

SEASONAL DIET OF MOUFLON (*OVIS GMELINI*): COMPARISON OF POPULATION SUB-UNITS AND SEX-AGE CLASSES

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INTRODUCTION

Although several methods exist to quantify the diet of herbivores, each has advantages and limitations, and none is entirely free from bias (Holeček *et al.*, 1982). Furthermore, some techniques are not applicable to free-ranging populations. Faecal analysis (Putman, 1984) and rumen analysis (Heroldova, 1988a) are the two most frequently used. Both techniques have been employed to describe mouflon diet. Faecal analysis was used in a study of a population in the Cazorla mountain range, southern Spain (García-González & Cuartas, 1989), while rumen analysis was carried out to quantify autumn and winter diet in Czechoslovakia (Heroldova, 1988b) and autumn diet only in Teneriffe, the Canary Isles (Luengo & Pinero, 1991). Other authors have relied on direct observation to provide an approximate estimate of diet composition in this species, on wild animals in Corsica (Pfeffer, 1967) and on enclosed animals in Germany (Briederman, 1988). This study concerns the largest population of mouflon in France, in and around a wildlife reserve in the Caroux-Espinouse mountain range. One previous study of mouflon from this area provided some preliminary information on diet composition by analysis of rumen contents (Faliu *et al.*, 1990).

In several species, differential dietary requirement is often hypothesized to explain sexual segregation (Main *et al.*, 1996). Neither Faliu *et al.* (1990) nor the other authors cited above attempted a comparison of male and female diet of mouflon. Such a comparison may provide interesting insights into the factors underlying sexual segregation commonly observed in this species (Bon, 1987; Dubois *et al.*, 1993; Le Pendu *et al.*, 1995). Here, we describe seasonal variation of mouflon diet from faecal micro-analysis for two socio-spatial sub-units of the Caroux-Espinouse population. Additionally, we present a re-analysis of rumen contents data (Faliu *et al.*, 1990), providing a comparison of diet composition for lambs and adult animals and for the two sexes.

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STUDY AREA

The study population was founded from 19 individuals introduced between 1956 and 1960 to the reserve (Cugnasse & Houssin, 1993). Currently, the population, estimated at 1 400 in 1981 (Cugnasse, 1982), consists of less than two thousands animals on an area of about 12 000 ha (Hewison, unpublished data). This site occurs on the southern border of the Massif Central in the south of France with altitude ranging from 600 to 1 124 m. Climatic conditions are a mixture of Mediterranean, Oceanic and Mountain influences, leading to hot dry summers, wet autumns and cold winters (Baudière, 1970). The vegetational cover is a mosaic of beech (*Fagus sylvatica*), chestnut (*Castanea sativa*) and evergreen oak (*Quercus ilex*) forests moving from north to south, heather (*Erica cinerea*, *Calluna vulgaris*) and broom (*Cytisus purgans*, *C. scoparius*) moorlands, and rocky slopes. Ancient meadows remain from pasture lands surrounding several abandoned villages in the valleys. The high plateaux have been replanted with coniferous trees (*Pinus sylvatica*, *P. nigrans*, *Picea excelsior*).

Three socio-spatial sub-units within the mouflon population were delimited by radio-tracking studies (Fig. 1) : Mascar, Vialais and Brus (Maublanc *et al.*, 1993). Each of these consists of valleys and plateaux inhabited throughout the year by mouflon females and young but by old males only during the rutting period from late September to January-March (Bon, 1987 ; Cransac & Maublanc, 1996). From a preliminary analysis of broad habitat types, it appears that there may be differences between these sub-units in habitat composition ; the Brus unit is more heavily wooded while the other two units are more open, with higher grass abundance (Maublanc *et al.*, 1993). Here we investigate the effect of habitat differences on the diet of the mouflon inhabiting two of these units.

MATERIAL AND METHODS

FAECAL ANALYSIS

The study was carried out from April 1994 to March 1995 in the national wildlife reserve and an adjacent valley. Data on the phenology of different plant species were collected each season. Seasons are delimited as winter from January to March, spring from April to June, summer from July to September and autumn from October to December.

The seasonal composition of mouflon diet was determined by microhistological faecal analysis. Samples of faeces were collected each month in two of the sub-units of the population (Vialais, Brus) in the valley bottoms, on slopes and on the plateaux. Fresh samples were taken as those still covered in mucus. Five to 10 pellets from single, well-defined groups were collected to ensure only one individual animal was sampled. Approximately 100 fresh pellet groups were collected per season, equally distributed between the two sub-units and preserved in a solution of 10 % formaline. For each sample, four slides were prepared following the technique used by Guilhem *et al.* (1995). For quantification, species fragments were counted on a video screen divided into a grid of squares. The number of grid squares covered by a given epidermic unit was recorded. A total of 800 grid squares selected at intervals of 1 mm on the slide were sampled and so

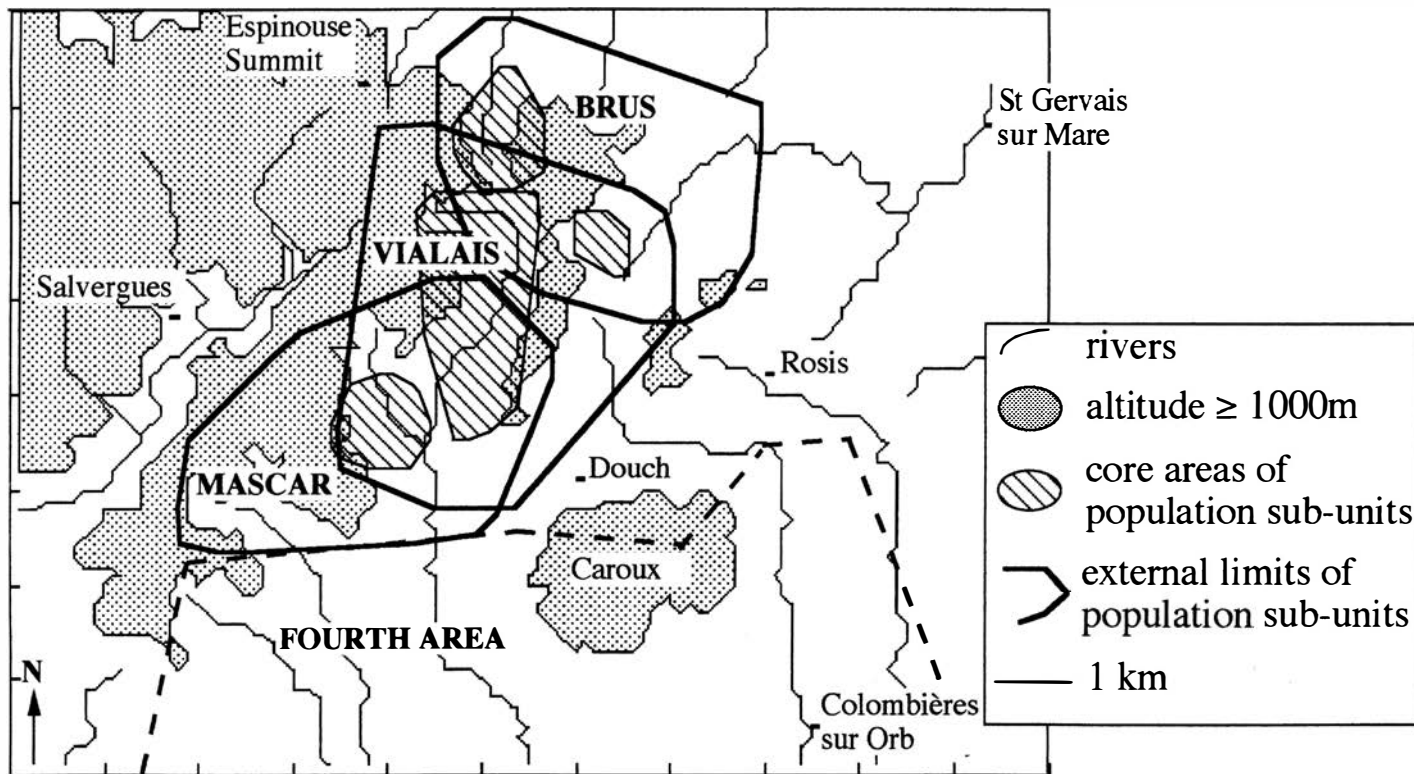


Figure 1. — Location of the three socio-spatial sub-units of the mouflon population determined by radiotracking in the Caroux-Espinouse massif. A fourth area is delimited, outside the reserve, from where additional rumen samples were taken.

the abundance of each species was expressed as a fraction of 800. Each epidermis was classified at the species level when this was possible or, in some cases, at the generic or other taxonomic level according to Bonnier (1990). The computer program « plantox » (Badia *et al.*, 1986) was used as an identification key for dicotyledons. This provides the plant family, genera or species name from codes of shapes of hairs, cells, stomata, etc... A classical reference atlas was compiled for monocotyledons. Soft fruits were identified by characteristics of their epidermis, but nuts were only identifiable by hairs and were quantified in four classes defined by the number of hairs : absent, present (< 50), abundant (from 50 to 300) and highly abundant (> 300). For each season and each of the two sub-units diet composition was evaluated in two ways. Firstly, each species was expressed in terms of presence/absence, i.e. the proportion of the faecal samples for a given sub-unit/season where that species was detected. Secondly, the contribution of a species in the mouflon diet was expressed quantitatively as the mean number of epidermic units per sample (average based on between 52 and 60 faecal samples). To evaluate possible bias in the quantitative analysis due to problems of species identification, these two variables were compared using regression of log-transformed variables. For example, such problems may lead to under-estimation of the number of epidermis units of a species which is not easily recognized and to over-estimation of a species with distinctive morphology, while in a qualitative study, this problem is less serious. In the statistical analysis, certain species were combined into broad categories whereas others, because they were an important part of the diet and/or they were representative of a particular habitat type, were considered separately. For example, fescue (*Festuca* sp.) is typical of dry meadows and mixed moorland, wavy-hair-grass (*Deschampsia flexuosa*) is typical of forest, while broom and heather are the main components of two types of moorland and *Rubus* sp. is a particularly important element in the diet. The degree of similarity of diet between seasons and sub-units was estimated by the similarity index of Gauch (1973) : $SI = 100 \times 2 \sum_{\min}(p_{ij}, p_{ik}) / \sum(p_{ij} + p_{ik})$ where p_{ij} and p_{ik} represent the proportion of the species i in the diet for season/sub-unit classes j and k . For comparing diet between sites for each season, differences were analysed statistically using χ^2 tests. Because of potential differential bias in the quantification of plant fragments, a comparison between plant groups was not considered possible.

RUMEN ANALYSIS

In order to compare diet composition of adults and lambs of both sexes, we re-analysed rumen contents data previously presented by Faliu *et al.* (1990) together with some additional samples. This comprised 145 rumens collected between 1973 and 1977 during the hunting season of October to March. Samples originated from each of the three population sub-units of the reserve plus a fourth area on its southern border (Fig. 1). Because of the small sample sizes, we considered autumn and winter for adults (for females : $n_{\text{autumn}} = 44$, $n_{\text{winter}} = 10$; for males : $n_{\text{autumn}} = 60$, $n_{\text{winter}} = 16$) but only autumn for lambs (females : $n = 9$, males : $n = 6$). Heroldova (1988b) considered that the minimum number of rumen samples per group needed for reliable analysis of diet was approximately ten. Samples of the content of each rumen (0.51) were filtered in sieves of 4, 2.5 and 1.6 mm. Large fragments were identified with the naked eye and a hand-held binocular lens if necessary, while small fragments were examined under the

microscope. Results were expressed as the percentage of fragments of each plant species as a function of the total number of fragments observed. Because we dealt with percentages, non parametric tests were used to compare male and female diet in winter (Kendall's rank correlation coefficient) and to compare diet between sub-units and between age-sex classes (Friedman's test).

RESULTS

Differences between seasons and sub-units are estimated from faecal analysis. Firstly, because of problems of species identification associated with microanalysis of faeces, we wanted to be sure that we could use the data in a quantitative manner. We compared the abundance of each species, expressed as the mean number of epidermic units (out of 800) per sample, and the frequency of occurrence (presence/absence) of that species in the faecal samples for a given season. Data were log-transformed to obtain normally distributed variables. These two variables were very highly correlated for each season : in spring $R^2 = 0.949$, $n = 70$, $p < 0.0001$; in summer $R^2 = 0.935$, $n = 67$, $p < 0.0001$; in autumn $R^2 = 0.959$, $n = 48$, $p < 0.0001$; in winter $R^2 = 0.957$, $n = 43$, $p < 0.0001$. This extremely close relationship between the measure of presence/absence and abundance supports the use of the latter in subsequent analysis. Abundance should be considered as a semi-quantitative variable because it is probable that not all plant species eaten by the animal were present in the faeces, some, such as lichens, ferns, mushrooms or some fruits, being entirely digested. Despite this, we use this variable for comparing seasons and/or areas.

GENERAL DIET

Globally, the main diet components of mouflon in the Caroux-Espinouse are grasses and shrubs while trees are not important (Table I). The proportion of unidentified fragments was fairly constant between the seasons (9.5 %), although slightly higher in spring (12 %). Generally, only a few species or families of each plant type made up a large part of the diet in each season. i) Among the grasses *Festuca* sp., *Deschampsia flexuosa* and *Brachypodium pinnatum* were abundant in all seasons and *Aira caryophyllea* in spring only ; ii) Among the forbs, Labiateae and *Teucrium scorodonia* were present all year round with Compositae and *Crepis* sp. in spring only ; iii) Among the shrubs, broom, heather and *Rubus* sp. were eaten throughout the year plus *Vaccinium myrtillus* in spring and summer ; iv) Among the trees, conifer needles occurred in the diet all year round and Fagaceae were present at a low level except in winter ; v) In the fruit category, nuts were important for mouflon in autumn and winter and soft fruits were eaten in spring and summer.

DIET VARIATION BETWEEN SUB-UNITS AND SEASONS

Mouflon diet composition differed significantly between the two study sub-units of the population (Fig. 2) in autumn ($\chi^2 = 63.819$, $p = 0.0001$, $df = 13$),

TABLE I

Seasonal variation in the diet of two sub-units of a mouflon population in the Caroux-Espinouse massif determined by faecal analysis expressed as the mean number of epidermis units of each species or family. (Species with all site-season averages less than 3 are regrouped as a separate category entitled « others »).

Season	Spring		Summer		Autumn		Winter	
	Brus	Vialaïs	Brus	Vialaïs	Brus	Vialaïs	Brus	Vialaïs
Population sub-unit								
Sample size	60	57	53	59	52	53	55	52
Gramineae	105	132	80	77	110	100	115	105
<i>Festuca</i> sp.	78	97	58	68	73	78	100	86
<i>Deschampsia flexuosa</i>	54	43	66	67	56	42	43	31
<i>Brachypodium pinnatum</i>	18	32	20	22	14	27	41	57
<i>Aira caryophylla</i>	15	23	4	7	3	3	5	8
<i>Poa</i> sp.	3	9	0	2	3	3	5	8
<i>Agrostis</i> sp.	5	2	4	3	3	4	2	4
<i>Holcus</i> sp.	7	6	1	0	1	2	3	4
<i>Bromus</i> sp.	1	2	1	1	0	0	0	4
Cyperaceae	1	0	1	1	2	1	1	2
Total Grasses	285	347	235	247	265	262	314	311
Labiatae	14	3	18	13	10	23	10	14
<i>Teucrium scorodonia</i>	5	4	14	18	7	17	11	9
Compositae	16	13	9	3	1	3	0	3
<i>Crepis</i> sp.	27	6	9	1	0	0	0	1
<i>Cerastium</i> sp.	1	2	15	3	2	6	1	4
<i>Lamium</i> sp.	2	1	3	2	3	4	0	1
Papilionaceae	5	5	2	2	0	0	0	0
<i>Glecoma</i> sp.	0	0	1	1	4	4	0	1
<i>Bellis</i> sp.	3	2	1	1	2	0	1	1
<i>Conopodium majus</i>	4	2	2	3	0	0	0	0
<i>Sedum</i> sp.	1	4	1	3	0	0	0	1
<i>Hieracium</i> sp.	1	0	3	5	0	0	0	0
Umbelliferae	3	2	1	0	1	0	0	0
<i>Arenaria</i> sp.	0	0	7	0	0	0	0	0
<i>Sisymbrium</i> sp.	1	0	2	3	0	0	0	0
Others	14	10	12	9	1	3	3	2
Total Forbs	96	54	98	68	31	63	28	36
Broom*	114	99	144	163	51	70	77	55
Heather**	55	44	29	28	139	117	158	175
<i>Rubus</i> sp.	50	35	90	99	85	101	52	64
<i>Vaccinium myrtillus</i>	30	16	13	7	1	2	0	1
Rosaceae	8	7	6	5	1	2	0	2
<i>Rosa canina</i>	5	6	9	3	0	0	0	0
<i>Crataegus</i> sp.	2	7	3	4	0	0	0	0
<i>Prunus</i> sp.	0	0	6	3	0	0	0	0
Total Shrubs	264	213	301	312	278	292	287	297

Season	Spring		Summer		Autumn		Winter	
Fagaceae	1	10	7	12	1	8	0	0
Others	1	0	5	2	2	0	0	2
Conifer	9	29	11	7	13	26	39	44
Total Tree leaves	12	39	23	22	15	34	39	46
Nuts***	0	0	0	0	101	32	23	1
Fruits	13	13	32	49	1	3	1	1
Total Fruits	13	13	32	49	102	35	24	3
Ligneous fragments	35	33	30	25	33	37	34	33
Unknown	96	101	81	77	75	77	74	74
Total	800	800	800	800	800	800	800	800
Nb of species/family	49	41	50	43	32	29	23	32

* *Genista pilosella* and *Genista anglica*

** *Calluna vulgaris* and *Erica cinerea*

*** Chestnuts and beechnuts

in winter ($\chi^2 = 34.449$, $p = 0.0006$, $df = 12$) and in spring ($\chi^2 = 43.492$, $p = 0.0001$, $df = 12$), but not in summer ($\chi^2 = 14.931$, $p = 0.2452$, $df = 12$). However, there is little variation in the total number of species occurring in the diet between sub-units (Table I). In general, it seems that the diet of animals in the Brus was more diverse than in the Vialaïs, except in winter. The biggest differences occurred in spring, when mouflon in the Vialaïs ate more grasses and less shrubs and forbs than mouflon in the Brus, and in autumn, when mouflon in the Brus ate twice the quantity of nuts than mouflon in the Vialaïs. In winter, differences between sub-units in diet composition of each species group were slight. In absolute terms, there was little real difference in seasonal diet between sub-units (Fig. 2).

Mouflon diet varied significantly between seasons in each sub-unit (Vialaïs : $\chi^2 = 659.53$, $p = 0.0001$, $df = 39$; Brus : $\chi^2 = 790.71$, $p = 0.0001$, $df = 39$). The mouflon diet is most diverse in spring and summer, comprising between 41 to 50 species or family groups, while this falls to between 23 to 32 in autumn and winter (Table I). According to the similarity index (Table II), winter and autumn diets are the most similar ($SI_{Brus} = 83.26$, $SI_{Vialaïs} = 85.85$). In these seasons, the mouflon ate 1/3 grasses (fescue and other unidentified monocotyledons) and 1/3 shrubs (heather plus *Rubus* sp. in autumn only). They also fed on nuts in autumn. The most marked difference in diet occurs in the comparison of summer with winter ($SI_{Brus} = 62.81$, $SI_{Vialaïs} = 62.37$) and with autumn ($SI_{Brus} = 66.60$, $SI_{Vialaïs} = 74.85$). In summer, grasses are less abundant in the diet, while broom and *Rubus* sp. become more prevalent. At this time of year, fruits are also an important component of the diet. Spring diet is essentially intermediate, comprising of the same proportion of grasses as, but less shrubs (essentially broom) than, in winter and autumn. At the same time, forbs make up a larger part of the diet in spring compared to autumn and winter.

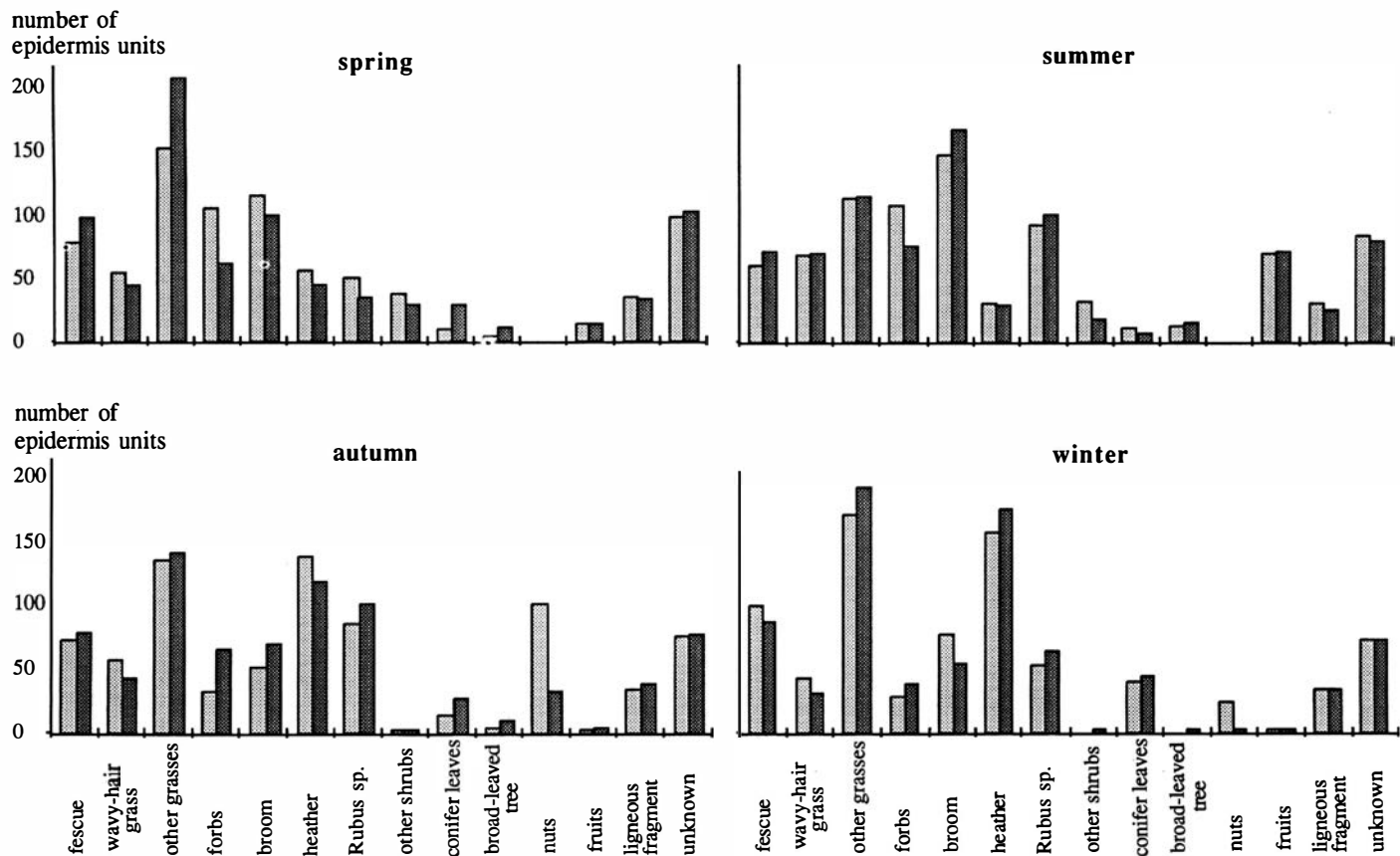


Figure 2. — Comparison of the seasonal diet of mouflon in two sub-units of a population in the Caroux-Espinouse massif determined by faecal analysis, expressed as the mean number of epidermis units (max. 800) of each plant group. Light bars represent the Brus sub-unit and dark bars represent the Vialais sub-unit.

TABLE II

A : Similarity index between seasonal diets in the Brus sub-unit of the mouflon population of the Caroux-Espinouse massif determined by faecal analysis (see text for formula).

B : Similarity index between seasonal diets in the Vialaïs sub-unit of the mouflon population of the Caroux-Espinouse massif determined by faecal analysis.

	A			B		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Summer	84.02	—	—	Summer	73.58	—
Autumn	71.74	66.60	—	Autumn	77.52	74.85
Winter	75.05	62.81	83.26	Winter	77.74	62.37
						85.85

DIET VARIATION BETWEEN DIFFERENT AGE-SEX CLASSES

To compare diet between age classes and sexes, data were derived from rumen analyses. Firstly, we tested for differences between the four areas (three socio-spatial sub-units and one additional area) from where the rumen samples originated. Because of the small sample sizes, we only used rumens collected during autumn from adult mouflon to assess variation between sub-units. With this data set no significant differences were found between diets of mouflon from the four areas (females : $H = 0.543$, $p > 0.05$, $df = 3$; males : $H = 0.245$, $p > 0.05$, $df = 3$). Therefore, in subsequent analysis, we pooled data for all four areas. Comparisons of the sexes were possible in autumn and winter for adults, and in autumn only for lambs. Diets were very similar both between male and female adults in winter (Kendall rank correlation coefficient : $\tau = 0.838$, $n = 15$, $p = 0.0001$) and among all four age-sex classes (adult, lamb, male, female) in autumn (Kendall concordance coefficient : $c = 0.869$, Friedman's test : $df = 14$, $p = 0.0001$). Keeping in mind that no significant differences appeared between sex-age classes, we could examine tendencies of differences. From the similarity index (Table III), it is clear that the diet of male lambs tends to differ the most from that of other sex-age classes, particularly in comparison with female lambs. Female lambs seem to select essentially nuts (autumn), whereas male lambs fed largely on *Rubus* sp. However, we should note that sample sizes are quite small for this age class ($n = 9$ for females, $n = 6$ for males).

DISCUSSION

The utility of faecal analysis to study herbivore diet has often been discussed (Putman, 1984 for a review). From an organisational point of view, faecal analysis has several advantages in that it is relatively simple to obtain a large sample size and the level of disturbance to the animals is minimal. The main disadvantages of this method are that it is difficult to classify samples by sex or age of the animal and the duration of analysis is considerable because a substantial training period is necessary to minimize errors in species determination and to collect a reference

TABLE III

Similarity index between autumn diets of adult and lamb mouflon of both sexes in the Caroux-Espinouse massif determined by rumen analysis.

	Adult females	Lamb females	Lamb males
Lamb females	82.29	—	—
Lamb males	79.14	70.26	—
Adult males	87.33	86.97	79.53

atlas of all plant species present on the particular study site. Several authors have tested the accuracy of this method by comparison with rumen analysis (Todd & Hansen, 1973 ; Anthony & Smith, 1974 ; Kessler *et al.*, 1981), with analysis of data from rumen-fistulated animals (Bartolome *et al.*, 1995 ; Mohammad *et al.*, 1995), with artificial digestion analysis (Dearden *et al.*, 1975) and by comparing results with a provided diet of known composition (Maizeret *et al.*, 1986). Overall, the method seems to provide a reasonable approximation of the general diet with the loss of certain details, especially in spring and summer. The two main sources of bias in the analysis of diet by faecal microhistology are the different sizes of species fragments and the variable digestibility of different species (Johnson & Wofford, 1983 ; Putman, 1984). We limited the first of these problems by quantifying the abundance of each species, not on the basis on the number of fragments present, but as a function of the proportion of the surface area of a microscope slide occupied (Chapuis, 1980). From studies carried out to estimate the differential digestibility of individual species, forbs are more digestible than other types of plants (Anthony & Smith, 1974 ; Kessler *et al.*, 1981 ; Leclerc, 1981). Their digestibility varies between seasons and according to the other species present in the rumen at the same time. Thus, it is probable that we under-estimated the abundance of forbs in our results on mouflon diet. In addition, quantification of the abundance of nuts may be difficult as they occur as partial elements only, such as hairs, so we counted these in four classes of abundance. We reduced potential for errors in plant identification by compiling keys using plant specimens collected from the field site itself and by performing determination at the family level when species characteristics were unclear or absent. A higher proportion of fragments were unidentifiable in spring due to the fact that, at this time of year, a greater proportion of the plant cells are not yet differentiated (Leclerc, 1981 ; Guilhem *et al.*, 1995). Due to such sources of error, certain authors question the validity of quantitative determination of diet composition using faecal analysis (Zyznar & Urness, 1969, Maizeret *et al.*, 1986), while others accept this approach (Garcia-Gonzalez, 1984). In our study, we have attempted to validate the use of a semi-quantitative analysis by comparing the mean number of epidermis units of each species with the frequency of occurrence in the sample set (presence/absence). The extremely close relationship between these two variables for our data support the use of a semi-quantitative analysis in this case.

The diet of mouflon in the Caroux-Espinouse massif comprises a wide variety of plant species, however, the bulk of food intake is made up of only a few species. Similar results were found in a study of the diet of Corsican mouflon by direct

observation by Pfeffer (1967), while Heroldova (1988b), analysing rumen contents, recorded a diet consisting of a large variety of species in approximately equal abundance in a Czech population. Despite differences inherent of the use of two methods, it seems that the composition of the mouflon diet has changed between 1975 and 1995 in our study population. Faliu *et al.* (1990) noted that the mouflon fed essentially on grasses (56.4 %) and completed their diet with forbs, shrubs and fruits in approximately equal amounts. In 1995, the mouflon fed on grasses and shrubs in equal proportions, completing their diet with forbs and fruits. This difference is probably linked to the loss of meadows which have been increasingly invaded by broom moor over this period (unpublished data). By comparing results on mouflon diet across studies (Table IV), it appears that this animal is an opportunistic feeder which is able to use very different kinds of habitats, which are sometimes far removed from its habitat of origin. Forbs were the major dietary component in the Cazorla mountain range (Garcia-Gonzalez & Cuartas, 1989) and in autumn in Tenerife (Luengo & Pinero, 1991), together with shrubs and fruits in autumn in Czechoslovakia (Heroldova, 1988b). In Corsica diet comprised essentially shrubs (Pfeffer, 1967), in Germany trees, shrubs and grasses (Briedermann, 1988) and in our study grasses and shrubs. It should be noted that this comparison incorporate studies using different techniques with different inherent biases, as described above. Importantly, in our study, tree leaves formed only a minor part of the diet and no bark-stripping damage was ever recorded in the Caroux massif such as that found in Czechoslovakia (Heroldova, 1988b).

There were dietary differences, although slight, between the two main sub-units of the Caroux mouflon population. They seemed to be related to differences in the overall abundance of different types of habitat in the two sub-units. Thus, mouflon in the Brus sub-unit, which live in woodier habitat, ate more chesnuts, whereas those in the Vialaïs ate more grasses. Clearly, it would be informative to compare plant availability of the two areas in more detail to determine if this is really the source of differences in diets between sub-units. Luengo & Pinero (1991), in the Canary Isles described different diet composition for mouflon which inhabited a high mountain open shrub area and those which lived in a pine forest. Similarly, in Spain, seasonal variation of mouflon diet is linked to plant availability (Garcia-Gonzalez & Cuartas, 1989). The three sub-units of our study site correspond to socio-spatial units defined by extensive long term radiotracking studies (Maublanc *et al.*, 1993). This highlights the fact that it is important to consider the spatial behaviour of animals when studying variation in diet.

Seasonal variation of diet may also be linked to plant phenology. Protein content is highest prior to flowering, during growth, but fiber content subsequently increases and plants become less digestible (Garcia-Gonzalez, pers.com.). Mouflon seem to select species according to their phenology ; fescue is dry in summer and autumn and was thus consumed mainly in spring and winter, broom is dry in autumn and winter and is eaten when leaves are present in spring and summer and heather is dry in summer and occurs in the diet mainly in winter. The absolute availability of heather, fescue, wavy-hair-grass and broom does not change over the year because they are perennial species, and only their phenology is variable. At the same time, because annual species are not present all year round, the relative availability of the four species mentioned above is variable. So we can assume that mouflon select species partly on the basis of the interaction between the animal's preference and partly on the basis of the phenological state of the

TABLE IV

Habitat characteristics of study sites and methods from several published investigations of mouflon diet.

Diet composition (%)												
Author	Country/Site	Method	Period	Vegetation	Climate	Altitude (m)	trees	shrubs	forbs	grasses	fruits	other
Pfeffer, 1967	France Corsica	direct observation wild animals	annual	pine, evergreen oak Arbutus, Cytisus	Mediterranean	600-1 300	43	31	*	25	1	0
Briedermann, 1968	Germany Niederfinow	direct observation enclosed animals	annual	pine, poplar pasture	Continental	8	38	30	*	25	0	3
Heroldova, 1988	Czechoslovakia	rumen analysis	Nov-Dec	coniferous, beech	Continental	280-596	5.7	24.3	35.7	4.2	17.1	13
Garcia-Gonzalez & Cuartas, 1989	South Spain Cazorla	faecal analysis	autumn	oak juniper, hawthorn	Mediterranean Mountain	1 300	**	7.8	63.7	28.2	0	0.3
Faliu <i>et al.</i> , 1990	France Caroux	rumen analysis	annual	beech, chestnut, evergreen oak broom, heather, meadow	Mediterranean Oceanique	600-1124	**	16.8	13.2	56.4	8	5.6
Luengo & Pinero, 1991	Canary Isles Tenerife	rumen analysis	autumn	pine open shrub	dry : May-Oct snow	1 000- > 2 000	2.2	16.3	*	67.1	0	14.4
Cransac <i>et al.</i> , 1996	France Caroux	faecal analysis	annual	beech, chestnut, evergreen oak broom, heather, meadow	Mediterranean Oceanique	600-1 124	5	32	10	35	5	13

* Forbs and grasses grouped.

** Trees and shrubs grouped.

plant. The seasonal variation of diet suggests that two limiting periods exist in Caroux. In summer, because of the Mediterranean influence, the grasses are dried out and these conditions would forced mouflon to feed on broom. In winter, when the mountain influences bring cold weather, some species of grasses and all forbs become frozen and these conditions would forced mouflon to feed on heather. However, the mouflon are also able to complement their diets with fruits in summer and nuts in autumn. In several mouflon populations (Heroldova, 1988b ; Briederman,1988), winter is a limiting period when snow covers the ground vegetation because mouflon do not scrape away deep snow as do other ungulates (Pfeffer, 1967). Snow cover in the Caroux- Espinouse is rarely substantial and lasts only for short periods (less than 20 days per year on average), essentially on hill tops and plateaus.

The rut in the Caroux-Espinouse is from October to December. At this time males, who live in peripheral areas separated from female home ranges during the rest of the year, join the female population sub-units (Dubois *et al.*, 1993). After the rut, males leave progressively from January to March. Thus, males and females share the same range in autumn, whereas in winter they tend to live in separate areas. Despite this, our comparison of the diet of adult males and females did not reveal any differences between the sexes in either of these two seasons. In this respect, mouflon differ from several species where the sexes occupy different home ranges and have different diet, for example red deer (Clutton-Brock & Albon, 1989) and bighorn sheep (Shank, 1982) Thus, it seems unlikely that sexual segregation of mouflon outside the rutting period is due to feeding considerations. In fact, results of studies testing the hypothesis of a link between sexual segregation and differential diet of the sexes are inconsistent between studies and this hypothesis may not be supported (Main *et al.*, 1996). It would clearly be interesting to compare male and female diets during spring or summer when their ranges are strictly separate, and also to investigate dietary differences between pregnant, lactating and non pregnant females. In the same population, Bon *et al.* (1995) found that females with lambs at foot do not feed in the same areas as other ewes.

Lambs are born in April in this population and are weaned in August or September (Bon *et al.*, 1993), but, according to Briedermann (1986), lambs begin to eat plant matter earlier than this. Our results show that lambs of six to eight months old have a diet similar to that of adults. In other studies, no significant differences of diet were found between animals of various ages in white-tailed deer (Weckerly & Nelson, 1990), or between lambs, yearlings and adult ewes in bighorn sheep (Shank, 1982). Leclerc (1981) observed the same pattern for goats and suggests that this is partly because feeding is a learned behaviour from the mother and partly because lambs share the same range as the mother. Indeed, Briederman (1986) showed that mouflon lambs of 4 months already ate 70 plant species of the 126 they use when 1 year old, indicating a wide feeding repertoire is developed at an early age linked to precocious exploratory behaviour in this species.

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SUMMARY

We studied the diet of mouflon using faecal and rumen contents analysis for the population of the Caroux-Espinouse mountains (south of France). There were slight intra-population differences in diet between the two major socio-spatial sub-units. Mouflon fed on a large number of plants, modifying their diet in relation to plant phenology. During seasons when grasses were less digestible, they were replaced in the diet by broom in summer and by heather in winter. Analysis of rumen contents did not reveal any dietary differences between males and females (in autumn and in winter) or between adults and lambs (in autumn). A comparison of published studies on mouflon diet shows that this species is able to adapt its foraging behaviour, permitting it to inhabit environments as varied as the continental German plains, Mediterranean Corsican high mountains and Mediterranean and Oceanic low altitude mountains. The mouflon can be considered an opportunistic feeder whose optimal habitat is a diverse one.

RÉSUMÉ

De nombreux facteurs interagissent pour expliquer les variations dans le régime alimentaire des herbivores. Par exemple, la disponibilité et la phénologie des plantes, l'état physiologique de l'animal, etc... Au cours de la présente étude, nous avons déterminé le régime alimentaire saisonnier du mouflon par analyse de fèces et de contenus de panses dans le massif du Caroux-Espinouse (Sud de la France). Nous avons discuté des limites de ces deux méthodes pour étudier le régime alimentaire. La comparaison des régimes alimentaires de deux sous-unités de population montrent quelques différences. Le mouflon se nourrit sur un grand nombre d'espèces et peut moduler son régime en relation avec la phénologie des plantes. Dans la population étudiée, le déficit en Graminées est compensé en été par une alimentation sur le genêt et en hiver sur la bruyère. En reprenant les données d'une étude des contenus de panses d'animaux issus de la même population, nous n'avons pas trouvé de différences entre les régimes des mâles et des femelles (en automne et hiver) et les régimes des agneaux et des adultes (en automne). La comparaison de différentes études sur le régime alimentaire du mouflon montre que cette espèce est capable de s'acclimater, entre autres, dans des habitats aussi différents qu'une plaine continentale en Allemagne, les hautes montagnes méditerranéennes de Corse ou les moyennes montagnes sous influence méditerranéenne et océanique du massif du Caroux-Espinouse. Le mouflon peut être considéré comme opportuniste dans le choix de son alimentation et l'habitat dont il a besoin doit offrir une certaine diversité.

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