1 **Seasonality and edge effect determine herbivory risk according**
2 **to different plant association models**

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Abstract

We report evidence of a hierarchical resource selection by large herbivores and plant neighbouring effects in a Mediterranean ecosystem. Plant palatability was assessed according to herbivore foraging decisions. We hypothesize that under natural conditions large herbivores follow a hierarchical foraging pattern, starting at the landscape scale, and then selecting patches and individual plants. A between- and within-patch selection study was carried out in an area formed by scrubland and pasture patches, connected by habitat edges. With regards to between-patch selection, quality-dependent resource selection is reported, herbivores mainly consuming pasture in spring, and woody plants in winter. Within-patch selection was also observed in scrub habitats, influenced by season, relative patch palatability, and edge effect. We defined a Proximity Index (PI) between palatable and unpalatable plants, which allowed the verification of neighbouring effects. In spring, when the preferred food resource (i.e., herbs) is abundant, we observed that in habitat edges large herbivores basically select the relatively scarce palatable shrubs whereas inside scrubland, unpalatable shrub consumption was related to increasing PI. In winter, a very different picture was observed. There was a low consumption of palatable species surrounded by unpalatable ones in habitat edges, where the latter were more abundant. All these outcomes can be explained by different plant associations described in the scientific literature. We conclude that optimal foraging theory provides the conceptual framework behind the observed interactions between plants and large herbivores in Mediterranean ecosystems.

Introduction

The study of plant-herbivore interactions is a crucial issue in ecology which is increasingly taking into consideration not only the individual plant species and its antiherbivory mechanisms, but also the surrounding plant stand and the role played by neighbouring plants (e.g. Atsatt and O'Dowd 1976; Brooker and Callaghan 1998; Grubb 1992; Hambäck and Beckerman 2003; Milchunas and Noy-Meir 2002; Gómez-Aparicio et al. 2008). Plants show different defence mechanisms against herbivory that influence their palatability, such as the production of secondary compounds, physical defences such as thorns and other morphological traits (see e.g. Vicari and Bazely 1993). Also, plant distribution in a given patch follows a series of rules mainly dependent on a balance between positive and negative interactions (Brooker and Callaghan 1998) as well as plant dispersal abilities (e.g., O'Connor 1994). In this context, herbivores play an important role in determining plant community composition (e.g., Augustine and McNaughton 1998).

Food resources for large herbivores can be identified at different ecological scales (reviewed by Bailey et al. 1996). Senft et al. (1987) applied a hierarchical approach to ungulate feeding behaviour, considering plant communities at the landscape scale, feeding stations within a plant community, and individual plants or plant parts at the bite scale. Moving from one hierarchical scale to another depends on animal perception and foraging responses (ibid.). Having the chance to choose between different patches, animals that make foraging decisions at the patch scale reject those ones with the lowest densities of palatable food (Shipley and Spalinger 1995). Also, at the feeding station or patch scale, interspecific plant selection will be expected for

very conspicuous (either visually or through olfactory clues)
defended/undefended plant species.

Since herbivores base their feeding decisions on plant palatability (Freeland and Janzen 1974), the composition of a given vegetation stand can influence plant-herbivore interactions at the species level (Atsatt and O'Dowd 1976; Augner et al. 1991; Baraza et al. 2006). Thus, the susceptibility of a plant to herbivory will partly depend on the characteristics or density of neighbouring plants (see Milchunas and Noy-Meir 2002; Palmer et al. 2003). According to the relative palatability of neighbouring plants and the hierarchical level at which herbivores make foraging decisions, plant neighbours may have different effects on herbivory rates, and a number of such plant associations have been described in the literature (e.g., Hjältén et al. 1993; Milchunas and Noy-Meir 2002).

When a low palatable plant is surrounded by highly palatable plants, i.e. the plant stand is highly attractive for herbivores, it might be at risk of being consumed if herbivores do not distinguish (or select) between individual plant species. This situation has been named associational susceptibility or associational damage; whereas the opposite situation, i.e., a highly palatable plant surrounded by non-palatable or low palatable plants (which would confer a certain protection for the former) is named associational defence or associational resistance. Both associations have been observed in studies with mammalian herbivores (Danell et al. 1991; Hjältén et al. 1993; McNaughton 1978; Smit et al. 2005).

However, when herbivores are selective within a patch, distinguishing between individual plant species at the feeding station scale, the final output of

these associations can be dramatically different. Under low-scale feeding decisions, and following Bergvall et al. (2006), an unpalatable plant surrounded by palatable plants may be safe due to the contrast between itself and its neighbours. This has been called neighbour contrast defence, a generalisation of the attractant-decoy hypothesis (see Atsatt and O'Dowd 1976); whereas neighbour contrast susceptibility would occur when a palatable plant is not safe in a mainly unpalatable patch, and can be selectively consumed by the herbivore (Bergvall et al. 2006). This last instance would imply that the herbivore's costs of feeding at a relatively low palatable patch are counterbalanced by the benefits obtained from the consumption of the palatable plant. Both neighbour contrast defence and susceptibility have been observed in pastures consumed by cattle (Hayakawa 1972, cited in Atsatt and O'Dowd 1976).

In sum, mixed (palatable/non-palatable) plant associations have been postulated as a mechanism that explains plant distribution and community structure (Hay 1986; Holmes and Jepsoninnes 1989; McNaughton 1978), maintaining the coexistence of different plant species (Holt and Kotler 1987).

Since palatability of a plant species is a trait that may vary depending on the plant community, associational susceptibility and associational defence can be regarded as two extremes of the same gradient (Brooker and Callaghan 1998), depending on the relative palatability of neighbours and the way in which herbivores are deterred (physically or chemically). Also, reported phenological changes in plant chemical composition suggest that palatability may vary seasonally (Codron et al. 2007; Marshal et al. 2005; O'Reagain 1993).

The study of plant-herbivore interactions in Mediterranean ecosystems has been scarcely undertaken, despite harbouring remarkable vegetation diversity and heterogeneity (Medail and Quezel 1997, 1999; Myers et al. 2000), and being characterized by a high degree of complexity (Perevolotsky 1994). Thus, these ecosystems constitute an ideal system to test the effects of neighbouring vegetation on plant-herbivore interactions, even at small spatial scales (Blondel and Aronson 1999). Also, Mediterranean habitats have been subjected to intense herbivorous pressure, from both wild and domestic herbivores, for thousands of years (Le Hourou 1981; Papanastasis and Peter 1998). This has promoted a high heterogeneity in plant communities at different levels, e.g., species diversity, spatial structure and ecological succession (see Le Hourou 1981).

In this study, carried out in a Mediterranean landscape, we analysed large herbivore foraging decisions in a natural plant community, considering both the spatial scale of food resources and the relative palatability of plant communities and individual plants, in two different seasons. Plant consumption rate was estimated through faecal contents and browse data (see Materials and methods). Plant associations were assessed both in a within-patch context (consumption of unpalatable and palatable plants), and a between-patch context (habitat foraging decisions) across seasons.

Materials and methods

Study area

The study was conducted during 2006 and 2007 in a hunting estate located in the province of Ciudad Real in Castile-La Mancha (south central Spain,

38°55'N 0°36'E, Figure 1). The estate is a 724 Ha. enclosure with altitude between 600 and 850 m. above sea level and is located in a region of Mediterranean-continental climate, characterized by summer droughts, cold winters and high summer temperatures.

The study area comprises pasture lands with scattered holm oaks (*Quercus ilex*), and Mediterranean perennial shrubs. The dominant shrub species are *Cistus ladanifer*, *Phillyrea angustifolia*, *Rosmarinus officinalis*, *Quercus ilex*, various species of *Erica* and *Genista hirsuta*. Trophic resources for herbivores are not limiting at any season. A cereal mix is grown in part of the study area, and supplementary food provided in troughs daily. Although the estate lacks natural water sources, there are a few artificial pools. The estate was established in 1988.

Three different habitats were identified:

- **Scrubland or woody plant areas:** areas covered by typical Mediterranean woody plants and shrubs.
- **Open areas:** pastures.
- **Habitat edges:** 5 m belts where the habitat abruptly changes from open areas to scrubland.

Study animals

Three sympatric large herbivore species live in the study area. One is a native species, red deer (*Cervus elaphus*), and the other two were introduced due to their relevance as game: the aoudad (*Ammotragus lervia*) and the European mouflon (*Ovis orientalis*).

Red deer are the most abundant species in the study area (over 400 individuals), followed by the European mouflon (over 40 individuals) and the aoudad (over 20 individuals), according to census counts carried out by the estate staff on July and September 2006 and 2007.

The aoudad is original from mountainous and desert areas in the North of Africa and has been successfully introduced in the USA and Spain (Cassinello 1998). The European mouflon is native to Corsica and Sardinia and has been repeatedly introduced in most of Europe since the second half of the nineteenth century (Cugnasse 2000; Markov and Penev 2000; Rodríguez-Luengo et al. 2002).

Field sampling

Plant availability in the study area was assessed by sampling along a series of transects, randomly located in the three vegetation types: open land, scrubland and habitat edges (along the edge). Vegetation cover and browse signs were recorded in winter and spring. These times of year were chosen in order to compare two seasons with different plant availability. Browsing evidence was only registered in scrubland and habitat edges, where shrubs were present.

Herbaceous plant availability was determined using the “*point quadrat method*” (Hanley 1978). Herb cover was registered every 10 cm in 10 m transects (62) laid out in the three habitat types. Points with bare ground or covered by leaf litter were also registered. Shrub availability was assessed using the “*line intercept*” method (Eberhardt 1978; Hanley 1978) along 50 m long and 60 cm wide transects (83). Parts of plants over 2 m were not registered, as they are out of reach from the study herbivores.

Browse data were collected while measuring shrub availability. Herbivory intensity was quantified by checking each individual woody plant within the transect and scoring it as browsed or unbrowsed. A woody plant was considered as browsed when showing any recent signs of having been consumed by large herbivores. Herbivory risk of each plant species was subsequently calculated as the proportion of browsed plant individuals of that species per transect and averaged over all the transects in the study area. As red deer are the most abundant species in the study site, registered browsing signs can be mainly attributed to deer foraging activity.

Laboratory analyses

Since it was impossible to distinguish consumption signs on herbs in the field, we evaluated the preference of herbivores for different resources (woody vs herbaceous species) by means of microhistological analysis of plant remains in faecal samples (Henley et al. 2001; Holeček et al. 1982; McInnis et al. 1983; Putman 1984).

Fresh faeces were collected during the spring of 2006 and winter of 2006 and 2007 from the three ungulate species under study. Faeces morphology and the direct observation of defecating animals allowed the identification of faeces origin. Once collected in the field, faeces were kept at a temperature of -20°C until they were processed and analysed in the laboratory. The method of analysis (Bartolomé et al. 1995) included a first stage in which samples were treated with nitric acid at 80°C and microscope slides were prepared. Epidermal plant fragments in faecal samples were then identified and recorded under a microscope. A reference collection of vegetation present in the study area was

used in order to classify plant fragments up to genus and, in some cases, species.

Selectivity index

In order to establish foraging preferences by herbivores living at the study site, we determined *selected*, *indifferent* and *refused* plants and patches using the Savage selectivity index (Manly et al. 2003), for each season. This index determines selectivity of a given resource ($w_i = U_i/p_i$) by relating its use (U_i) with its availability (p_i). When comparing herbaceous and shrub selectivity, “use” refers to the percentage of their content in faeces, and “availability” to their proportional cover in the study site; whereas in the shrub species selection analysis, “use” refers to browsed proportion of the plant, and “availability” to plant species cover. The Savage index varies from zero (maximum refusal) to infinite (maximum selection), where 1 is the value defining the selection expected by chance.

The statistical significance of this index was tested by comparing the Savage statistic (see formula below) with that corresponding to the critical value of a χ^2 distribution with one degree of freedom (Savage 1931; Manly et al. 1993):

$$\text{Savage statistic} = \frac{(w_i - 1)^2}{\text{se}(w_i)^2}$$

The standard error of the index is: $\text{se}(w_i) = \sqrt{\frac{(1 - p_i)^2}{u_t * p_i}}$, where u_t is the total amount of plants registered with browse signs or total plant fragments counted in faeces.

Plants actively *selected* according to the Savage index were considered palatable, while *refused* plants and those consumed in the same proportion as their availability (*indifferent* plants) were considered as unpalatable (Gómez et al.

2001). Therefore, palatability was not only defined by plant traits, but also by other factors that may affect herbivore foraging decisions.

Assessment of neighbouring effects

Neighbouring effects at the plant scale were assessed by determining the proximity to browsed palatable plants. Thus, a Proximity Index (PI) was developed to determine the degree of vicinity between unpalatable and browsed palatable plants. We calculated the PI for each transect as:

$$PI = \frac{\text{number of unpalatable individuals neighbouring browsed palatable plants}}{\text{total number of unpalatable individuals}}$$

where neighbouring plants are those overlapping or less than one centimetre away from the target individual.

PI provides an overall measure of nearness between plants with differing relative palatability within a determinate patch, habitat or a whole plant community. PI lets us assess the neighbouring context with a continuous variable. This index is therefore advantageous when shrub diversity is high and associational effects at the plant species scale want to be studied.

Statistical analyses

In order to test which were the factors determining herbivory risk of plants at different scales, general linear models (GLM) were used. Previously, the ratio variables were arcsine transformed and log transformations were applied to the remaining variables when they departed from normality (Zar 1984). Multivariate ANOVAs were used to determine: the effect of season on the selection of herbs or shrubs by ungulates; herbivory risk for shrub species at the habitat scale; and the availability of palatable and unpalatable shrubs within the study area.

A separate slope design was used to analyze herbivory risk of unpalatable shrub species at the patch scale according to the PI. Separate slope designs should be used when categorical and continuous predictors interact, influencing the responses on the outcome of the model, as the traditional analysis of covariance is inappropriate in this situation (Statsoft 2001). This type of design is a within subject design identical to a nested ANOVA, since the effect of the continuous predictor across the levels of the categorical predictor (Quinn and Keough 2002) is tested. As a result, the main effect of the continuous predictor is omitted from the model.

To control the error produced by multiple comparisons while analysing the significance of the Savage index, we used Bonferroni's correction, adjusting the significance of the statistical test. All analyses were performed using (procedures in) JMP 6.0.3 (SAS Institute Inc.) and Statistica (packages) (Statsoft 2001).

Results

Herbivore between-patch selection: scrubland and pasture

The percentage of herbaceous fragments in ungulate faeces was significantly higher than that of woody plant fragments (plant type: $F_{(1,111)}=33.14$; $R^2=0.08$; $p<0.0001$). Season was not significant *per se* in determining total plant content (season: $F_{(1,111)}=0.99$; $p=0.996$). However, the interaction term between plant type and season was highly significant (plant type*season: $F_{(1,111)}=291.08$; $R^2=0.73$; $p<0.0001$), indicating that the effect of season depended on which plant type was considered. Hence, shrubs were more consumed than herbaceous plants in winter, while the opposite was

observed in spring (see Figure 2). This model accounted for up to 81% of the internal variability of the data ($F_{(3,111)}=97.38$; $p<0.0001$).

The Savage index results showed that both shrubs and herbs were actively selected in winter and spring, respectively (see Table 1).

Herbivore within-patch selection: scrubland

Season, habitat and palatability effects

Shrub species were classified into unpalatable and palatable species (see Methods). The main palatable species during winter were: *Cistus salviifolius*, *Quercus faginea*, *Rosa canina* and *Rubus ulmifolius*, and the most unpalatable was *Genista hirsuta*; whereas in spring the most palatable species were *Asparagus acutifolius*, *Cytisus* sp., *Erica* sp. and *Phyllirea angustifolia*, whereas *Cistus ladanifer* was the most unpalatable.

Overall, browsing of unpalatable shrub species ($F_{(3,78)}=40.51$; $R^2=0.61$; $p<0.0001$) was better explained by seasonality and edge effect than that of palatable ones ($F_{(3,78)}=4.47$; $R^2=0.17$; $p=0.01$).

Browsing of unpalatable shrubs varied depending on the habitat considered, as it was higher in edge areas with respect to scrub areas (habitat: $F_{(1,78)}=7.53$; $R^2=0.03$; $p=0.01$) and this effect was maintained across seasons (habitat*season: $F_{(1,78)}=2.88$; $R^2=0.01$; $p>0.05$). Also, in general, unpalatable species were browsed more intensely in winter compared to spring (season: $F_{(1,78)}=111.87$; $R^2=0.56$; $p<0.0001$; see Figure 3).

In contrast, the effect of season on the probability of palatable shrubs being browsed varied according to habitat type (habitat*season: $F_{(1,77)}=7.65$; $R^2=0.08$; $p=0.01$). In general, palatable species were slightly more browsed

when located in scrubland patches than in edges (habitat: $F_{(1,77)}=5.40$; $R^2=0.06$; $p=0.02$). However, this effect was diluted in spring, when palatable species were similarly consumed, regardless of their location (season: $F_{(1,77)}=3.17$; $R^2=0.03$; $p>0.05$; see Figure 3).

Overall, unpalatable species were more readily available in the study area than palatable ones ($F_{(1,192)}=35.71$; $R^2=0.12$; $p<0.0001$). However, their respective availability depended on the season or the habitat, since only in edges ($F_{(1,192)}=14.65$; $R^2=0.05$; $p=0.0001$) and in winter ($F_{(1,192)}=62.89$; $R^2=0.21$; $p<0.0001$) were unpalatable species more abundant than palatable ones (see Figure 4).

Neighbouring effects

Browsing of unpalatable woody plants was significantly explained by season, habitat and the third order interaction term between season, habitat and proximity index ($F_{(7,74)}=20.56$; $R^2=0.66$; $p<0.0001$; see Table 2).

Unpalatable shrubs were more heavily browsed in habitat edges and during winter, as stated above (see Figure 3). However, there was a neighbouring effect to be considered. In scrubland and during spring, the proximity to a browsed palatable plant would lead to a higher probability of unpalatable plants being browsed (associational susceptibility evidence), whereas in habitat edges this relationship presented a negative trend (neighbour contrast defence, see Table 3). In contrast, in both habitat types and during winter, this neighbouring effect was not detected (Figure 5).

Discussion

Evidence of the co-occurrence of different plant neighbouring effects is provided in a natural plant community subjected to herbivory, with seasonality and edge effect as determinant factors. Also, a hierarchical resource selection is reported, where herbivores first select high-quality patches, and then individual plants according to their palatability.

Palatability

Most plant-herbivore interaction studies determine plant palatability according to plant chemical composition and physical defences (e.g., Baraza et al. 2006; Rousset and Lepart 2002). However, palatability is a varying, season-dependent trait (O'Reagain and Schwartz, 1995; Meissner et al. 1999). Therefore, we have assessed plant palatability on the basis of foraging decisions (Owen-Smith & Cooper 1987; Gómez et al. 2001), so that in this study palatability is not an absolute but a relative trait. Palatability depends on season and plant community composition, being the result of the different factors that may affect herbivore foraging decisions (see Gomez et al. 2001).

It has been carried out in a Mediterranean ecosystem, characteristic of the centre of the Iberian Peninsula where *Cistus* spp. and *Erica* spp. prevail. Thus, plant associations reported here are based on a natural system, contrary to experimental studies which have been carried out under relatively artificial conditions where animals were offered a priori assumed palatable and non-palatable plants (see, e.g., Milchunas and Noy-Meir 2002).

Factors that determine between- and within-patch selection

Our results indicate that, at the patch scale, herbs are significantly selected in comparison to woody plants and shrubs in spring (e.g., Bugalho and Milne 2003), whereas the opposite occurs in winter. *Seasonal fluctuations of diet selection appear to be consistent with the variation in the nutritive value of herbaceous plants*, which during the wet season show an increase in nitrogen and minerals and a reduction in fibre (e.g., Codron et al. 2007; Marshal et al. 2005; Rogosic et al. 2006). In habitats where plant palatability is season-dependent, such as the Mediterranean habitats, herbivores tend to occupy alternative patches (e.g., scrubland), when pastures are not productive. Scoones (1991, 1995) defined key resource habitats as those that retain good quality resources during lean seasons.

Herbivory risk of palatable and unpalatable plants is influenced by habitat type and season (see Figure 3). In winter, woody plant species were consumed according to their palatability but showing opposite trends in scrubland and habitat edges, i.e., palatable species were more browsed in scrubland and unpalatable ones in edges. To understand these differences in browsing behaviour we must consider plant availability, as there is a higher density of unpalatable shrubs in edge areas in winter (Figure 4). In spring, unpalatable plants were hardly consumed in both habitats, whereas palatable plants were consumed in high proportions. As we have already seen, during spring herbivores are basically grazers, foraging on pastures which offer the highest quality food; thus, when browsing in scrubland, they choose mainly palatable plant species.

Neighbouring effects

395 **Season-dependent** neighbouring effects were detected. In spring, we
396 found a relationship between the probability of unpalatable shrubs being
397 browsed and the proximity to browsed palatable shrubs, although its nature
398 varied with habitat type. However, this relationship disappeared in winter.

399 **In spring herbivores actively selected nutritious food resources, feeding on**
400 **pastures first, and then browsing preferentially on palatable shrubs. In habitat**
401 **edges and during spring, palatable plants were largely selected, despite being**
402 **less abundant than unpalatable ones.** Also, being in the vicinity of browsed
403 palatable plants reduced the risk of being consumed for unpalatable ones,
404 **which is evidence of neighbour contrast defence (Bergvall et al. 2006).**

405 Conversely, plant associational susceptibility was detected in scrubland
406 habitats, where unpalatable plants were consumed at a higher rate when in the
407 vicinity of browsed palatable plants.

408 In winter, unpalatable plants were more abundant than palatable ones in
409 scrubland areas and habitat edges, so that associational susceptibility events
410 were not expected, given the relatively low palatability of patches.

411 All these plant associations can be explained by optimal foraging theory
412 (McArthur and Pianka 1966). This is the case, for example, of the associational
413 susceptibility registered during spring in scrubland, where herbivores
414 consuming a given palatable plant would continue using the same feeding
415 station, foraging on unpalatable plants. This takes place whenever searching
416 and finding a new, optimal, more nutritive patch is costlier than feeding on
417 unpalatable resources (Bailey et al. 1996). Prior studies also document co-
418 occurring plant neighbouring effects such as Hjältén et al. (1993) who found both

associational defence and associational susceptibility promoted by voles and hares.

Hierarchical resource selection

Previous studies on interactions between plants and large herbivores have reported contradictory results with regards to the scale of resource selection. Some authors have stated that herbivorous mammals are generally more selective at the patch or plant community scale than at the landscape scale (Bergvall et al. 2006; Danell et al. 1991; Milchunas and Noy-Meir 2002). Our results, instead, suggest that both types of behaviour do not have to be regarded as mutually exclusive, being the ratio of palatable/unpalatable plants in a patch the factor that determines final foraging pattern. Other authors have equally suggested that between- and within-patch selection are two different processes that may occur simultaneously (Edwards et al. 1994; Wallis De Vries 1999; Bee et al. 2009). Additionally, evidence that large herbivores can be selective exclusively within patches has mainly been based on experimental setups (e.g., Bergvall et al. 2006), where patches do not resemble real plant communities (Bailey et al. 1996; O'Reagain 1993). Thus, arguing that large herbivores are not selective between patches but only within patches would only apply when no apparent patch differences are found (Bergvall et al. 2006; Miller et al. 2007).

Our results support the hierarchy theory (Senft et al. 1987), where optimal foraging promotes resource selection at different spatio-temporal scales, starting at the regional scale and downscaling sequentially, from landscapes to plant communities or patches, to feeding stations or individual

plants (bite level) (Bailey et al. 1996; Senft et al. 1987). This foraging behaviour is common in social groups of herbivores, where decisions are taken hierarchically, with group leaders choosing resource patches, and where each herdmate occupies specific feeding stations (e.g., Owen Smith 1994; Perez-Barberia et al. 2007).

As Hjältén et al. (1993) suggest, plant associational events may provide a mechanism, not only to explain plant distribution and community structure (Holmes and Jepsoninnes 1989; McNaughton 1978), but also for promoting the coexistence of different plant species (Holt and Kotler 1987).

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Figure captions

Figure 1. Location of the study area in the Iberian Peninsula

Figure 2. Seasonal content of herbaceous and woody plants in faeces

Figure 3. Seasonal browsing of unpalatable (a) and palatable (b) plants at each habitat type (habitat edge and scrubland)

Figure 4. Availability of unpalatable and palatable shrub species at each season (a) and habitat type (b). Model parameters: $F(7,192)= 15.91$; $R^2= 0.39$; $p<0.0001$

Figure 5. Seasonal browsing of unpalatable plants according to proximity index in scrubland and habitat edges. Confidence intervals were set to 95%. Sample size = 81. r-Pearson and p-values are provided

Table 1. Seasonal resource selection based on the Savage index ($X^2=6.239$, d.f.=1, $p=0,0125$, Bonferroni correction applied).

Season	Plant type	U _i	p _i	Savage index	Statistic	Selection
Spring 2006	Herbs	0,745	0,725	1,027	15,81	+
Winter 2007	Herbs	0,379	0,710	0,533	2828,54	-
Spring 2006	Shrubs	0,255	0,632	0,404	5233,92	-
Winter 2007	Shrubs	0,621	0,550	1,130	109,46	+

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Table 2. Parameters of the separate slope GLM design explaining browsing of unpalatable shrubs according to seasonality (winter and spring), habitat (habitat edge and scrubland) and proximity to browsed palatable shrub species (proximity index).

Variables	R ²	df	F	p
season	0.22	1	12.80	0.001
habitat	0.23	1	13.14	0.0005
season*habitat	0.00	1	0.32	0.57
season*habitat*proximity index	0.20	4	2.79	0.03

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Table 3. Parameters of the separate slopes design describing the relationship between browsing of unpalatable plants and proximity index across seasons and habitat types. See also Figure 5.

Season	Habitat type	β	t	p
Spring	Scrubland	0,30	2,05	0,0436
	Edge	-0,33	-2,43	0,0175
Winter	Scrubland	0,21	1,01	0,3140
	Edge	0,02	0,19	0,8519

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