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COMPARISON AND OVERLAP OF SYMPATRIC WILD UNGULATE DIET IN CAZORLA, SEGURA AND LAS VILLAS NATURAL PARK

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ABSTRACT.– This paper analyses the trophic relationships and the degree of overlap between the diet of Spanish ibex (Capra pyrenaica), *red deer* (Cervus elaphus), *fallow deer* (Dama dama) *and mouflon* (Ovis musimon) *in the Cazorla, Segura and Las Villas National Park (Southeastern of Spain). Stomach content was used as the basis for diet evaluation. The most heavily consumed plant species by the four herbivores were* Quercus rotundifolia, Phillyrea latifolia, Rosmarinus officinalis, Oryzopsis paradoxa *and* Festuca arundinacea. *Spanish ibex and red deer were the ungulates with the most similar diet (53.7% overlap), both were browsers and consumed large amounts of woody matter. Fallow deer and mouflon had similar feeding habits, both are grazers and have a high intake of grasses. There were very low levels of overlap between the ibex and red deer diet with that of fallow deer and mouflon, respectively. Mouflon was the largest forbs consumer, fallow deer consumed most camephytes and red deer consumed most trees and shrubs. None of the four ungulates had absolutely definitive diets that could class them strictly as browsers or grazers, however certain trends suggested that ibex and red deer primarily behave as browsers while fallow deer and mouflon are grazers, although this was not a strict division.*

RÉSUMÉ.– Nous avons étudié le degré de superposition entre la diète du bouquetin (Capra pyrenaica), *cerf* (Cervus elaphus), *daim* (Dama dama) *et mouflon* (Ovis musimon) *dans le Parc National de Cazorla, Segura et Las Villas (SE de l'Espagne). Pour l'évaluation de la diète, nous nous sommes basés sur les contenus stomachaux. Les espèces les plus consommées par les quatre herbivores étaient* Quercus rotundifolia, Phillyrea latifolia, Rosmarinus officinalis, Oryzopsis paradoxa *et* Festuca arundinacea. *Le bouquetin et le cerf montraient la diète la plus semblable (53,7% de superposition) puisque tous deux broutaient une grande quantité de matière ligneuse. Le mouflon et le daim montraient des habitudes similaires au niveau de l'alimentation, mangeant des herbes et consommant une gran-*

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de quantité de graminées. Les diètes du bouquetin et du cerf ne se superposaient que très peu avec celles, respectivement, du daim et mouflon. Le mouflon consommait beaucoup de mégaphorbes tandis que le daim consommait surtout des chamaephytes et le cerf principalement arbres et arbrisseaux. Aucun des quatre ongulés étudiés montrait des diètes très strictes (broutage ou consommateur de graminées); cependant, on peut signaler que le bouquetin et le cerf présentaient plus des caractères de brouteurs tandis que le mouflon et le daim mangeaient casi-exclusivement des herbes.

RESUMEN.– En el presente estudio se analiza la relación trófica y el grado de solapamiento de dieta entre la cabra montés (Capra pyrenaica)*, el ciervo* (Cervus elaphus)*, el gamo* (Dama dama) *y el muflón* (Ovis musimon) *en el Parque Nacional de Cazorla, Segura y Las Villas. La dieta se evaluó a partir de los contenidos gástricos. La especies más consumidas por los cuatro herbívoros fueron* Quercus rotundifolia, Phillyrea latifolia, Rosmarinus officinalis, Oryzopsis paradoxa *y* Festuca arundinacea. *Los dos ungulados con la dieta más similar fueron el ciervo y la cabra montés (53,7% de solapamiento), de hábitos ramoneadores y consumidores de grandes cantidades de leñosas. El gamo y el muflón tienen dietas similares, comportándose como pastadores y consumiendo principalmente gramíneas. Los niveles de solapamiento entre la dieta de la cabra montés y el ciervo por un lado, y el gamo y muflón por otro, son muy bajos. El muflón ha sido el mayor consumidor de herbáceas no graminoides, el gamo consume mayoritariamente caméfitos y el ciervo árboles y arbustos principalmente. Ninguno de los cuatro mostró una dieta estrictamente ramoneadora o pastadora, aunque el ciervo y la cabra montés se comportan básicamente como ramoneadores, mientras que el gamo y el muflón principalmente como pastadores.*

Key-words: Diet overlap, Spanish ibex, mouflon, fallow deer, red deer.

1. Introduction

Herbivores are usually separated ecologically in accordance with their feeding habits (LAMPREY, 1963). There are browsers, browser-grazers and strict grazers. These categories are neither strict nor specific and can be varied in accordance with habitat, availability of forage classes and local herbivore population densities. They may also include sub-classifications of trophic resource usage: the use of certain plant species, different tissues and grass height (JARMAN & SINCLAIR, 1979). Generalisations about the feeding patterns of particular species are difficult, however, as their choice of forage obeys different criteria. Ruminants such as sheep are highly selective in Australian grasslands (ARNOLD, 1964) but on North American prairies prove to be even less selective than cattle (SCHWARTZ & ELLIS, 1981). SORIGUER *et al.* (1992) state that foraging is one of the most decisive ecolo-

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gy-related aspects in herbivore breeding ability and demography. Similarly, the trophic relationships amongst herbivores sharing a natural environment are decisive in the state of their populations. Knowledge of their feeding habits and trophic relationships is thus a fundamental aspect in the management of wild ungulate populations. There are four wild ungulate species in the Cazorla, Segura and Las Villas Natural Park: Spanish ibex (an endemic species of considerable scientific and hunting importance), mouflon, fallow deer and red deer. The purpose of this study was to compare the diet of these wild herbivores and define their overlap in order to detect potential interference or competition between the sympatric wild ungulates in the area.

2. Material and methods

The study area is in the southeastern part of Jaen Province (Spain) in the Cazorla, Segura and Las Villas Nature Park. The local climate has extremely hot summers and frequent frosts in winter, with snow on the higher ground. There are two bioclimatic pictures: Supramediterranean, defined by the Betic Supramesomediterranean, basophyle-*Quercus faginea* and Betic Supramediterranean, basophyle-*Q. rotundifolia* vegetation series, and the Oromediterranean defined by the Betic Oromediterranean, basophyle-*Juniperus sabina* series (RIVAS-MARTÍNEZ, 1987).

The diet of all four ungulates was estimated from rumen analysis. The 105 Spanish ibex samples were collected in April, June, July, August, November and December; the 15 mouflon samples were collected in spring and winter; the 24 fallow deer samples were collected at the end of winter, in summer and autumn; and the 16 red deer samples were collected in spring, summer and winter. A sample of 1 l was taken from each rumen, washed under pressure over a fine mesh sieve (1 mm^2) and separated into fragments corresponding to each species or/and plant group, after was obtained the volume and dry weight. Dicotyledon species were identified using herbarium material from the study area and macroscopic techniques. Microscopic techniques were used to identify and quantify the monocotyledon species on the basis of their epidermis cellular structure. For this purpose, a reference collection was obtained of leaves and stems epidermis samples from plants found in the study area. Monocotyledon fragments from each stomach content were grouped to obtain individual subsamples that was dried, crushed (to homogenise the size of vegetal fragments), washed and prepared for microscopic identification and quantification following CAVENDER & HANSEN (1970). Relative density of plant species was expressed by a fragment count (SPARKS & MALECHEK,

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1968; STEWART, 1967; CAVENDER & HANSEN, 1970). In each subsample 200 epidermis fragments (randomly distributed in the microscope fields) were counted at a magnification of 125x, usually considered sufficient for the evaluation of an anima'l diet from excrement samples (MAIZERET *et al.*, 1986). This permitted an estimate to be made of the dry weight contribution of each monocotyledon to the diet of each individual animal. Final data were expressed as percentage dry weights of dicotyledon and monocotyledon species in the total sample.

Diet composition was analysed by plant species and trophic or plant groups, broken down into: trees/shrubs, chamaephytes/dwarf-shrubs, graminoids (grasses, sedges, rushes) and forbs (herbaceous species, except the graminoids); and also woody plants (trees, shrubs and chamaephytes) and herbaceous plants (graminoids and forbs). The comparison and overlap between diets was estimated using the Spearman' s Correlation Rank Coefficient (r_s) and the Kulczynski's Similarity Index (KSI) (OOSTING, 1956), KSI=[Σ2W/Σ (a+b)](100, where W= the lesser percentage of a common component in the two diets to be compared and (a+b) is the sum of percentages of components of the two diets being compared. Diet diversity was calculated using the Shannon-Weaver index: $H' = - \sum P_i \log_{10} P_i$.

3. Results

3.1. Diet of Spanish ibex, mouflon, fallow deer and red deer

The diet composition (biomass percentages), diet diversity, species richness and biomass percentages of each plant group consumed by four wild ungulates are shown in Table 1.

In the Spanish ibex diet, trees and shrubs were the most heavily consumed plant group, particularly *Quercus rotundifolia, Phillyrea latifolia* and *Juniperus oxycedrus*. The second group was graminoids, particularly *Oryzopsis paradoxa* (5.2%) and *Festuca arundinacea* (3.7%). Chamaephytes and non-graminoids made a much smaller contribution to the diet than these two groups, the main species being *Helianthemum croceum, Teucrium carthaginense, Aphyllanthes monspeliensis* and *Asphodelus cerasifer* (1.8% to 0.9%). Woody plants comprised 61.3% of diet, herbaceous plants 38.3% and cryptogams 0.4%.

In the mouflon diet, graminoids was the most heavily consumed group (53%), particularly *Oryzopsis paradoxa* (10.9%) and smaller amounts of *Festuca rivularis, F. plicata, Carex hallerana, F. arundinacea* and *Helictotrichon filifolium*. Non-graminoids was the second most important group, the major species

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being *Cirsium hispanicum* (5.7%) and *Asphodelus cerasifer* (3.3%). Trees and shrubs formed almost the same proportion of diet as the above group, primarily consisting of *Quercus rotundifolia* (6.6%), *Cytisus reverchonii* (2.2%) and *Crataegus monogyna* (1.5%). Chamephytes were less heavily consumed than the above groups, most notably *Echinospartum boissieri* (3.3%). Woody plants formed 28.6% of the diet, herbaceous plants 70.4% and cryptogams 1%.

Table 1. Diversity of diet, species richness and diet composition (biomass percentage) of Spanish ibex (SI), red deer (RD), fallow deer (FD) and mouflon (M) in Cazorla, Segura and Las Villas Natural Park. Species of plants with input $0.5% in at least one diet.

TROPHIC RESOURCES	SI	RD	FD	M
Diet diversity	1.70	1.25	1.55	1.43
Species richness	305	56	98	107
WOODY PLANTS				
Trees/Shrubs				
Quercus rotundifolia	13.4	29.0	0.9	6.6
Phillyrea latifolia	9.2	9.5	+	0.1
Juniperus oxycedrus	6.8	3.0	-	+
Rosmarinus officinalis	2.8	12.5	-	+
Rubus ulmifolius	2.7	1.7	0.2	0.1
Hedera helix	2.1	0.5	+	0.4
Pinus nigra	1.5	3.4	6.2	2.0
Rosa canina	1.3	0.5	0.1	0.1
Olea europaea	1.3	-	-	-
Viburnum tinus	1.2	3.7	-	-
Juniperus sabina	1.2	-	-	+
Quercus coccifera	1.1	0.3	+	-
Jasminum fruticans	1.0	+	+	+
Arbutus unedo	0.7	2.1	-	-
Crataegus monogyna	0.7	1.7	0.6	1.8
Quercus faginea	0.4	1.4	0.3	0.2
Prunus mahaleb	0.2	-	0.8	1.5
Cytisus reverchonii	+	1.3	0.2	2.2
Others	5.4	1.5	0.5	2.1
Total	**53.3**	**72. 1**	**11.8**	**17.1**
Chamaephytes/dwarf-shrubs				
Helianthemum croceum	0.8	0.2	0.9	1.2
Teucrium carthaginense	0.6	-	0.2	0.9
Salvia lavandulifolia	0.6	-	+	0.1
Genista cazorlana	0.5	-	2.5	+
Teucrium multiflorum	0.2	-	2.2	0.3
Erinacea anthyllis	0.1	-	9.4	0.9
Echinospartum boissieri	+	-	4.7	3.3
Others	5.2	1.4	0.9	4.8
Total	**8.0**	**1.6**	**20.8**	**11.5**
Viscum album	0.8	-	-	-

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HERBACEOUS PLANTS				
Graminoids				
Oryzopsis paradoxa	5.2	3.0	5.2	10.9
Festuca arundinacea	3.7	3.5	4.7	4.7
Carex hallerana	2.3	1.5	3.7	5.5
Helictotrichon filifolium	1.9	-	1.7	3.0
Sesleria argentea	1.9	1.0	2.6	-
Brachypodium sylvaticum	1.5	1.0	1.8	2.4
Carex sp.	1.2	1.1	2.2	0.7
Cynosurus echinatus	1.1	1.3	2.7	1.2
Festuca plicata	0.8	0.5	2.3	6.2
Aegilops triaristata	0.7	1.2	2.3	1.1
Brachypodium ramosum	0.7	1.3	1.7	-
Festuca rubra	0.6	-	-	1.3
Festuca scariosa	0.5	1.0	1.7	1.4
Arrhenatherum bulbosum	0.5	0.8	2.0	-
Poa bulbosa	0.5	0.5	2.8	1.7
Dactylis glomerata	0.4	1.1	2.1	1.4
Koeleria hispanica	0.3	0.6	2.0	2.5
Bromus sp.	0.3	-	1.7	-
Festuca hystrix	0.3	-	-	1.6
Stipa aristella	0.2	2.5	2.7	+
Aegilops ovata	0.2	-	2.0	-
Avena sp.	0.2	-	1.7	-
Festuca rivularis	-	-	0.7	6.4
Others	3.7	2.4	7.1	1.0
Total	**28.7**	**24.3**	**57.4**	**53.0**
Forbs				
Aphyllantes monspeliensis	1.8	-	1.0	-
Asphodelus cerasifer	0.9	-	5.3	3.3
Rubia peregrina	0.9	0.2	-	1.0
Sanguisorba lateriflora	0.7	0.2	0.3	1.2
Cirsium hispanicum	0.2	-	0.5	5.7
Others	5.1	1.4	1.9	6.2
Total	**9.6**	**1.5**	**9.0**	**17.4**
Total	**100.0**	**100.0**	**100.0**	**100.0**

Graminoids were the largest component of fallow deer diet, particularly *Oryzopsis paradoxa, Festuca arundinacea, Carex hallerana, Aegilops triaristata, Poa bulbosa, Cynosorus echinatus* and *Stipa aristella* (2.7% to 5.2%), followed by chamephytes (20.8%) including *Erinacea anthyllis* (9.4%), the most heavily consumed individual species, *Echynospartum boissieri* (4.7%) and *Genista cazorlana* (2.5%). Trees and shrubs were less important than camephytes, with only *Pinus nigra* making a relevant contribution (6.2%). Non-graminoids was the least consumed group, primarily via *Asphodelus cerasifer* and *Aphyllathes monspeliensis*.

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Woody plants formed 32.6% of the diet, herbaceous plants 66.4% and cryptogams 0.9%.

Trees and shrubs formed by far the largest component of red deer diet (72.1%), most notably *Quercus rotundifolia* (29%), *Rosmarinus officinalis* (12.5%) and *Phillyrea latifolia* (9.5%), while 16 graminoids were identified, the largest component being *Festuca arundinacea* and *Oryzopsis paradoxa*. Chamaephytes and non-graminoids carried little weight in red deer diet. For red deer, the most heavily consumed plant components were *Q. rotundifolia* leaves, shrub and grass leaves, dry pine needles, *Crataegus monogyna* fruits and *Rosmarinus officinalis* flowers. Woody plants formed 73.7% of the diet, herbaceous plants 25.8% and cryptogams 0.5%.

3.2. Diet comparison and overlap

The overlap of each plant group in the ungulate diets is shown in Table 2. No significant correlation was detected between Spanish ibex and mouflon diets, and overlap was relatively low (36.5%). The woody component of the two diets was also non-correlated with little overlap. There was, however, a significant correlation for the herbaceous component (r_s=0.47, P<0.05, n=25), and overlap was higher than for woody species (38.0%). Diet breadth (diversity) and species richness were greater for Spanish ibex than for mouflon.

Table 2. Degree of overlap in percentage (ISK) of each group of plants consumed by wild ungulates in Cazorla Segura and Las Villas Natural Park. Spanish ibex (SI), red deer (RD), fallow deer (FD) and mouflon (M).

	SI-M	*SI-FD*	*SI-RD*	*M-FD*	*M-RD*	*FD-RD*
PLANT GROUPS						
Trees and shrubs	31.3	8.9	58.6	20.8	26.5	14.3
Chamaephytes/dwarf-shrubs	27.7	17.3	20.8	53.0	21.4	10.7
Graminoides	45.8	53.2	55.1	57.2	34.4	49.0
Forbs	35.4	37.6	27.0	45.4	15.9	24.7
Woody	30.2	10.6	55.7	40.0	25.7	13.4
Herbaceous	38.0	50.4	50.3	52.5	30.6	40.0
Total Diet	36.5	26.0	53.7	51.0	28.0	26.4

No significant correlation was found between Spanish ibex and fallow deer diet, and overlap was small (26%). Woody resources consumed by the two species were unrelated and overlap was quite small. There was, however, a correlation between the herbaceous component of the two diets (r_s=0.67, P<0.001, n=25), with a relatively high overlap (50.4%). Diet breadth and species richness was greater for Spanish ibex than for fallow deer.

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In contrast, the Spanish ibex and red deer diets did correlate significantly (r_s=0.67, P<0.001, n=51), and overlap was the highest of the herbivore diet comparisons (53.7%). There was also a correlation in the woody component of the two diets (r_s=0.75, P<0.001, n=26) as well as in the herbaceous component (r_s=0.60, P<0.007, n=25), with a relatively high overlap. Diet breadth and species richness were considerably greater in Spanish ibex than in red deer.

A correlation was found between mouflon and fallow deer diet (r_s=0.59, P<0.001, n=51), with a relatively large overlap (51%). The woody and herbaceous components of the two diets correlated (r_s=0.74, P<0.001, n=26) and (r_s=0.52, P<0.05, n=25) respectively. Diet diversity and proportions of each plant group were all similar in the two ungulates.

The composition of mouflon and red deer diets differed considerably, with a 28% overlap. No correlation was found between diets, herbaceous or woody components. Dietary diversity and species richness was greater in mouflon than red deer.

A significant correlation was detected between red deer and fallow deer diets (r_s=0.31, P<0.05, n=51), but overlap was low (26.4%). The woody component did not yield any correlation and overlap was very low, while the herbaceous component of the two diets did correlate (r_s=0.65, P< 0.01, n=25) and overlap was 40%. Diet breadth and species richness were greater for fallow deer than for red deer, and the consumption of each plant group differed considerably.

4. Discussion

Similarities in the diets of sympatric ungulate species can be influenced by several factors including food availability and quality, population density and specialisation of each species' feeding habits. On the basis of the latter premise, the analysis of the Spanish ibex and mouflon diets revealed different feeding habits, with the Spanish ibex consuming more woody vegetation while the mouflon consumed more herbaceous plants, with a large grass component. This pattern in caprine and ovine feeding habits was clearer in this area, a Mediterranean forest, than in other mountain zones (Sierra Nevada), where the Spanish ibex cohabits with the domestic sheep (*Ovis aries*) and a 56.3% diet overlap and a significant correlation between diets was been detected (MARTÍNEZ, 2002). This is understandable given that the study area is largely covered by alpine grasslands and the Spanish ibex feeding pattern was also primarily as a grazer. In the UK, BULLOCK (1985) detected low levels of overlap between domestic sheep and goats in certain zones and time periods. Considerable differences were found in woody and

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herbaceous plant consumption. Similar results were presented by CUARTAS (1992). However, this author detected lower consumption of grasses in both ungulates than the level found in the present study. This may have been due to a more restricted or localised research zone in the former case. The importance of grasses in Spanish ibex diet contributes to the positive relationship found between the herbaceous component in its own diet and that of mouflon and fallow deer.

Red deer had the most similar diet to that of the Spanish ibex in terms of amounts contributed by each plant group and the degree of diet overlap. In this context, *Quercus rotundifolia* and *Phillyrea latifolia* were important woody species for both ungulates. CUARTAS (1992) also noted high degree of overlap between the two diets, and McMAHAN (1964) observed this pattern between the browsing habits of domestic goat and red deer. There is a heavy consumption of shrub and tree matter by red deer and Spanish ibex in Spanish Mediterranean habitats (MARTÍNEZ *et al.*, 1985; PALACIOS *et al.*, 1989; GARCÍA-GONZÁLEZ & CUARTAS, 1992; MARTÍNEZ, 1994, 1996). The importance of herbaceous vegetation for red deer and Spanish ibex in different periods and environments has also been suggested by several authors (PALACIOS *et al.*, 1980; JENSEN, 1968; KAY & STAINES, 1981; MARTÍNEZ, 2000, 2001). In this case, red deer and Spanish ibex primarily behaved as browsers, although grasses formed a considerable group in the diet of both, especially in spring, suggesting that they should be considered in the transitory forms of the HOFMANN (1973) classification

The fallow red deer and mouflon had similar diets and a substantial overlap. The two phytophaga were heavy grazers and consumed large amounts of grasses. This implies that there could be competition for food in cases of a broad overlap between their distribution areas, as the grassland zones in the study area are not abundant. However, they tend to occupy different altitude-related habitats with only a limited overlap in certain areas and periods (FANDOS, 1986). In addition to their consumption of abundant herbaceous material (70%), it is curious to note that woody vegetation (especially subshrubs and camephytes) comprised roughly 30 % of the mouflon and fallow deer diet, as noted also by other authors including CALDWEL *et al.* (1983) for fallow deer and CUARTAS (1992) for both species.

When comparing mouflon and red deer diets, we found that the latter diet primarily consisted of shrub while the former mainly consumed herbaceous plants. Their feeding habits were quite different, with red deer primarily consuming trees and shrubs and almost no camephytes or forbs, while forbs and to a lesser extent chamaephytes formed a substantial part of the mouflon diet. Other authors including GEIST (1974) have identified *Ovis canadiensis* as one of the most selective grazers in warm climates, while HANSEN & MARTIN

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(1973) have noted that grasses are the most important food source in the annual diet of the species in the Grand Canyon. In the present study area, *Ovis musimon* consumed the largest amount of forbs amongst the four ungulates, and also had a grasses-rich diet. In contrast, the red deer was identified as a major browser and consumer of woody plants. There was little potential competition between red deer and mouflon in the light of their diet composition, their feeding specialisation and the fact that they tend to occupy different habitats (FANDOS, 1986).

Red deer and fallow deer also differed in feeding habits. The former ungulate had a primarily browsing behaviour while the fallow deer was primarily a grazer, with a grass-rich diet. This group of plants is attractive to red deer (25%) and leads to a correlation between the herbaceous components of the two diets. The importance of herbaceous vegetation for red deer and particularly for fallow red deer has also been detected by PALACIOS *et al.* (1980) in Doñana National Park. There is potential competition between the two species for herbaceous vegetation, given that their use of the habitat with respect to altitude is practically the same, with a greater breadth in the case of the fallow deer (FANDOS, 1986).

The degree of dietary overlap amongst the herbivores in Cazorla was quite low. There was only some overlap between Spanish ibex and red deer and between fallow deer and mouflon. The estimates revealed a greater overlap amongst the herbaceous components of their diets than between the woody plants (with the exception of the Spanish ibex and red deer diets), suggesting that grasslands are in heavy demand by these herbivores for forage and that there may be competition for herbaceous vegetation in cases of substantial habitat overlap. According to SQUIRES (1982) in BULLOCK (1985), divergence in feeding strategies only gives rise to a small dietary overlap between herbivores. On the basis of this premise, diet similarity or overlap amongst the ungulates in Cazorla was relatively low, they followed a generalist foraging pattern and some, particularly the Spanish ibex and to a lesser extent the mouflon, diversified their diet considerably. All of these patterns are probably linked to the different feeding trends and specialisations of the herbivores, along with the feeding strategies they must use due to heavy herbivore densities which lead to a resource shortfall. This coincides with results and suggestions by several authors that overlap declines with resource scarcity. In the present study area, dietary overlap between Spanish ibex and mouflon was greater in spring than in winter (the period of lowest vegetation availability) (MARTÍNEZ, 1992). In Cazorla, there is evidence of a resource distribution amongst sympatric herbivores due to their high density, which also indicates a substantial diversification of species diet and the occupation of different habitats by ungulates with similar feeding habits.

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