

Diet selection by Spanish ibex in early summer in Sierra Nevada

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Feeding strategy of the Spanish ibex *Capra pyrenaica* Schinz, 1838 was compared in two altitudinal zones of the Sierra Nevada, the high zone between 2700 and 3300 m a.s.l. and the mid-altitude zone between 2000 and 2700 m a.s.l. The study was carried out in July, and primarily focused on diet selection. Food availability, diet composition, species selection indices, and the effect of plant availability and chemical composition on diet selection in each zone were analysed. In the high zone, the availability of herbaceous resources was much greater than that of woody species, while in the mid-altitude zone, both resource types were almost equally abundant. Resource availability in both zones had a 36% index of similarity. Herbaceous plants were the predominant dietary component in both zones, and diet similarity was 51%. The greater similarity found between the two diet compositions than between the two resource availabilities revealed preferences for common species in both zones. The Spanish ibex selected food items with moderate levels in diet composition, a degree of quality (high protein content and digestibility) and moderate availability. In the high zone, the ibex selected its diet according to the protein content, while in the mid-altitude zone the food choice was mainly influenced by availability. Spatial heterogeneity probably influenced the difference detected in terms of the feeding strategy used in each area.

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Introduction

Previous analyses of the Spanish ibex *Capra pyrenaica* Schinz, 1838 feeding habits have revealed variations between locations, seasons and sexes (Martínez 1988, 1989a, 1990, 1992, 1994, 1997, Martínez *et al.* 1985), indicating that the diet selection is influenced by a range of factors. However, these species choice processes are very little-known. Westoby (1978) and Belovsky (1985) found that herbivores adopt feeding strategies that maximise the ingestion of digestible energy and essential nutrients. Other authors such as Maizeret (1988) suggest that diet diversification is one of the fundamentals of feeding behaviour.

According to Guillingham and Bunnell (1989), knowledge of the types and quantity of consumed food is an important aspect for understanding the natural history of animals, but a list of diet components reveals little about the selection processes. Analyses of the Spanish ibex diet composition in Sierra Nevada (Martínez

1988, 1989b, 1990) have served as a basis for understanding the species' feeding habits during the summer period (July and August) in areas above 2000 m a.s.l. However, recognising that a wide range of factors is involved in a herbivore's diet selection (feed availability, plant chemical composition, digestibility, palatability, physiological state of the animal, digestive capacity and efficiency), this paper investigates some of the mechanisms used by the Spanish ibex to choose its food. For this purpose, parameters such as plant resource availability and chemical composition were analysed in the study area.

In the Sierra Nevada, the Spanish ibex is one of the most important fauna species. In this habitat, both animal and plant communities are extremely vulnerable due to adverse environment conditions throughout the year, and vegetation and animal species are intimately linked through the feeding process. Consequently, it is important to determine the feeding strategy used by the Spanish ibex populations in this type of habitat. The study, which focuses on the high and mid-altitude zones of the study area, seeks to understand and compare the Spanish ibex feeding strategy at the start of the summer in the two zones. The diet selection is analysed on the basis of the availability and chemical composition of the plant species.

Study area

The study area was located in Sierra Nevada (south-eastern Spain). Two zones defined in terms of altitude (the factor influencing the climate and consequently the vegetation) were analysed. The high zone, covering the highest parts of the mountain (a key habitat for the Spanish ibex in summer), was on the S side of the Sierra between 2700 and 3000 m a.s.l. The mid-altitude zone was on the N-NW side between 2000 and 2700 m a.s.l. Geologically, the area has a central nucleus of Palaeozoic origin formed by acidic rock which reaches the highest elevations. It is surrounded by a Mesozoic belt of Dolomite, limestone, and marble, which only extrudes at the W-NW end (Rodríguez de la Zubia 1969). The area is snow-covered for 8 to 9 months of the year, with a mean annual precipitation (10-year average) of 694 mm and a mean temperature of 4.7°C (Prieto 1983).

On the basis of Valle (1985), the study area is represented by two vegetation series: The *Genisto baeticae-Juniperetum nanae sigmetum* series is widely distributed between 2000 and 2800 m and is defined by several plant communities. Broom-juniper fields which previously had *Juniperus communis*, *J. sabina* and *Pinus silvestris* as abundant species, but currently this type of vegetation is heavily degraded and has been replaced by thorny-padded chamaephytes. Thyme-pasture includes communities of *Thymus sephylloides*, and also herbaceous species such as *Agrostis nevadensis* and *Ameria filicaulis*. Wet meadows include communities formed by *A. nevadensis* and *Herniaria boissieri*, which mark the transition to other hygrophyllous communities with *Nardus stricta* and *Festuca iberica*.

The second series: *Erigeronto frigidi-Festucetum clementei sigmetum*, lies above 2700 m a.s.l. Its communities include pastures which are subject to strong winds, snow during most of the year and summer drought, typical species include *Festuca clementei*, *F. pseudeskia* and *A. nevadensis*, wet meadows formed by the communities defined in the above series and by characteristic species such as *Armeria splendens*, and rocky outcrops which tend to be colonised by low pioneer species.

Material and methods

Several methods and techniques were used due to the large number of parameters analysed. These are described in detail in Martínez (1992). A résumé is given here.

The vegetation was sampled systematically in the two zones, using sampling transects and plots set in different types of vegetation in accordance with the altitudinal gradient and its heterogeneity. Following Walker (1976) with certain modifications, the floristic composition of the herbaceous and woody strata were evaluated independently. Data from the two strata and the area covered by each type of vegetation (1:50 000 map of crops and land uses in Guedar-Sierra) were used to estimate the biomass contribution by each vegetation species in proportion to the total vegetation.

The botanical composition of the herbaceous stratum was evaluated using the ranking method (Mannetje and Haydock 1963) to calculate the specific constants for each study area. The sampling transects measured 500 m by 1 m, with 1 m² sampling units set every 20 m along the line. The biomass of the shrub species was evaluated on the basis of their volume, and linked to weight using regression equations. A series of 10 m² sub-plots were set every 25 m along each 189 × 5 m sampling plot. The height and largest and smallest diameters of all plants found were measured in each sub-plot. The volume was subsequently estimated on the basis of these parameters.

The Spanish ibex diet was studied using fecal analysis. The technique described by Cavender and Hansen (1970) was employed with minor modifications in both the physical and chemical treatments, which facilitated identification and quantification of species, as described in Martínez (1988). Twenty-five samples collected from each zone in July (taken directly from groups of previously located individuals) were analysed.

The degree of overlap between the diets was estimated using Kulczynski's Similarity Index (Oosting 1956), $KSI = [\Sigma 2W/\Sigma(a+b)] \times 100$, where W is 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. The similarity between food availability in two zones was also estimated using KSI. The diversity of plant species in the diets and availability was estimated according to the Shannon-Weaver Index (Pielou 1975), $H' = -\Sigma p_i \log_{10} p_i$, where p_i is the proportion of the total diet or availability belonging to the i th species.

Both diet composition and resource availability were analysed by species, by trophic or plant groups: shrubs, chamaephytes, graminoids (grasses, sedges and rushes) and forbs (total herbaceous excepting for grasses, sedges and rushes), and also by woody and herbaceous plants. Particular plant species were evaluated on the basis of the corresponding chemical analyses. Protein content (PROT) was estimated using the Kjeldahl method with an Kjeldahl Bouat-Afora air-dragging device. Other parameters: cellular content (CC), neutral-detergent fibre (NDF), acid-detergent fibre (ADF), hemicellulose (HEM), cellulose (CE), lignin (LIG), and apparent digestibility of dry matter (DDM) were determined by the method of Goering and Van Soest (1970) with modifications suggested by García-Criado (1974). The selection of plant species was estimated by the Ivlev's Selectivity Index, $ISI = (D - A)/(D + A)$, where D - diet (consumption) and A - availability.

The influence of different factors or variables on diet selection by the Spanish ibex in both zones was determined on the basis of three statistical approaches: Spearman's Correlation Rank Coefficient (r_s), Multiple Step-wise Regression (R^2) and Principal Components Analysis (PCA). Spanish ibex diet (SII) was the dependent variable, while the independent variables were: plant availability (A) and the parameters of the chemical composition of the previously defined plants. In the PCA, the variables were: Spanish ibex diet, plant availability and chemical composition parameters of plant species.

Results

Herbaceous and shrub strata

In the high zone herbaceous stratum, 68 species with an estimated biomass of 1497 kg/ha were evaluated. The diversity was 1.28 bits. The graminoid group was the most abundant, representing 69% of the total biomass and having diversity of 1.0 bits. The forbs represented the remaining biomass (31%) and their diversity was 1.2 bits. In the mid-altitude zone, 52 species with an estimated biomass of 342 kg/ha were recorded. The diversity was 1.05 bits. The graminoid group

comprised 85.9% of the total biomass and its diversity was 0.97 bits. Forbs comprised the rest of biomass (14.1%), with a diversity of 0.95 bits.

In the high zone, the shrub stratum only covers a small zone in the study area and is very little developed, being restricted to diverse chamaephyte species and a few low prostrate shrubs which reflect the harsh, adverse climatic conditions. Seven species were found, the estimated volume was 422.9 m³/ha and the estimated biomass was 4191.6 kg/ha. The density was 25 000 plants/ha and the species diversity was 0.42 bits. Six woody species were evaluated in the mid-altitude zone, with a plant density of 50 000 individuals/ha. The estimated volume was 1406.6 m³/ha of shrub matter and dry weight biomass of 14 963.3 kg/ha. The diversity was 0.41 bits.

Floristic composition and total plants availability

Table 1 shows the most abundant species in the study area (percentages $\geq 0.5\%$). In the high zone, the herbaceous vegetation formed the largest part of the plant biomass (87%). In contrast, the biomass contributed by the woody vegetation (shrubs-chamaephytes) constituted 13%. In the biomass of each trophic group, graminoids were the most abundant, followed by forbs, shrubs and chamaephytes (Fig. 1).

The species composition of the mid-altitude zone is summarised in Table 1. Herbaceous plants comprised 57.3% of the total biomass and woody plants comprised the remaining (42.7%). Figure 1 shows biomass separated into trophic groups. The most abundant group was graminoids, followed closely by shrubs, then forbs and finally chamaephytes, which were not abundant.

Quantitative and qualitative differences were found between the availability of food resources of the two zones (Table 1). These differences are reflected in the low similarity index between respective food supplies (36%). The similarity indices amongst the corresponding plant groups did not exceed 50%, except amongst the chamaephytes (57.9%) which was the highest. The group of graminoids had a mid-range similarity index (49.5%), while those of shrubs and forbs were quite low (28.5%). In both zones, herbaceous vegetation contributed more biomass than woody vegetation, although the latter was considerably more abundant in the mid-altitude zone. The estimated biomass per hectare in the two zones differed considerably. Herbaceous vegetation biomass/ha in the mid-altitude zone was double that of the high zone, and woody vegetation biomass/ha was four times higher. Influential factors were vegetation density, form of growth, and type of species found in each zone. The diversity index and species richness were greater in the high zone.

Spanish ibex diet

The Spanish ibex diet in the mid- and high-altitude zones was described by Martínez (1988, 1990). For illustrative purposes, however, Table 1 summarises the diet composition in each zone, and Fig. 1 shows the importance of each plant group. Essentially, 39 plant species were identified in the upper zone, with a diversity of

Table 1. Resource availability (A), Spanish ibex diet (D) and species selection (ISI) in the high and mid-altitude zones of Sierra Nevada.

Plant species	Biomass (%)					
	High zone			Mid-altitude zone		
	A	D	ISI	A	D	ISI
1	2	3	4	5	6	7
Shrubs						
<i>Cytisus purgan</i>	7.9	1.0	-0.75	-	-	-
<i>Juniperus nana</i>	2.5	5.5	0.37	10.4	4.0	-0.45
<i>J. sabina</i>	0.4	4.0	0.80	2.0	3.0	0.20
<i>Genista baetica</i>	-	-	-	28.7	3.5	-0.78
<i>Pinus sylvestris</i>	-	-	-	-	5.7	-
Chamaephytes						
<i>Thymus serpylloides</i>	1.4	1.1	-0.12	1.0	0.3	-0.50
<i>Sideritis glacialis</i>	0.4	0.4	0	-	-	-
<i>Ptilotrichum spinosum</i>	0.2	3.0	0.88	0.1	1.2	0.85
<i>Reseda complicata</i>	-	1.8	-	-	-	-
<i>Helianthemum</i> sp.	-	-	-	0.5	1.0	0.33
Others	0.2	0.2	-	-	-	-
Graminoids						
<i>Festuca pseudeskia</i>	13.3	1.0	-0.86	2.4	-	-
<i>Agrostis nevadensis</i>	11.4	16.0	0.17	9.7	16.6	0.26
<i>Nardus stricta</i>	5.5	10.0	0.29	2.3	-	-
<i>Festuca clementei</i>	5.0	5.3	0.03	-	-	-
<i>F. iberica</i>	3.5	9.5	0.46	2.9	14.5	0.65
<i>Carex nevadensis</i>	2.7	3.0	0.05	-	-	-
<i>Koeleria caudata</i>	2.7	-	-	0.5	3.3	0.74
<i>Festuca nevadensis</i>	2.6	-	-	1.8	3.0	0.25
<i>Dactylis glomerata</i>	2.3	7.7	0.54	2.2	6.9	0.52
<i>Festuca ovina</i>	1.4	3.7	0.45	1.8	6.5	0.57
<i>Deschampsia flexuosa</i>	1.3	1.6	0.10	5.1	8.6	0.25
<i>Holcus caespitosus</i>	1.3	0.2	-0.73	-	-	-
<i>Carex nigra</i>	1.1	1.2	0.04	-	-	-
<i>Poa alpina</i>	1.0	-	-	-	-	-
<i>Festuca frigida</i>	0.5	2.7	0.68	-	-	-
<i>Trisetum glaciale</i>	0.5	1.6	0.52	-	-	-
<i>Festuca indigesta</i>	-	0.5	-	12.1	3.2	-0.57
<i>Anthoxantum odoratum</i>	0.5	1.3	0.42	0.2	0.6	0.50
<i>Luzula spicata</i>	-	0.8	0.45	-	-	-
<i>Festuca scariosa</i>	-	-	-	5.0	3.3	-0.20
<i>F. rivularis</i>	-	-	-	0.5	0.6	0.09
<i>Arrhenatherum elatius</i>	-	-	-	0.8	1.8	0.38
<i>Carex</i> sp.	-	-	-	-	1.2	-
<i>Luzula</i> sp.	-	-	-	-	0.6	0.50
<i>Trisetum</i> sp.	-	-	-	-	0.6	0.50
Others	2.9	1.5	-	2.0	2.0	-

Table 1 – concluded.

	1	2	3	4	5	6	7
Forbs							
<i>Arenaria tetraquetra</i>		7.6	1.1	-0.75	1.2	0.6	-0.33
<i>Lotus glareosus</i>		2.8	1.2	-0.53	0.1	0.5	0.42
<i>Senecio pyrenaicus</i>		2.2	0.5	-0.64	-	-	-
<i>Leontodon microcephalus</i>		1.7	0.3	-0.70	-	-	-
<i>Plantago alpina</i>		1.6	-	-	1.1	-	-
<i>Crepis oporinoides</i>		1.5	1.0	-0.20	-	-	-
<i>Leontodon boryi</i>		1.3	-	-	-	-	-
<i>Reseda complicata</i>		1.4	1.8	0.13	-	-	-
<i>Sempervivum nevadense</i>		1.0	-	-	1.3	-	-
<i>Plantago nivalis</i>		0.9	-	-	-	-	-
<i>Jasione crispa</i>		0.9	-	-	-	-	-
<i>Herniaria boissieri</i>		0.6	-	-	-	0.5	-
<i>Eryngium glaciale</i>		0.5	1.8	0.56	0.7	-	-
<i>Ranunculus demissus</i>		0.4	0.6	0.20	-	-	-
<i>R. acetosellifolius</i>		0.4	2.5	0.78	-	-	-
<i>Anthyllis vulneraria</i>		0.1	1.3	0.73	-	-	-
<i>Rumex acetosella</i>		0.1	0.5	0.66	0.1	1.3	0.70
<i>Silene boryi</i>		0.1	0.1	0.00	0.2	0.6	0.50
<i>Cardus</i> sp.		-	-	-	0.7	-	-
<i>Dianthus</i> sp.		-	-	-	0.6	-	-
<i>Hieracium pilosella</i>		-	-	-	0.2	0.8	0.60
Others		1.7	2.7	-	2.8	3.8	-
<i>Sphagnum</i> sp.		0.7	-	-	-	-	-

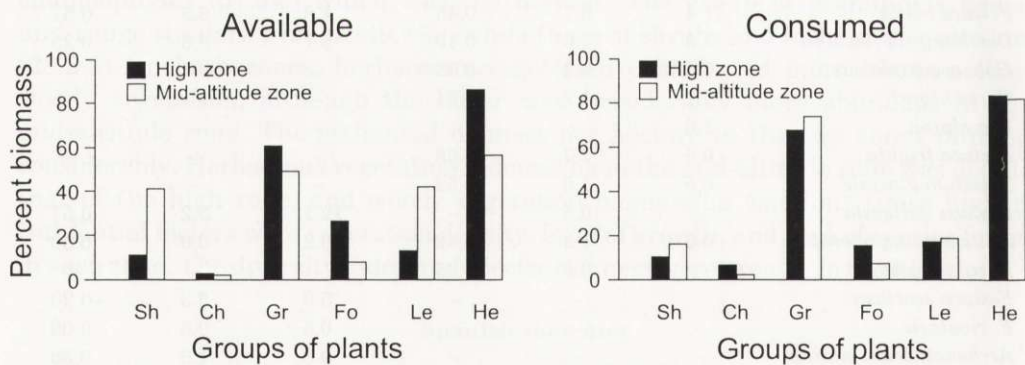


Fig. 1. Groups of plants available and consumed by Spanish ibex in high and mid-altitude zones of Sierra Nevada. Sh – shrubs, Ch – chamaephytes, Gr – graminoids, Fo – forbs, Le – ligneous plants, He – herbaceous plants.

1.13 bits. The most heavily consumed plant group was the graminoids, followed by forbs and shrubs, while the chamaephytes were the least used group. In the mid-altitude zone, 34 species were identified with a diversity of 1.19 bits. The trophic group contributing most to the Spanish ibex diet was the graminoids, followed by trees and shrubs, then forbs and finally chamaephytes.

The similarity between the ibex diet in two zones was 51.1%. It was low amongst the forbs group (23.6%) and amongst the chamaephytes (33.3%). However, it was higher amongst the shrubs (52.4%), and particularly amongst the graminoids (57%). The chamaephyte and forb groups were consumed twice as much in the high as in the mid-altitude zone. In contrast, the consumption level of the most important group (graminoids) in the diet of both zones was similar, with no significant difference to the consumption of trophic groups ($\chi^2 = 6$, $df = 3$, $p > 0.05$) or to woody and herbaceous plants consumed in the two zones ($\chi^2 = 0.1$, $df = 1$, $p > 0.05$). The diet diversity was greater in the high than the mid-altitude zone.

Food chemical composition

Table 2 lists several chemical components of various plant species available to and consumed by the Spanish ibex in the two study zones. *Agrostis nevadensis* had a high protein content and digestibility. Other species with relatively high protein or digestibility values were *Festuca clementei*, *Carex* sp., *Anthoxantum odoratum*, *Eryngium glaciale*, *Festuca iberica*, *Nardus stricta*, *Dactylis glomerata* and *Senecio pyrenaicus*. Another important chemical component in the plants, which may influence herbivore dietary selection, is lignin content. Woody plants had the highest content, especially *Juniperus sabina* and *Cytisus purgans*, while in herbaceous plants this component ranged between 5.8% and 1.7%, corresponding respectively to *Festuca pseudeskia*, a little consumed item, and *A. nevadensis*, a heavily consumed item.

Plants species selected by the Spanish ibex

Table 1 shows the Ivlev's Selectivity Indices for plant species consumed by the Spanish ibex in the high and mid-altitude zones. Amongst the woody plants in the high zone, the plant species with the highest indices were not abundant, but were relatively important in the diet; this was the case with *Juniperus sabina* and *Ptilotrichum spinosum*. The graminoids group had the largest number of positively selected species, although species with the highest indices were not particularly abundant. In contrast, species such as *F. pseudeskia*, an abundant resource in the zone, had an extremely negative index. This plant, unpalatable due to its spiny leaves, was very little consumed. The forbs included species with extremely high and extremely low indices, the latter corresponding to relatively abundant resources and low consumption.

In the mid-altitude zone, shrub plants were avoided, except for *J. sabina*. In contrast, the group of chamaephytes was preferred, except for *Thymus serpylloides*.

Table 2. Chemical composition of plant species important in availability and in Spanish ibex diet in Sierra Nevada. PROT – protein, CC – cellular content, NDF – neutral-detergent fibre, ADF – acid-detergent fibre, HEM – hemicellulose, CE – cellulose, LIG – lignin, DDM – apparent digestibility of dry matter.

Plant species	Components (%)							
	PROT	CC	NDF	ADF	HEM	CE	LIG	DDM
Woody plants								
<i>Cytisus purgans</i>	10.4	57.4	42.6	48.8	8.6	19.7	29.1	40.7
<i>Sideritis glacialis</i>	9.5	43.0	57.0	38.5	4.5	12.5	26.0	55.1
<i>Juniperus sabina</i>	7.5	29.9	70.2	40.8	10.9	21.7	19.1	59.2
<i>Juniperus nana</i>	7.1	37.9	62.1	36.1	1.9	12.2	23.9	58.1
Herbaceous plants								
<i>Agrostis nevadensis</i>	24.0	41.1	58.9	23.0	18.1	1.7	21.3	77.4
<i>Festuca clementei</i>	15.9	62.9	37.1	37.5	25.4	4.9	32.6	60.5
<i>Carex nigra</i>	14.3	56.5	43.5	32.4	24.2	5.1	27.6	59.6
<i>Anthoxanthum odoratum</i>	14.2	51.6	48.4	29.2	22.4	2.7	26.5	71.2
<i>Festuca iberica</i>	12.6	58.7	41.4	34.1	24.5	3.9	30.3	65.2
<i>Nardus stricta</i>	12.5	57.2	42.8	29.2	28.1	2.6	26.6	70.4
<i>Dactylis glomerata</i>	12.3	54.3	45.7	30.8	23.5	3.0	27.8	69.5
<i>Festuca nevadensis</i>	11.6	52.4	47.6	31.9	20.5	2.7	29.2	72.6
<i>Deschampsia flexuosa</i>	10.6	62.4	37.6	43.4	19.1	5.0	38.3	63.5
<i>Festuca ovina</i>	10.5	71.5	28.6	45.0	26.5	3.5	41.5	70.3
<i>Koeleria caudata</i>	9.8	60.5	39.5	36.4	24.1	3.4	33.0	67.0
<i>Festuca indigesta</i>	9.1	57.8	42.2	31.9	25.9	3.4	28.5	66.9
<i>Festuca pseudeskia</i>	7.3	69.5	30.5	42.5	27.1	7.1	35.4	52.4
<i>Eryngium glaciale</i>	13.3	33.2	66.8	30.9	2.3	5.3	25.6	69.2
<i>Senecio pyrenaicus</i>	12.2	20.9	79.1	20.5	0.4	3.2	17.3	75.7
<i>Rumex acetosella</i>	10.5	30.4	69.7	26.1	4.3	5.8	20.4	67.9

Almost all species forming the graminoids group were preferred, except for *Festuca scariosa*, and *F. indigesta* which was consumed very little although it is quite abundant in the zone.

The selection indices of consumed species revealed that the Spanish ibex generally followed a similar species selection pattern in the two zones. The grass species with a high protein content or digestibility were positively selected in both zones. The most abundant forb species were avoided. The highest quality woody plants were preferred, except for the most abundant items. Amongst the trophic groups, the chamaephytes and graminoids were preferred in both zones, while shrubs and forbs were avoided.

Influence of availability and chemical composition on food on diet selection

The selection of the herbaceous component of the diet was analysed after finding that herbaceous vegetation formed the majority of the Spanish ibex diet in both the

high and mid-altitude zones (83% and 81.3%, respectively). In the mid-altitude zone, only the selection of the herbaceous component could be analysed, as chemical parameters of *Pinus silvestris* and *Genista baetica*, and availability of *P. silvestris* were not available.

In the high zone, the herbaceous component of the Spanish ibex diet correlates with its protein content ($r_s = 0.54$, $n = 19$, $p < 0.05$). No correlation was observed with any other parameter. The regression analysis revealed that the herbaceous component of the diet was influenced by the protein content, the only variable entering in the configuration of the model ($R^2 = 0.48$, $F = 12.3$, $p < 0.01$). The Principal Components Analysis (PCA) (Table 3), also revealed important information. The herbaceous component of the diet and the protein content of the resources had positive scores on Component II. The lignin content had positive scores on Component III, while digestibility had negative scores. In the mid-altitude zone, the herbaceous component of the diet correlated with its availability ($r_s = 0.54$, $n = 16$, $p < 0.05$). Stepwise regression analysis indicated that protein content is the only variable included in the model ($R^2 = 0.34$, $F = 7.3$, $p < 0.05$). The PCA (Table 3), provides important information: diet and availability scored positively on Component II.

In the high zone, no correlation was found in the diet with either availability or the chemical composition parameters. According to the stepwise regression analysis, the protein content of the Spanish ibex food influences its diet selection ($R^2 = 0.37$, $F = 10.2$, $p < 0.01$). The PCA (Table 3) provides similar results to those of the

Table 3. Principal Components Analysis (PCA). Loading factors of variables in the 3 principal axes. SID - Spanish ibex diet, A - availability, PROT - protein, NDF - neutral-detergent fibre, CC - cellular content, ADF - acid-detergent fibre, HEM - hemicellulose, LIG - lignin, CE - cellulose, DDM - apparent digestibility of dry matter. Herbaceous component of diet (DHC) and total diet (TD). * - load factors defined.

Components	High zone (DHC)			Mid-altitude zone (DHC)			High zone (TD)		
	I	II	III	I	II	III	I	II	III
SID	-0.05	0.44*	0.08	0.22	0.47*	0.29	-0.08	0.42*	0.32
A	0.06	0.25	0.50	0.11	0.39*	0.11	-0.20	0.14	0.39
PROT	-0.19	0.36*	0.05	0.36	0.22	-0.09	-0.01	0.44*	0.05
NDF	-0.41	0.11	-0.07	-0.43	0.26	-0.12	-0.48	-0.04	-0.01
CC	-0.41	-0.11	0.07	0.43	-0.26	0.12	0.48	0.03	0.01
ADF	0.39	-0.06	0.03	-0.28	-0.28	0.55	-0.28	-0.35	0.23
HEM	0.33	0.21	-0.13	-0.30	0.28	-0.47	-0.41	0.15	-0.19
LIG	0.14	-0.28	0.55*	-0.28	-0.28	0.55	0.10	-0.34	0.50*
CE	0.39	-0.00	-0.09	-0.40	0.25	0.09	-0.43	-0.12	-0.19
DDM	-0.29	0.10	-0.50*	0.38	0.15	-0.35	0.14	0.35	-0.44*
% of explained variance	41.7	33.0	10.6	46.3	24.4	13.8	34.9	31.8	15.6

herbaceous component. Ibex diet and protein content of plants had positive scores on Component II. Component III groups lignin food content in the positive region and digestibility in the negative region. None of the analyses revealed any influence of availability in diet selection.

Discussion

Despite their relative proximity to each other, the two zones have several ecological differences. The altitudinal variable influences climatic conditions and causes variation in the vegetation composition and structure. This variation influenced the Spanish ibex diet and feeding strategy in the two zones.

Diet composition

The fact that the similarity index between the Spanish ibex diet in the two zones was moderate (51%), underscores the quantitative and qualitative similarities and differences between the diets in the two zones. Amongst the differences, some resources were consumed in different percentages in one of the two zones, or were part of the diet in one zone and not the other. This may be due to several reasons: more palatable and preferred plants may grow in the zone where they are less heavily consumed, or are unavailable in the area where they are not consumed, as is the case with *F. clementei* and *F. frigida* in the mid-altitude zone, and *F. indigesta*, *P. sylvestris* and *G. baetica* in the high zone. The lower availability of one resource in one of the zones or its advanced phenological state (lower palatability) may influence its consumption. This was probably the case for *Nardus stricta*, consumed in the high zone but unconsumed in the mid-altitude zone.

Amongst the similarities, some of the most representative species of the study area were consumed in large proportions in both zones. This was the case for *A. nevadensis*, *F. iberica*, *D. glomerata* and *F. ovina*, some of which, such as *A. nevadensis* and *D. glomerata* had high selection indices. This suggests that the ibex has preferences for certain common trophic resources in both zones, and in fact the similarity between the diets was higher than between the food availabilities. It should be noted that almost the same amount of woody plants was consumed in both zones, although they were much more abundant in the mid-altitude zone. Unlike this study area, the woody plants in low zones of lower altitude areas, such as the Sierras de Beceite or Sierras de Cazorla (Mediterranean areas), are substantially more consumed than in the high zones (Martínez 1994, 1997). In Sierra Nevada, the Spanish ibex has a different feeding pattern: richer in grasses and similar to the mountain areas of the Sierra de Gredos (Martínez and Martínez 1987), which are more similar by climatic and edaphic conditions.

Feeding strategy

The Spanish ibex feeding strategy differs somewhat in the two zones, with certain common traits. According to Owen-Smith (1979), the feeding efficiency of

large herbivores is affected by the state of their food resources. Similarly, Skogland (1980) claims that if the state of the vegetation changes, the width of trophic niche can undergo changes, along with the food intake. In the high zone, both the composition of the entire diet and its herbaceous component were influenced by resources quality. The ibex consumed the most protein-rich and digestible food, while the species with the highest cellulose and lignin content were consumed very little and not selected. In the mid-altitude zone, on the other hand, the selection of the herbaceous component of the Ibex diet was influenced by resource availability, although protein content was also important to some extent. Thus, the Spanish ibex consumed food that was protein-rich but also had a higher lignin content and a lower digestibility, as it ingested a larger amount of shrubs than in the high zone. The fact that the protein content of the food is reflected in the diet selection in both zones is important, as nitrogen plays a key role in all metabolic processes, especially in growth (Mattson 1980). It is also fundamental in reproductive mechanisms: the fertility of several ungulates correlates with plant nitrogen content (Crawley 1983).

The diet diversity and the number of species consumed were higher in the high zone than the mid-altitude zone (as was the case with resource availability), suggesting that the Spanish ibex tended towards a greater diet diversity in habitats where the species diversity was also greater. The greater trophic niche width, as with the influence of food quality, suggests a greater degree of diet selection in the high zone. However, although the Spanish ibex may use slightly different strategies in each zone, I conclude that in the Sierra Nevada, at altitudes above 2500 m, the Spanish ibex has similar feeding habits in both zones and primarily selects its diet on the basis of quality (protein content). In both the upper and the mid-altitude zone, the Spanish ibex tries to optimise its use of the available resources (some of which have a high fibre and lignin content). In the high zone it has a more diverse and selective diet with a higher protein content and a lower shrub consumption; while in the mid-altitude zone it ingests a larger amount of shrubs, consuming the most abundant herbaceous resources and at the same time selecting those with the highest quality. By this means, it acquires the nutrients necessary to cover its needs, as the food intake changes in response to the prevailing state of the food resources (Skogland 1984).

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