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DIET SELECTION OF THE ALPINE MARMOT (*MARMOTA M. MARMOTA* L.) IN THE PYRENEES

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RÉSUMÉ. — *Sélection du régime alimentaire chez la Marmotte des Alpes (*Marmota m. marmota *L.) dans les Pyrénées.*— Nous avons étudié de mai à septembre dans les Pyrénées occidentales la composition du régime alimentaire et la sélection des plantes dans deux groupes familiaux de Marmotte des Alpes *Marmota m. marmota*. La nourriture consommée a été déterminée par analyse des fèces et la sélection des plantes en comparant la composition des fèces au cortège de plantes disponibles dans la zone entourant les terriers des marmottes. La plupart des plantes disponibles n'appartenaient qu'à quelques familles dont l'abondance ne changea pas de manière remarquable durant les mois d'étude contrairement aux stades phénologiques des plantes. Les marmottes ont surtout consommé des végétaux consistant en une grande variété de feuilles, de fleurs et de graines de graminées et autres herbes, les feuilles de dicotylédones dominant nettement dans le régime. Les Légumineuses, Composées, Liliacées, Plantaginacées et Ombellifères étaient positivement sélectionnées ; les Labiées et les Rubiacées étaient évitées. Les fleurs étaient activement choisies sur la base de leur abondance relative et de leur phénologie. L'ingestion de proies animales (Arthropodes) a été confirmée au début de la saison d'activité.

SUMMARY. — We studied the diet composition and selection of plants in the Alpine marmot *Marmota m. marmota* of two family groups in the Western Pyrenees from May to September. The food consumed was determined by faecal analysis, and the plant selection was determined comparing the plant composition in faeces and plant availability in the area surrounding the marmot burrows, which was measured by the point-intercept method. Most of the available plants belonged to a few families whose abundance did not change remarkably through the studied months, although the plants' phenological stage changed considerably. The Alpine marmots primarily ate plants, consisting of a wide variety of leaves, flowers, and fruits of grasses and forbs, although the leaves of dicotyledonous herbs clearly dominated in the overall diet. Leguminosae, Compositae, Liliaceae, Plantaginaceae, and Umbelliferae were positively selected, and Labiatae and Rubiaceae were avoided. Flowers were actively chosen on the basis of relative abundance and phenology. The ingestion of animal prey (Arthropoda) was confirmed at the beginning of the active season.

The Alpine marmot *Marmota marmota* Linnaeus, 1758 inhabited the Pyrenees during the Pleistocene (Besson, 1971). At the end of that period, it disappeared from the Pyrenees, only persisting in the Alps (*M. m. marmota*) and in the Carpathian mountains (*M. m. latirostris*). When available, Alpine marmots prefer to settle in east– and south-facing slopes, and in areas

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with high plant cover and low human disturbance (Allainé *et al*. 1994). Seemingly, the size of the home range, through its effect on the availability of high quality plants, is a factor limiting their reproductive success. Since its first release in the Pyrenees in 1948 (Couturier, 1955) the Alpine marmot (ssp. *marmota*) has been introduced several times onto the French slope, and it subsequently spread throughout the entire mountain range (Herrero *et al*., 1994a). Its colonization success was probably linked to the availability of a broad deforested sub-alpine and montane belt originally created to provide summer ranges for livestock (Herrero *et al*., 1994b). However, the animal's relationship with its new environment is largely unstudied.

The feeding behaviour of marmots (genus *Marmota*) has been largely surveyed throughout most of their distribution range (*i.e.*, North America: Fall, 1971; Hansen, 1975; Armitage, 1979; Frase & Armitage, 1989; Barash, 1989; Eurasia: Bibikov, 1989; Semenov, *et al*., 2001). However, only three studies have investigated so far the diet of Alpine marmots in the Alps (Bassano *et al*., 1996; Massemin *et al.*, 1996; Rudatis & De Battisti, 2005) and to our knowledge no study has been published on the food habits of marmots in the Pyrenees.

Marmots are primarily herbivorous (Frase & Armitage, 1989; Mann *et al*., 1993; Bassano *et al*., 1996). Their diet appears to change seasonally, as they often eat roots, presumably when leaving hibernation, whereas they browse widely during summer (Mann *et al*., 1993). During the active period, they feed on a number of plant parts and species, although the specific contributions of plant taxa as well as flowers, fruits, leaves, and stems to the diet is unknown. They may eat flesh in captivity, and in several cases cannibalism has been reported (Armitage *et al*., 1979; J. Herrero, *pers. obs.*); in the wild, insects and worms are also consumed prey.

Our aim was to thoroughly characterize the diet of the Alpine marmot in the Pyrenees and to analyse the seasonal feeding strategy of this species through plant selection analysis.

MATERIALS AND METHODS

The study was conducted in Larra-Belagoa Nature Reserve (LBNR), a rough karstic mountain area of 57.4 km^2 in the Southwestern Pyrenees. Altitude range in LBNR is 1,100–2,442 m, annual precipitation is 2,500 mm, and mean annual temperature at 1,500 m is 7°C. Main vegetation types are mixed forest of beech *Fagus sylvatica* and fir *Abies alba*, mountain pine woodland *Pinus uncinata*, cliffs, and meadows (Elósegui *et al*., 1986).

We preselected three marmot groups; however, in one of the groups, only one individual emerged after hibernation and disappeared by late June, so we studied only the remaining two groups. One group was composed of two adults (probably a female and a male) and the other of one adult female and four young after July. The two family groups were contiguous and inhabited a gap in the mountain pine forest.

The diet of these marmots was analysed by microhistological examination of their faeces (Stewart, 1967; Sparks & Malechek, 1968; Holechek *et al.,* 1982). Every two weeks from May to September 1994, we collected fresh droppings from two known group latrines. Due to the shyness of marmots while defecating, it was not possible to assign the faeces to particular individuals; therefore, we analysed a mixture of the droppings found in the latrines. In May, we gathered five latrine mixtures and 15 droppings in total; in June, five mixtures and 14 droppings; in July, three mixtures and 16 droppings; in August, four mixtures and 10 droppings; and in September, four mixtures and five droppings.

Faecal fragments of plant origin were categorized as vegetative or floral parts and subsequently classified to at least the family level. Difficulties of identification prevented classification of most of the flower and inflorescence remnants into a specific taxon.

From mid-June 1994 to September 1994, we estimated the abundance of plant taxa around the surveyed marmot burrows through the point-intercept method (Knapp, 1984). For that purpose, we selected four plots in the most representative vegetation communities (two herbaceous and two shruby) that covered all the area occupied by the two family groups. We distributed four fixed transect lines of 25 m across the herbaceous plots and two 25 m lines in the shruby plots. As we assumed that the developmental dynamics would be faster in grass and herbs than in shrubs we sampled the herbaceous plots twice a month and the shruby once a month. In every sampling we determined the species and the developmental stage of the plant intersected by points distributed every 20 cm along those lines. Categories of developmental stages were as follows: vegetative, flowering, with flowers and fruits, fruiting, with fruits but without seeds, and decaying. The frecuency of species and developmental stages by plots was weighed according to the surface occupied by each plot type within the area occupied by each family group.

A chi-squared test between plant availability and diet composition was used to analyse diet selection under a null hypothesis of no difference between the two distributions (Manly *et al*., 1993). Rejection of the null hypothesis was followed by computation of 95 % simultaneous confidence intervals (Cherry, 1996) to estimate the true proportion of use in every plant category. If the proportion available of a specific category fell below (or above) the lower (or upper) limit of its associated confidence interval, we concluded that the marmot was selecting that plant category positively (or negatively).

Presence of large herbivores was rare, although Pyrenean chamois *Rupicapra p. pyrenaica* and roe deer *Capreolus capreolus* were occasionally seen in the marmots' feeding areas.

RESULTS

Plant availability

Although more than 30 plant families were identified around the marmot burrows, 12 families accounted for more than 90 % of all plant intercepts along transect lines (Table I). The most abundant plant family was Gramineae (monthly comprising more than 20 % of all plant intercepts), followed by Leguminosae (range 15 – 20 % and composed primarily of the shrub *Genista occidentalis*), Rubiaceae (9 – 14 %), Labiatae (7 – 10 %), Compositae (4 – 9 %), and Scrophulariaceae (2 – 5 %). There were significant changes in the frequency of the most abundant plant families through the months of the study (Pearson's Goodness of fit $\chi^2 = 218$, df = 33; $p < 0.001$; Table I), although the differences in frequency within any family or group seldom reached the 5 %.

TABLE I

Percentage availability of plant families around marmot burrows. Only those plants with values >2 % in any month are shown

	June	July	August	September
Caryophyllaceae	3.4	4.6	1.8	2.5
Cistaceae	0.9	1.9	2.7	3.7
Compositae	9.4	6.4	5.5	3.9
Cyperaceae	1.6	0.5	1.2	2.2
Gramineae	24.2	21.4	27.6	28.6
Labiatae	8.6	7.6	8.9	9.9
Herb Leguminosae	5.4	4.1	1.3	3.3
Woody Leguminosae	15.5	15.1	14.6	16.4
Polygonaceae	4.2	3.9	5.7	3.9
Rubiaceae	9.8	14.0	11.4	8.9
Scrophulariaceae	1.9	5.6	5.6	4.8
Umbelliferae	4.5	6.0	6.9	7.2
Total	91.0	93.1	94.2	96.0

The phenological stage of available plants changed considerably through the studied months (Fig. 1). The abundance of green plants without flowers or fruits fell abruptly between June and July, and steadily decreased thereafter. The abundance of plants flowering or fruiting peaked in July, and then almost disappeared by September. The abundance of decaying plants was negligible in July, but increased noticeably thereafter.

Diet

Most of the remnants found in the marmots' faeces were of plant origin (Table II). Among them, those from vegetative portions (i.e., leaves and stems, seasonal mean 84 %, SD = 8.0 %) appeared more often in faeces than those associated with flowers and fruits (seasonal mean 13.5 %, SD = 9.8 %; Mann-Whitney U = 441, $p < 0.001$). Both vegetative and floral/fruit portions changed significantly over the course of the study period (Kruskall-Wallis test, $H_{veg} = 10.2$ and $H_{flo} = 13.9$, df = 4 and $p < 0.05$ for both), with a slight decline of vegetative fragments in July and August, while floral parts correspondingly increased (Table II). The remainder consisted of invertebrates (Arthropoda) and hairs (mean 2.3 %, SD = 3.0 %), and to a lesser extent, fungi and Pterodophyta (mean = 0.2 %, SD = 0.5 %), both appearing appreciably only in May.

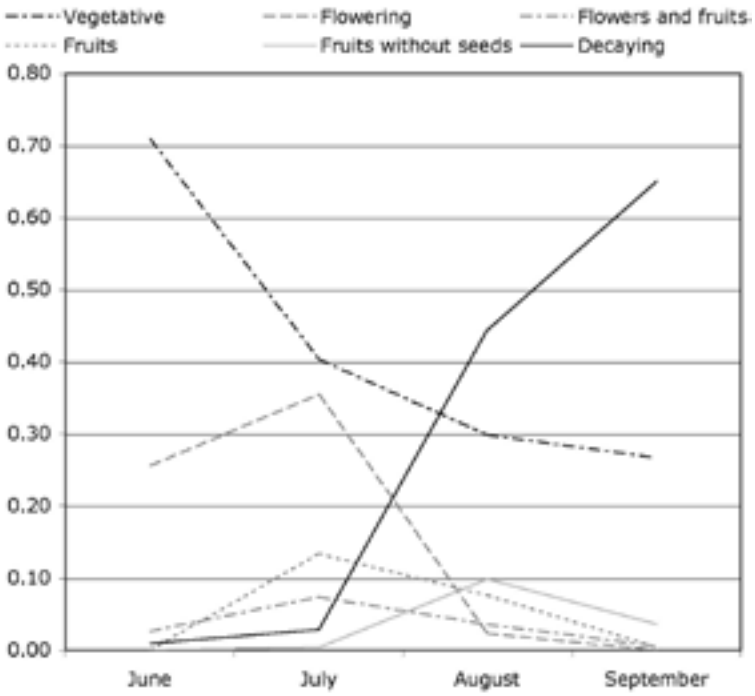

Figure 1. — Proportions of available plants at different phenological stages around marmot burrows.

TABLE II

Mean (SD) frequency percentages of food categories in marmot faeces

	May	June	July	August	September
Vegetative Parts	87.7 (16.76)	92.3 (2.84)	77.6 (3.23)	73.7 (12.29)	88.8 (5.24)
Flowers and Fruits	3.6 (2.56)	6.9 (3.04)	21.9 (2.97)	25.9 (11.92)	9.2 (6.89)
Fungi and Ferns	1.1 (2.56)	0.0 (–)	0.0 (–)	0.0 (–)	0.0 (–)
Animals	7.5 (15.43)	0.8 (0.41)	0.5 (0.30)	0.4 (0.40)	2.0 (2.50)

We found 42 plant genera and 18 plant families among the faeces analysed. Among the vegetative parts, the most frequent families were Gramineae, Leguminosae, Compositae, and Umbelliferae. The first two families comprised a substantial portion of plant fragments throughout the study period (Table III).

The species often observed in the faeces were *Festuca rubra-nigrescens* group, *Nardus stricta*, and *Poa pratense-alpina* group among Gramineae; *Anthyllis vulneraria-montana* group, *Medicago* ssp., and *Astragalus monspessulanus* among Leguminosae; *Crepis albida*, *Centaurea scabiosa*, *Achillea millefolium*, and *Hieracium* ssp. among Compositae; genus *Silene*, *Arenaria* ssp., *Cerastium* ssp., and *Saponaria* ssp. among Caryophyllaceae; *Laserpitium siler*, *Seseli montanum*, and *Bupleurum angulosum* among Umbelliferae; genera *Galium* and *Asperula* among Rubiaceae; and *Plantago alpina* among Plantaginaceae.

Woody plants composed a very small portion of the faeces; consequently, the amounts of monocotyledonous plants (Gramineae, Cyperaceae, Juncaceae, and Liliaceae) and herbaceous

dicotyledonous plants showed opposite trends through the surveyed months (Table III). The content of dicots in faeces was significantly higher than that of monocots (Mann-Whitney $U = 12$, $p < 0.001$), and the former composed, in all samples, more than 50 % of the vegetative fragments (leaves). However, the faecal proportion of neither monocots nor dicots changed significantly through the marmots' active period (Kruskall-Wallis test, $H_{monocot} = 6.8$, $df = 4$, $p = 0.15$; $H_{dicot} = 6.7$, $df = 4$, $p = 0.15$).

TABLE III

Mean (SD) frequency percentages of plant taxa in marmot faeces

		May	June	July	August	September
Monocots						
	Gramineae	21.42 (6.21)	28.20 (11.27)	6.27 (6.71)	21.72 (33.88)	17.02 (20.50)
	Others	2.44 (1.55)	2.18 (1.57)	1.07 (0.22)	0.64 (0.40)	0.29 (0.21)
	Unidentified	2.59 (1.95)	0.71 (0.40)	0.17 (0.30)	0.70 (1.14)	1.00 (0.90)
	Total Monocots	26.17 (8.18)	31.09 (10.30)	7.51 (7.21)	23.07 (34.10)	18.31 (20.14)
Herbaceous Dicots						
	Caryophyllaceae	12.24 (10.41)	1.58 (1.55)	0.43 (0.39)	0.25 (0.30)	4.98 (5.93)
	Compositae	2.51 (1.55)	2.15 (1.27)	26.54 (7.35)	9.07 (4.84)	6.51 (5.35)
	Leguminosae	19.29 (8.24)	14.94 (2.03)	25.53 (7.45)	20.72 (7.61)	14.76 (9.45)
	Plantaginaceae	0.11 (0.14)	6.45 (4.46)	0.40 (0.56)	0.07 (0.15)	0.11 (0.22)
	Rubiaceae	0.76 (0.82)	4.43 (4.42)	0.45 (0.21)	3.26 (4.50)	1.67 (1.99)
	Umbelliferae	1.23 (1.72)	5.16 (5.19)	1.59 (0.65)	7.74 (8.23)	12.31 (17.75)
	Others	4.23 (3.70)	1.17 (1.32)	0.83 (0.22)	1.06 (0.76)	5.82 (4.84)
	Unidentified	31.78 (5.52)	31.86 (4.73)	35.38 (8.48)	34.76 (16.66)	34.20 (9.01)
	Total Dicots	72.14 (8.59)	67.73 (11.36)	91.03 (7.95)	76.93 (34.10)	80.37 (22.50)
Woody Plants		1.69 (0.97)	1.19 (2.24)	1.46 (0.80)	0.00 (–)	1.32 (2.37)

FOOD SELECTION

Distribution of frequencies of leaves and flowers/fruits in faeces did not mirror their frequencies in the available vegetation (Chi-squared test, $\chi^2 > 13$, $df = 1$, $p < 0.01$ in all cases). Selection of foliar parts was positive in all months except September, while the selection of floral/fruit parts showed the opposite trend. Dicotyledonous plants were positively selected in all months, but monocotyledonous plants were only positively selected in June, whereas woody plants were negatively selected from June to September (Chi-squared test, $\chi^2 > 302$, $df = 2$, $p < 0.001$ in all cases).

Considering only the plant families whose relative abundance in faeces or around burrows was greater than 2 %, their frequencies in faeces did not correspond to those expected from their availability in any month (Chi-squared test, $\chi^2 > 500$, $df = 12$, $p < 0.001$ in all cases). Herbaceous Leguminosae were positively selected in all months, Gramineae were positively selected only in June, selection for Compositae changed from negative in June to positive in the other three months, and Umbelliferae were positively selected in all months but July (Table IV). One the other hand, several widely available plant groups such as the woody Leguminosae, Labiatae, Polygonaceae, Rubiaceae, and Scrophulariaceae were negatively selected in almost all months of the study.

TABLE IV

Marmot selection of plant taxa. Only those whose frequency in faeces or abundance was greater than 2 % were shown. + indicates positive selection, – indicates negative selection, and 0 indicates no difference between frequencies in diet and availability

	June	July	August	September
Caryophyllaceae	–	–	–	+
Cistaceae	–	–	–	0
Compositae	–	+	+	+
Cyperaceae	–	0	0	–
Gramineae	+	–	0	–
Herb Leguminosae	+	+	+	+
Labiatae	–	–	–	–
Plantaginaceae	+	0	–	–
Polygonaceae	–	–	–	–
Rubiaceae	–	–	–	–
Scrophulariaceae	–	–	–	0
Umbelliferae	+	–	+	+
Woody Leguminosae	–	–	–	–

DISCUSSION

In the Pyrenees the diet of the Alpine marmot is based mostly on dicotyledonous herbs and, to a lesser extent, monocotyledonous plants. The preference for dicot herbs has been previously described in individuals of the genus *Marmota* (Hansen, 1975; Bassano *et al*., 1996; Massemin *et al*., 1996; Rudatis & De Battisti, 2005). Other foods include woody plants, invertebrates, fungi, and ferns; however, these contributed little to the diet and their consumption was primarily restricted to the first weeks after arousal from hibernation. Carey (1985) argued that the preference for forbs over graminoids exhibited by marmots appears to be related to the differences in the nutritional quality of the two plant types. Forbs generally contained higher concentrations of nutrient (in particular phosphorus, calcium and sodium and possibly protein) and lower contents of cell wall components (fiber). Because the extent of fermentation of fibrous foods varies inversely with passage rate through the gut, and passage rate varies directly with body size (Demment & Van Soest, 1985), it is often argued that small non-ruminant hervibores should select foods of high digestibility which can have much faster fermentation rates (Van Soest, 1994). However, Stallman & Holmes (2002) postulated that the choice of forbs over graminoids could be explained because of the higher water content of forbs (not investigated here).

Overall, plant frequency in faeces varied remarkably across families and between months in any family. Only the consumption of Leguminosae and Gramineae was consistently high across the studied months, whereas other families reached that level of consumption only in certain months (Compositae in July, Caryophyllaceae in May, and Umbelliferae in September). Moreover, marmots did not select for most of the consumed families, and only Leguminosae, Compositae, and Umbelliferae were positively selected in at least three of the four studied months. These three dicot families, together with the readily available Gramineae, seemed to constitute the bulk of the marmots'diet through the active period. Other works have also remarked that marmots forage selectively on Leguminosae species (Carey, 1985; Stallman & Holmes, 2002). Although graminoids always made up at least 20 % of the diets (except in July), marmots only chose them actively at the beginning of the growing season (June), when graminoids offer the best nutritive value. Accordingly, in the Alps the relevance of graminoids in the diet of marmots fall from May to July (Massemin *et al*., 1996). Some of the plant species found in our study have been previously reported in the diet of Alpine

marmots, *e.g., Plantago alpina*, *Achillea millefolium,* and several species of *Festuca* genus (Bassano *et al*., 1996).

Leaves were the most consumed plant part in all four months, while flowers and seeds (the latter classed as fruits) rose above the 20 % availability threshold only in July and August. It is important to note, however, that the flowers and fleshy fruits (berries and drupes) leave relatively fewer identifiable fragments in faeces than the leaves, stems and seeds do. In addition, when various plant parts are eaten together, the retention time in the gut is determined by the less-digestible parts, increasing the digestion of the softest parts. For this reason, it is certain that we underestimated the proportions of flowers in the marmots' faeces; it is likely that this underestimation was more pronounced when their consumption was lowest, *i.e.,* in May, June, and September. Taking into account that foraging is enhanced in July and August (Sala *et al*., 1992) due to an increase in the marmots' digestive tract capacity (Hume *et al*., 2002), the annual significance of flowers in dietary bulk is likely to be higher than that indicated by percentage frequencies in faeces. Interestingly, Massemin *et al*. (1996) found that in the Alps the proportion of flowers was predominant in faeces and that it seemed to peak in June and July. A high consumption of flowers and seeds may provide the depot fats (adipose tissue, primarily composed by triacylglycerol, a three-carbon skeleton to which three fatty acids are attached) with a higher proportion of polyunsaturated fatty acids (PUFA), as these plant parts are rich in PUFA (Hill & Florant, 1999). An increased level of flowers and seeds in the diet may enhance the marmots' chances of survival, as PUFA reduce their energy expenditure and increase torpor depth during hibernation (Arnold, 1992; Munro & Thomas, 2004).

We found an appreciable amount of animal remains (primarily Insecta: Arthropoda) in faeces in May. At that time, marmots were emerging from hibernation, snow still covered a considerable part of the study area, and green plants were not yet available. Availability of insects is not expected to be higher in May than in later months, and thus marmots would be likely to show a preference for foods of animal origin in May. In addition, marmots may feed underground in the weeks following emergence from hibernation, consuming animal prey as well as roots and bulbs (J. Herrero, *pers. obs.*); however, we were not able to identify underground plant parts in faeces in this study.

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