and the species × treatment interaction; individual animals were nested within treatment and species. The model also used days as a repeated measure with all other interactions included. The protected LSD procedure was used to compare individual means (SAS, 2000). All analyses on shrub intake were adjusted for body weight (g/kg BW).

3. Results

Analyses of the first three experiments revealed both main effects (treatment and days) and their interaction were significant ($P < 0.01$). Sheep ate substantially more total biomass of the mixture of high-tannin shrubs plus the high-saponin *H. helix* than did sheep offered an equal number of only high-tannin shrubs (Fig. 1). A day × treatment interaction was observed ($P = 0.01$), with sheep consuming more high-tannin shrubs when fed with *H. helix* on days 8 and 10 in Exp. 1; on days 11, 12, 14, and 18 in Exp. 2; and on days 21, 22, 24, 28, and 30 in Exp. 3 (Fig. 1). There was a trend ($P = 0.01$) for a positive effect of the saponin-containing *H. helix* on total shrub intake (30.9 ± 2.0 g/kg BW versus 21.4 ± 2.2 g/kg BW). In general, intake of shrub mixtures tended to increase over time and as number of species fed increased, regardless of treatment in Exps. 1–3 (Fig. 1). In all experiments, there was a day effect and a day × treatment interaction ($P < 0.05$), and sheep ate more biomass of the mixture of high-tannin shrubs plus the high-saponin shrub than did sheep offered an equal number of only high-tannin shrubs as the trials progressed (Fig. 1).

In Exp. 1, sheep offered a high-tannin shrub (*P. lentiscus*) and a high-saponin shrub (*H. helix*) consumed more foliage ($P < 0.01$) than sheep offered two shrubs containing different concentrations of tannins (*P. lentiscus* and *A. unedo*; 20.9 ± 1.5 g/kg BW versus 16.6 ± 1.5 g/kg BW; Fig. 2). Intake of *P. lentiscus* by sheep receiving *H. helix* was higher than intake of *P. lentiscus* by sheep receiving two tannin-containing species (8.2 ± 1.4 g/kg BW versus 5.0 ± 1.3 g/kg BW; $P < 0.01$), indicating a complementary interaction between *P. lentiscus*

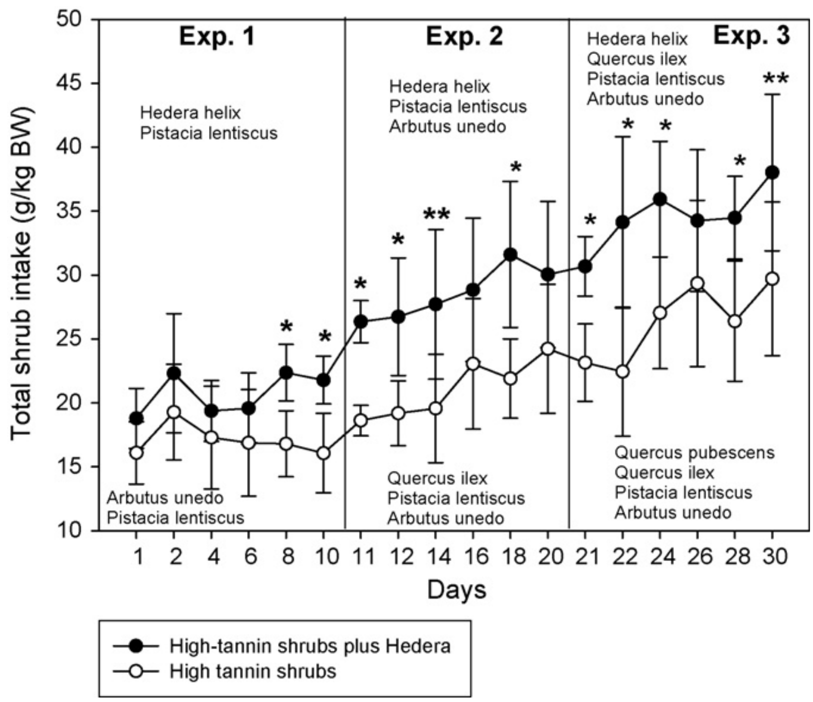

Fig. 1. Total daily intake (g/kg BW ± S.E.) of sheep fed different combinations of high-tannin shrubs (*Quercus ilex*, *Quercus pubescens*, *Arbutus unedo*, and *Pistacia lentiscus*) with or without the high-saponin shrub *Hedera helix*. Asterisks indicated significant ($^{*}P < 0.01$; $^{**}P < 0.05$) differences on a specific day between groups 1 and 2.

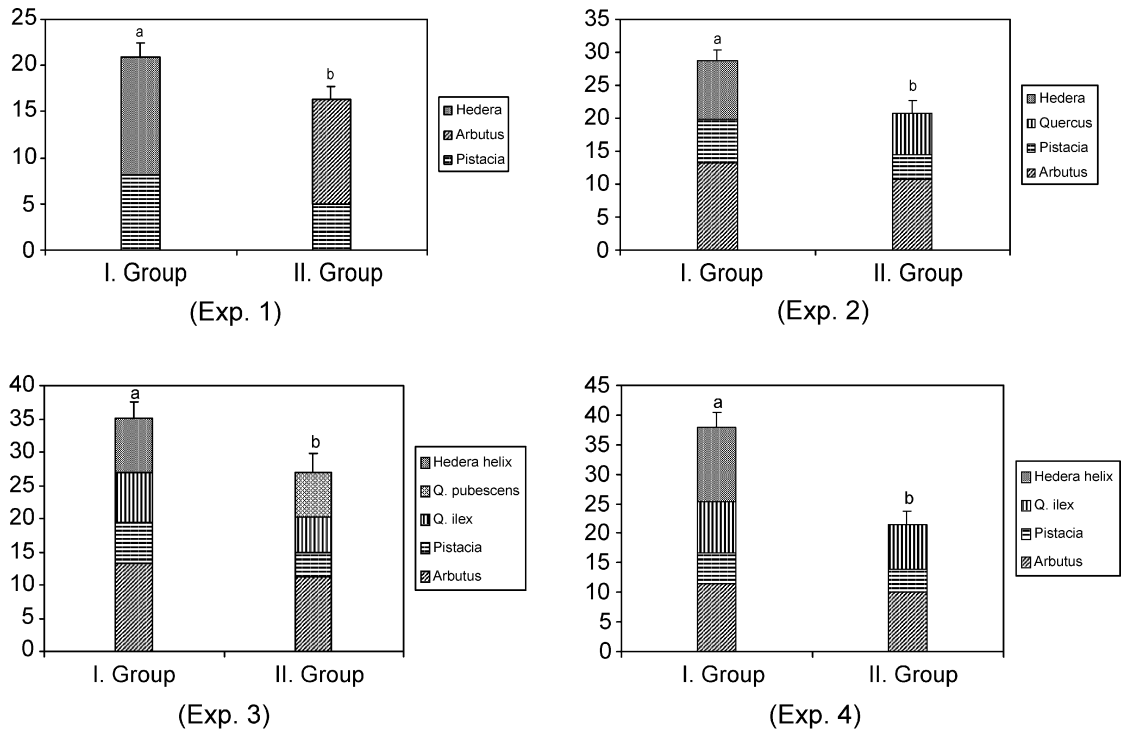

Fig. 2. Intake (g/kg BW) of sheep fed different combinations of high-tannin (*Quercus ilex*, *Quercus pubescens*, *Arbutus unedo*, and *Pistacia lentiscus*) and/or high-saponin *Hedera helix* shrubs; $n = 6$ per treatment group; $P < 0.01$.

and *H. helix*. In Exp. 2, sheep offered two tannin-rich shrubs (*P. lentiscus* and *A. unedo*) plus the saponin-rich *H. helix* ate more foliage ($P < 0.01$) than sheep offered three high-tannin shrubs (*P. lentiscus*, *A. unedo*, and *Q. ilex*; 28.8 ± 1.6 g/kg BW versus 20.8 ± 1.8 g/kg BW; Fig. 2). Again, animals receiving *H. helix* consumed more foliage ($P < 0.01$) of both *P. lentiscus* and *A. unedo* than those fed three tannin-containing shrubs (6.6 ± 1.2 g/kg BW versus 3.7 ± 1.3 g/kg BW; 13.3 ± 1.5 g/kg BW versus 10.7 ± 1.1 g/kg BW, respectively). Intake of *H. helix* was remarkably less ($P < 0.01$) in Exp. 2 than Exp. 1 (8.9 ± 0.7 versus 12.8 ± 0.7).

In Exp. 3, sheep provided a mixture of three high-tannin shrubs (*Q. ilex*, *A. unedo*, and *P. lentiscus*) plus the saponin-rich *H. helix* consumed more total foliage ($P < 0.01$) than a mixture of four tannin-rich shrubs (*Q. ilex*, *Q. pubescens*, *A. unedo*, and *P. lentiscus*; 35.3 ± 2.3 g/kg BW versus 26.9 ± 3.0 g/kg BW; Fig. 2). Sheep also ate more *A. unedo*, *P. lentiscus*, and *Q. ilex* when fed with *H. helix* ($P < 0.01$) than when fed in a mixture of four high-tannin shrubs (13.3 ± 0.6 g/kg BW versus 11.3 ± 0.6 g/kg BW; 6.0 ± 0.9 g/kg BW versus 3.7 ± 0.7 g/kg BW; 7.6 ± 0.9 g/kg BW versus 5.2 ± 0.8 g/kg BW, respectively).

Sheep in Exp. 4 also ate more foliage ($P < 0.01$) of the mixture of three high-tannin shrubs with *H. helix* than those fed a mixture of only the three high-tannin shrubs (*Q. ilex*, *P. lentiscus*, and *A. unedo*). The intake difference was much greater between experimental groups (38.6 ± 2.5 g/kg BW versus 21.5 ± 2.4 g/kg BW) in Exp. 4 when the number of shrubs in the mixture differed. Sheep again ate more *P. lentiscus* when fed with *H. helix* than when fed only with high-tannin shrubs (5.4 ± 1.1 g/kg BW versus 4.0 ± 0.3 g/kg BW; $P < 0.01$), but intake of the other two high-tannin shrubs (*A. unedo* and *Q. ilex*) did not differ between groups (11.4 ± 1.4 versus 10.1 ± 1.6; 8.7 ± 1.9 versus 7.5 ± 1.0; $P > 0.05$; Fig. 2).

Although intake of the five shrubs differed among experiments, the rank order of amount of each shrub species eaten was similar across experiments. The mean amount of shrubs consumed across all experiments and treatments was: *A. unedo* (11.6 ± 1.1 g/kg BW), *H. helix*

(10.6 ± 0.9 g/kg BW), *Q. ilex* (7.1 ± 1.0 g/kg BW), *Q. pubescens* (6.7 ± 1.7 g/kg BW), and *P. lentiscus* (5.3 ± 1.0 g/kg BW).

4. Discussion

Complementary resources are very common in nature (Schmidt et al., 1998). Herbivores may select different plants that provide a balanced mixture of nutrients (Westoby, 1978; Wilmshurst et al., 1995) or reduce the intake of any one allelochemical (Freeland and Janzen, 1974). Many studies have shown that mammalian herbivores perform better when fed mixed diets (Freeland et al., 1985; Pennings et al., 1993; Bernays et al., 1994). Balancing nutrients and minimizing harmful effects of toxins are two alternative (but not mutually exclusive) hypotheses for explaining food complementarity.

Tannins and saponins are two major classes of phytochemicals that are prevalent in Mediterranean shrubs. Sheep provided with a choice of shrubs containing tannins or saponins consumed combinations of the shrubs that presumably reduced adverse effects associated with consumption of either toxin alone. In the first three experiments, sheep consumed more total shrubs when fed a mixture containing both high-tannin and high-saponin shrubs than an equal number of only tannin-containing shrubs. These results suggest a complementary interaction of shrubs containing both classes of secondary compounds, particularly considering that *P. lentiscus* intake (the shrub with the highest tannin index) was increased in all experiments when fed in combination with *H. helix*.

Each shrub has a unique combination of primary and secondary compounds, and therefore, presumably a unique flavor and nutrient profile. We predicted that the positive effect of saponins in *H. helix* would be reduced as the number of shrubs and biological diversity of the diet increased (Rogosic et al., in press-b,c); however, this hypothesis was rejected based on our results. In contrast, increasing the number of Mediterranean shrubs (three versus six) offered to sheep and goats did stimulate intake in our previous studies (Rogosic et al., in press-b,c).

The phytochemical complementarity hypothesis assumes that different plant species contain different amounts and classes of allelochemicals that enable different combinations of secondary compounds to be selected in order to minimize toxic effects. The positive effects are obviously dependent on the relative proportions of the toxins ingested (Pfister et al., 1997). Tannins, saponins, and other phytochemicals likely form chemical complexes within the intestinal tract, since tannins and saponins have been shown to form chelation complexes in ‘‘in vitro’’ systems (Freeland et al., 1985). Formation of intestinal complexes would be expected to reduce absorption of these compounds.

Total shrub intake increased numerically as the number of shrubs increased over the course of Exps. 1–3. Although these experiments are not compared statistically, Fig. 2 illustrates that increasing number of shrubs offered increased intake. Sheep eat more when offered several foods ($3 > 2 > 1$) that contain complementary toxins (Burritt and Provenza, 2000; Villalba et al., 2002, 2004) or as the number of shrubs offered increases ($1 < 2 < 3 < 6$; Rogosic et al., in press-b,c). Under this framework, herbivores would be expected to eat small amounts of poor quality foods even though other palatable feeds are available for consumption (Rogosic et al., in press-a,b,c). Mammalian herbivores possess many mechanisms for detoxifying or tolerating phytotoxins and these various detoxification pathways are generally specific to a single phytochemical or class of phytochemicals. Some authors have suggested that herbivores can consume a variety of plant species to spread ingestion of phytotoxins over a great number of detoxification pathways (Freeland, 1991; Bernays et al., 1992). In this manner, herbivores might avoid overloading a particular detoxification pathway and thus avoid toxicosis. Furthermore, complementary interactions between high-tannin shrubs and the high-saponin shrub as observed in this study may reduce toxicity if herbivores select diets that take advantage of these beneficial interactions (Freeland et al., 1985; Burritt and Provenza, 2000; Rogosic et al., 2003). The fact that the high-saponin *H. helix* positively influenced biomass intake in Exps. 1–3 may have implications for coevolution between plant and animals in grazed ecosystems (i.e., if herbivores capitalize on complementary interactions among secondary compounds as a means of neutralizing negative effects of toxins). Flavor–nutrient–phytotoxin interactions within a plant community may also partially explain why effectiveness of plant defenses varies with the mixture of plant species (Rogosic et al., in press-c).

Total shrub intake was numerically much lower for sheep receiving the treatment without *H. helix* in Exps. 2 and 4 (three tannin-containing species) compared to the treatment without *H. helix* in Exp. 3 (four tannin-containing species), but total shrub intake remained similar for sheep fed the treatments containing *H. helix* in Exps. 3 and 4. Although total intake differed between treatment groups in Exps. 1–3, total intake differed to a greater extent in Exp. 4 when number of shrubs fed decreased. Moreover, the numerical increase in total intake as number of species fed increased (Fig. 2) further supports an increased intake as biological diversity of the diet increased. Variable nutrient concentrations in plant species may have different effects on diet selection by herbivores depending on the classes and concentration of phytotoxins in the plant community. Thus, relationships among shrubs are likely to vary on a case-by-case basis depending on biochemical composition.

The variety of shrubs species in the maquis plant community may present a challenge for herbivores to determine which combinations of shrubs will best meet nutritional needs, minimize intake of toxins, optimize interactions between nutrients and toxins, and optimize interactions between multiple toxins. While much more work needs to be done, it is clear that herbivores learn from the postingestive consequences of antagonistic and complementary interactions between nutrients/toxins and toxins/toxins.

5. Conclusions

Plants produce diverse mixtures of biochemicals that provide herbivores with nutrients for survival and reproduction and secondary metabolites that can both cause toxicity and yield health benefits. Biochemical diversity in a plant community may enable herbivores to eat combinations of foods that are complementary, and result in improved performance. Our results suggest a complementary interaction exists between tannins and saponins contained in five dominant shrubs of the Mediterranean maquis plant community when fed to sheep, and increasing number of shrubs offered to sheep also appeared to increase shrub intake. Complementary interactions between phytochemicals may influence how herbivores mix their diets and use food resources. Outcomes of their interactions may help to explain the dietary choices of herbivores. Exposure to a variety of plant species may allow herbivores to select mixtures that result in more balanced diets with fewer harmful effects of phytotoxins in chemically defended environments.

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