# Impact of season, habitat and research techniques on diet composition of roe deer (*Capreolus capreolus*): a review

Johnny Cornelis, Jim Casaer* and Martin Hermy

Laboratory for Forest, Nature and Landscape Research, Katholieke Universiteit Leuven, Vita! Decosterstraat 102, B-3000 Leuven, Belgium

Abstract

We summarize the information on the diet of roe deer *Capreolus capreolus* found in 33 European studies. After giving a short overview of the differences between the existing studies, we compare the information for each season. We submit the information, summarized in a matrix of 83 cases on 10 food groups, to a detrended correspondence analysis (DCA) and a two-way indicator species analysis (TWINSPAN). We calculate weighted averages grouping the information by season, habitat, research method and their cross-products. The weighted averages are also used as input for a multivariate ratio analysis. Since the available food items dictate the possible diet composition we further investigate the influence of the habitat on the reported food selection. The influence of season on the diet composition is compared with the effect of the habitat, and other factors such as research method and geographical location of the study site. The review shows that there is relatively little seasonal variation in the diet composition, which is more closely correlated to the habitat than to the season.

Key words: roe deer, *Capreolus capreolus,* diet composition

## INTRODUCTION

Roe deer *Capreolus capreolus* are widely distributed high impact herbivores that use a range of lowland and mountain habitats including large forests and unwooded field areas (Danilkin, 1996). An understanding of feeding habits is essential when considering carrying capacities, improvement of deer habitat and reduction of damage to forestry, agriculture or horticulture (Jackson, 1974). Hence it is not surprising that all over Europe considerable attention has been devoted to the biology of roe deer, in particular their feeding ecology.

To draw some general conclusions on the annual diet of roe deer, it is necessary to review the available literature. The review of Tixier & Duncan (1996) considered only the results of studies based on stomach content analysis. Faecal analyses were not included because the composition of the plant fragments in faecal samples differs considerably from stomach samples. Consequently, the authors could not investigate whether the research technique was a main source of variation in diets. It also means that a lot of valuable studies were not included. In this paper we review 33 different studies on the food selection by roe deer (see Table 2). The aim is to summarize the most recurring trends in their annual diet. We also searched for factors to explain the variation in food selection (habitat, season, research method and geographical location). For a better understanding of the studies cited, we start with a short overview of the research techniques used to examine herbivore food selection.

### Research techniques

The diet composition of roe deer, or herbivores in general, can be examined in a variety of ways: direct observation of the animals, description of feeding traces, analysis of the rumen content, sampling of rumen or oesophageal fistulae, faecal analysis or feeding experiments (Table 1) (Jackson, 1974; Goffin & de Crombrugghe, 1976; Staines, 1976; Maillard & Picard, 1987; Roelvink, 1988; Birkenstock & Maillard, 1989). Some additional remarks are summarized in the following paragraphs.

The most common method is the analysis of rumen contents (e.g. Gaare, Sörensen & White, 1977; Puglisi, Liscinsky & Harlow, 1978). Many samples can be supplied from animals killed by hunters or by traffic accidents. However, this restricts the sample period mainly to the hunting season. This method can result in two types of data. The first yields only the presence or

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*All correspondence to: Jim Casaer, Laboratory for Forest, Nature and Landscape Research, Katholieke Universiteit Leuven, Vita! Decosterstraat 102, B-3000, Leuven, Belgium.
E-mail: jim.casaer@agr.kuleuven.ac. be

**Table 1.** Summary of some benefits and drawbacks of several research techniques to examine the food selection of herbivores (adapted from Roelvink, 1988)

| Technique | Benefits | Drawbacks |
|---|---|---|
| Rumen or gullet fistulas | Results are precise and accurate | Requires expensive surgical operation<br>Not applicable to wild animals |
| Analysis of rumen contents | Quantitative and qualitative results<br>No expensive equipment required | Animal has to be killed<br>Feeding place is not known<br>Rumen content changes all the time<br>Difficult to identify food particles |
| Faecal analysis | Easy to collect and store material<br>Applicable to all animal species, at any time<br>No disturbance | Intensive work<br>Feeding place is not known<br>The ratio of faecal fragments does not reflect the ratio of food intake<br>Difficult to identify food particles |
| Direct observation | Simple and cheap<br>Gives also other information about the examined animal species | Difficult to execute with shy animals or in unsurveyable sites<br>Identification problems if observation distance is large |
| Analysis of feeding traces | Cheap<br>Little disturbance for the animal<br>Gives also information about the vegetation on the feeding place | Difficult to classify traces on the level of animal species<br>Traces are not always perceptible or disappear fast in the growing season |
| Feeding experiment | Accurate results<br>Each species can be tested apart from the others | Food has to be collected<br>Animals have to be captured<br>Results do not represent feeding behaviour under free-ranging conditions |

absence of a certain plant species in the examined rumen (e.g. Jackson, 1980; Fandos, Martinez & Palacios, 1987; Maillard & Picard, 1987; Maillard, Picard & Noël, 1989) and consequently gives the percentage of the animals ( = frequency) that ate a certain plant species. It does not reveal any information concerning the amount of the plant eaten. The second type of data gives the amount of each plant species expressed as a percentage of the examined rumen content. The percentage can be the number of fragments compared with the total number of fragments as well as a volume percentage or a percentage of the dry weight. When both types of data are available one can distinguish between plants often eaten in very low quantities, plants that are sporadically eaten in large amounts, and plants that are often eaten in large amounts (Cederlund *et al.*, 1980). However, the method requires a good knowledge of plant morphology and anatomy in order to recognize the different plant species in the rumen content.

A second, common method is faecal analysis (e.g. Alipayo *et al., 1992).* The same population of herbivores can be continuously sampled without direct interference (Bhadresa, 1986) and no animals have to be killed. The method can rarely take into account any information concerning the sex, age or physical condition of the animals, unless the faecal samples were collected from the spot on which the animal was observed defecating (Holisova, Kozena & Obrtel, 1986a).

Basically, two methods are used for quantifying proportions of different epidermis fragments in faeces: counting the number of fragments and estimating or measuring the surface areas of fragments. Of course, it is also possible to record only the presence or absence of species in faecal samples (e.g. Hearney & Jennings, 1983). Because of the differential interspecies digestibility of epidermis structures, difficulties in recognizing certain fragments (Stewart, 1967), the variability of fragment size and the poor correlation between epidermal surface areas and dry weights of plants, large discrepancies are found when comparing the. results from faecal analysis and those from the analysis of rumen contents. Holisova *et al.* (1986a) and Fitzgerald & Waddington (1979) suggest that an index of digestion must be used to correct the proportions of cuticle fragments if faecal analysis is to give an accurate estimate of the diet. Degrez & Libois (1991) conclude that faecal analysis and rumen analysis are complementary methods.

Direct observation of the animals is a simple and cheap method to determine which plants are important in the diet composition, but it is difficult to achieve with shy animals or in unsurveyable terrain, without the use of special equipment (e.g. Boag, Macfarlane Smith & Griffiths, 1990). Results from Wallmo *et al.* (1973) suggest that the observer must be within 23 m of the deer to identify more than 80% of the grazed plant species correctly. Multiplying the time spent feeding on a certain species with the average intake rate allows the translation of direct observations into consumed dry weight of a certain plant species and consequently to analyse the diet composition. Tixier *et al.* (1997) determined the average intake rate by supplying branches to tame animals during a fixed period and subsequently comparing the weight of the branches before and after consumption by the animals.

Analysis of feeding traces provides little disturbance for the animal, but it is difficult to make a distinction between related animal species (Birkenstock & Maillard, 1989). Furthermore, this method is unreliable for herbs and it gives no information about fungi and fruits (Maillard & Picard, 1987). Feeding traces cannot be recognized for all plants and they disappear fast in the growing season (Roelvink, 1988).

When excluding deer from certain areas by fencing and afterwards comparing the vegetation in and outside these enclosures, it is possible not only to deduce the influence of the animals on certain individual plant species, but also to analyse the influence of the animals on vegetation composition in general and on vegetative growth (Jackson, 1974; Hollins & Carroll, 1997).

The main problem when using feeding experiments to analyse diet composition is to decide which plant species and how much of each species should be offered to the animals.

Diet composition studies can, for all methods, only be translated into feeding preferences when there is also information on the availability of the different plant species. If there is no information concerning the exact place of food intake one can use the average availability of the different plant species in the study area.

All methods are likely to yield some valuable information, but they also each have their theoretical and practical benefits and drawbacks.

## METHODS AND ASSUMPTIONS

In order to compare the results of the food selection of roe deer in different studies, we reclassified food items into 10 groups: graminoids, herbs, ferns, fungi, half-woody plants, dwarf shrubs, coniferous browse, deciduous browse, cultivated plants and others. Graminoids comprise all kinds of wild grasses, sedges and rushes. Half-woody plants are *Rubus* spp., *Rosa* spp., *Hedera helix, Lonicera periclymenum, Ulex europaeus* and *Ribes* spp. Dwarf shrubs include all kinds of heather (*Calluna, Erica)* and bilberry (*Vaccinium myrtillus).* The category of coniferous browse contains needles, twigs and sprouts of conifers, and that of deciduous browse twigs, sprouts, fruits (e.g. acorns, beech nuts, horse chestnuts, apples) and green leaves of broad-leaved trees and shrubs. Cultivated plants include rye, barley, wheat, potatoes, beets, maize, lucerne, rape-seed and clover. The category 'others' contains mosses and all material that does not fit under one of the other categories (e.g. *Ilex aquifolium)* or that could not be identified. Gebczynska (1980) could not identify more than half of the rumen contents that she examined, because the particles were too small. That is why the category 'others' is so large in that study. These 10 categories were chosen because they were quite consistent between the studies reviewed, although some studies still did not fit into it. Therefore the results of Matrai & Kabai (1989) and Homolka (1991) are not included in the data analysis. Since the categories are broader than the ones used in the original papers, not all differences between the studies will be clear. Fruits, for example, are now included in the category of deciduous browse, but some authors distinguish fruits as a separate group (e.g. Fichant, 1974; Jackson, 1980; Maillard & Picard, 1987; Maillard *et al.*, 1989).

The results of different studies can be compared only if they are expressed in the same units. So, only those studies with quantitative results expressed as a percentage of the total amount of food intake are taken into account. This means that all results are expressed as a percentage of the dry weight of the rumen content, the volume of the rumen content, the total number of faecal fragments or the total faecal fragment area (see Table 2).

Another problem is that the different studies are not all expressed in the same time units. Therefore, we divided all data into 4 seasons. For studies with monthly data, April, May and June are combined (to form the spring season), July, August and September (summer), October, November and December (autumn), and January, February and March (winter) (see Table 3). This division agrees best with those studies already divided into seasons. Thus the data of Holisova, Obrtel & Kozena (1986b) are divided into 2 categories: the average of January, February and March forms the winter diet and the results for April are used as spring diet. Although Holisova, Obrtel & Kozena (1982) discuss the winter diet of roe deer, their results fall into the autumn period in this review, since the animals examined were shot between 20 September and 31 December. Holisova, Kozena & Obrtel (1984) divided their data into early and late summer; we took the average of both. Maizeret *et al.* (1991) investigated the summer and winter diet, but only the summer data are presented in their paper. Sometimes, however, it was impossible to divide the data into those four seasons. Hazebroek & Groot Bruinderink (1995), for example, divided their results into spring/summer, summer/autumn, winter and late winter. Maillard (1987) made no distinction between autumn and winter diet and Homolka (1991) used 6 periods of 2 months.

Since from the 33 studies only 29 expressed the data in percentages, from which 2 could not be rescaled into the time units used here and the results of 2 other studies could not be reclassified into the chosen food item categories, only 25 studies could be used for the statistical analysis. Because de Jong *et al.* (1995) had results from 2 sites in Kielder Forest, we named the results from Highfield, de Jong *et al.* 1 (1995) and those from Pundershaw, de Jong *et al.* 2 (1995). We divided the 4 sites of Fandos *et al.* (1987) in the same way. Thus our final data matrix included 29 studies (marked * in Table 2).

**Table** 2. Summary of the literature on the food selection of roe deer

| Author (* = used in the statistica] analysis) | Research method | Habitat | Region | Latitude | Longitude |
|---|---|---|---|---|---|
| * Birkenstock & Maillard (1989) | Rumen analysis (dry weight) | Deciduous forest | The Vosges, north-east France | 48 °12'N | 7°20'E |
| * Boag *et al.* (1990) | Rumen analysis (volume) | Agricultural area | East Scotland | 57°N | 3 °W |
| Borowski & Kossak (1975) | Analysis of feeding traces | Mixed forest | Bialowieza, Poland | 52 °40'N | 24 °E |
| * Cederlund *et al.* (1980) | Rumen analysis (dry weight) | Mixed forest | Grimsö, centra! Sweden | 59 "30'N | I?°30'E |
| * Degrez & Libois (1991) | Faecal analysis (number of fragments) | Mixed forest | The Ardennes, Belgium | 50 °l 5'N | 5 °27'E |
| * de Jong *et al.* 1 (1995) | Faecal analysis (area) | Coniferous forest | Highfield, Northumberland, England | 55°30'N | 2:°E |
| * de Jong *et al.* 2 (1995) | Faecal analysis (area) | Coniferous forest | Pundershaw, Northumberland, England | 55 °30'N | 2 °E |
| * Fandos *et al.* 1 (1987) | Rumen analysis (dry weight) | Deciduous forest | Cantabrian mountains, Spain | 43 °N | 6$^{10}$W |
| * Fandos *et al.* 2 (1987) | Rumen analysis (dry weight) | Deciduous forest | Iberian system, Spain | 42 °N | 2 °40'W |
| * Fandos *et al* 3 (1987) | Rumen analysis (dry weight) | Mixed forest | Guadarram mountains, Spain | 47 °N | 4 °W |
| * Fandos *et al.* 4 (1987) | Rumen analysis (dry weight) | Deciduous forest | Southem mountains enclaves, Spain | 39 °N | 4 °30'W |
| * Fichant (1974) | Rumen analysis (volume) | Mixed forest | The Ardennes, Belgium | 49 °40'N | 5 °40'E |
| * Gebczynska (1980) | Rumen analysis (dry weight) | Mixed forest | Bialowieza, Poland | 52 °38'N | 24 °E |
| * Grigorov (1976) | Rumen analysis (dry weight) | Mixed forest | Gabrovo, Bulgaria | 42 °52'N | 25 °19'E |
| Hazebroek & Groot Bruinderink (1995) | Rumcn analysis (volume) | Mixed forest | Veluwe, the Nether!ands | 52°IO'N | 5 °50'E |
| Heamey & Jennings (1983) | Faecal analysis (frequency) | Mixed forest | Norfolk/Suffolk, east England | 52 °30'N | l "E |
| * Helle (1980) | Faecal analysis (number of fragments) | Mixed forest | Muhos, centra! Finland | 64 °45'N | 26 °1 l'E |
| * Henry (1978a) | Rumen analysis (volume) | Coniferous forest | Durham, north-east England | 54 °41'N | 1 °50'E |
| * Henry (1978h) | Faecal analysis (number of fragments) | Coniferous forest | Durham, north-east England | 54 °4l 'N | 1:° 50'E |
| * Holisova *et al.* (1982) | Rumen analysis (volume) | Agricultural area | Southem Moravia, Czech Republic | 48 °57'N | l6 °29'E |
| * Holisova *et al.* (1984) | Rumen analysis (volume) | Agricultural area | Southem Moravia, Czech Republic | 48 °57'N | 16 °29'E |
| * Holisova *et al.* (l986h) | Faecal analysis (area) | Agricultural area | Southern Moravia, Czech Republic | 48 °57 N | 16 °29 E |
| Homolka (1991) | Faecal analysis (area) | Mixed forest | Southem Moravia, Czech Republic | 49 °N | 16 °30'E |
| * Hosey (1981) | Faecal analysis (number of fragments) | Mixed forest | Dorset, south England | 51 °N | °40'W |
| * Jackson (1980) | Rumen analysis (dry weight) | Mixed forest | Hampshire, south England | 51 °06'N | 1 °19'W |
| * Kaluzinski (1982) | Rumen analysis (dry weight) | Agricultural area | Czempin, west Poland | 58 °08'N | 16 °45'E |
| * Mail!ard & Picard (1987) | Rumen analysis (dry weight) | Deciduous forest | The Vosges, north-east France | 48 °42 N | 6 °12 E |
| Maillard (1987) | Rumen analysis (dry wcight) | Deciduous forest | The Vosges, north-east France | 48 "42'N | q ° 12'E |
| * Maillard *et al* (1989) | Rumen analysis (dry weight) | Deciduous forest | The Vosges, north-east France | 48 °42'N | 6 "12'E |
| ' Maizeret *et al* (1986) | Faecal analysis (number of fragments) | Mixed forest | Landes, south-wcst France | 44 °N | 0 °20'W |

**Table** 2. *(cont.)*

| Author (* = used in the statistical analysis) | Research method | Habitat | Region | Latitude | Longitude |
|---|---|---|---|---|---|
| * Maizeret *et al.* (1991) | Rumen analysis (dry weight) | Deciduous forest | Chizé, west France | 46°10'N | 0°20'W |
| * Maizeret & Tran Manh Sung (1984) | Rumen analysis (dry weight) | Mixed forest | Laudes, south-west France | 44°N | 0°20'W |
| Matrai & Kabai (1989) | Rumen analysis (number of fragments) | Mixed forest | Budapest, Hungary | 47°28'N | 19°26'E |
| Papageorgiou *et al.* (1981) | Feeding experiment | Mixed forest | Serres, north Greece | 41°N | 23°E |
| Poutsma (1977) | Direct observation | Mixed forest | Eeldo, the Netherlands | 53°10'N | 6°40'E |
| * Siuda *et al.* (1969) | Rumen analysis (volume) | Mixed forest | Olsztyn, Poland | 53°43'N | 21°36'E |
| * Tixier *et al.* (1997) | Direct observation transformed into consumed dry weight | Deciduous forest | Chizé, west France | 46°10'N | 0°20'E |

**Table** 3. Period and number of samples of each study used in the statistical analysis for each season

| Season | No. | Author | Period | No. of samples |
|---|---|---|---|---|
| Spring | 1 | Cederlund *et al.* (1980) | Apr - Jun 1973-79 | 20 |
| | 2 | Degrez & Libois (1991) | Apr-Jun 1988 | 29 |
| | 3 | de Jong *et al.* 1 (1995) | May 1993 | 3 |
| | 4 | de Jong *et al.* 2 (1995) | May 1993 | 1 |
| | 5 | Fandos *et al.* 1 (1987) | 28 Apr--20 Jun 1972-80 | 7 |
| | 6 | Fandos *et al.* 2 (1987) | 17 Apr-18 Jun 1976-80 | 4 |
| | 7 | Fandos *et al.* 3 (1987) | 25 Apr-29 May 1971-80 | 8 |
| | 8 | Fandos *et al.* 4 (1987) | 23 Mar-22 May 1979-80 | 3 |
| | 9 | Gebczynska (1980) | 11 Apr-1 Jun | 15 |
| | 10 | Henry (1978a) | May 1973-74 | 35 |
| | 11 | Holisova *et al.* (1986b) | Apr 1977, 1979-82, 1984 | 33 |
| | 12 | Hosey (1981) | Apr-Jun 1972 | 34 |
| | 13 | Jackson (1980) | Apr-Jun 1971-72 | 31 |
| | 14 | Kaluzinski (1982) | 11 May--21 Jun | 34 |
| | 15 | Maizeret & Tran Manh Sung (1984) | 15 Mar-- 30 Jun | 14 |
| | 16 | Maizeret *et al.* (1986) | Apr-Jun | 30 |
| | 17 | Siuda *et al.* (1969) | 22 Mar-21 Jun | 9 |
| | 18 | Tixier *et al.* (1997) | Apr-Jun | 7 |
| Summer | 19 | Birkenstock & Maillard (1989) | 1 Jun-30 Aug 1986 | 20 |
| | 20 | Cederlund *et al.* (1980) | Jul -Sep 1973-77 | 20 |
| | 21 | Degrez & Libois (1991) | Aug-Sep 1988 | 19 |
| | 22 | de Jong *et al.* 1 (1995) | Jul-Sep 1992 | 9-30 |
| | 23 | de Jong *et al.* 2 (1995) | Sep 1992 | 9-30 |
| | 24 | Fandos *et al.* 1 (1987) | 24 Jun-19 Sep 1974-80 | 25 |
| | 25 | Fandos *et al.* 2 (1987) | 29 Jun-10 Aug 1971-80 | 9 |
| | 26 | Fandos *et al.* 3 (1987) | 11 Sep-15 Sep 1981 | 2 |
| | 27 | Fandos *et al.* 4 (1987) | Aug 1980 | 5 |
| | 28 | Gebczynska (1980) | 2 Jun-10 Aug | 19 |
| | 29 | Henry (1978a) | Jul 1973-74 | 8 |
| | 30 | Holisova *et al.* (1984) | 19 May-18 Sep 1981-83 | 29 |
| | 31 | Hosey (1981) | Jul-Sep 1972 | 24 |
| | 32 | Jackson (1980) | Jul-Sep 1971 - 72 | 8 |
| | 33 | Kaluzinski (1982) | 22 Jun-21 Aug | 11 |
| | 34 | Maillard *et al.* (1989) | Jun-Aug 1985 87 | 13 |
| | 35 | Maizeret & Tran Manh Sung (1984) | 1 Jul-30 Sep | 17 |
| | 36 | Maizeret *et al.* (1986) | Jun--Sep | 30 |
| | 37 | Maizeret *et al.* (1991) | Jun--Sep 1985-87 | 39 |
| | 38 | Siuda *et al.* (1969) | 22 Jun-21 Sep | 9 |
| | 39 | Tixier *et al.* (1997) | Jul-Sep | 7 |

**Table 3.** *(cont.)*

| Season | No. | Author | Period | No. of samples |
|---|---|---|---|---|
| Autumn | 40 | Birkenstock & Maillard (1989) | 19 Oct-23 Dec 1985 | 17 |
| | 41 | Cederlund *et al.* (1980) | Oct-Dec 1973--75 | 43 |
| | 42 | Degrez & Libois (1991) | Oct - Dec 1987 | 19 |
| | 43 | de Jong *et al.* 1 (1995) | Nov 1992 | 9 30 |
| | 44 | de Jong *et al.* 2 (1995) | Nov 1992 | 9 -30 |
| | 45 | Fandos *et al.* 1 (1987) | 4 Oct-8 Dec 1970 -79 | 21 |
| | 46 | Fandos *et al.* 2 (1987) | 3 Oct- 21 Nov 1974-79 | 6 |
| | 47 | Fandos *et al.* 4 (1987) | 27 Nov-28 Nov 1978 79 | 2 |
| | 48 | Fichant (1974) | 5 Oct 27 Nov 1973 | 32 |
| | 49 | Gebczynska (1980) | 11 Aug-21 Dec | 33 |
| | 50 | Henry (1978a) | Nov 1973 | 24 |
| | 51 | Holisova *et al.* (1982) | 20 Sep 31 Dec 1980 | 32 |
| | 52 | Hosey (1981) | Oct -Dec 1972 | 24 |
| | 53 | Jackson (1980) | Oct-Dec 1970-72 | 22 |
| | 54 | Kaluzinski (1982) | 22 Aug-21 Nov | 16 |
| | 55 | Maillard & Picard (1987) | 12 Oct- 20 Nov 1983 | 33 |
| | 56 | Maizeret & Tran Manh Sung (1984) | 1 Oct-30 Nov | 37 |
| | 57 | Maizeret *et al.* (1986) | Oct- Dec | 30 |
| | 58 | Siuda *et al.* (1969) | 22 Sep-21 Dec | 7 |
| | 59 | Tixier *et al.* (1997) | Oct-Dec | 7 |
| Winter | 60 | Birkenstock & Maillard (1989) | 24 Dec 1985--31 Mar 1986 | 34 |
| | 61 | Boag *et al.* (1990) | Feb 1989 | 3 |
| | 62 | Cederlund *et al.* (1980) | Jan-Mar 1973-77 | 12 |
| | 63 | Degrez & Lihois (1991) | Jan-Mar 1988 | 25 |
| | 64 | de Jong *et al.* **1** (1995) | Jan-Mar 1993 | 9-30 |
| | 65 | de Jong *et al.* 2 (1995) | Jan-Mar 1993 | 9 30 |
| | 66 | Fandos *et al.* 1 (1987) | 25 Dec - 8 Mar 1970-80 | 14 |
| | 67 | Fandos *et al.* 2 (1987) | 30 Dec-14 Feb 1973--78 | 3 |
| | 68 | Fandos *et al.* 3 (1987) | 17 Feb -18 Mar 1979 | 2 |
| | 69 | Fandos *et al.* 4 (1987) | 20 Jan 1980 | |
| | 70 | Gebczynska (1980) | 21 Dec - 10 Apr | 24 |
| | 71 | Grigorov (1976) | Nov-Mar 1973-76 | 27 |
| | 72 | Helle (1980) | Jan-Apr 1976-77 | 77 |
| | 73 | Henry (l978a) | Jan-Feb 1973 74 | 16 |
| | 74 | Henry (1978b) | Jan- Mar 1974 | 105 |
| | 75 | Holisova *et al.* (1986b) | Jan-Mar 1977, 1979--80, 1982, 1984 | 150 |
| | 76 | Hosey (1981) | Jan-Mar 1972 | 37 |
| | 77 | Jackson (1980) | Jan-Mar 1971-73 | 44 |
| | 78 | Kaluzinski (1982) | 22 Nov-31 Jan | 64 |
| | 79 | Maillard & Picard (1987) | 21 Nov 1983-9 Jan 1984 | 34 |
| | 80 | Maizeret & Tran Manh Sung (1984) | 1 Dec --15 Mar | 21 |
| | 81 | Maizeret *et al.* (1986) | Jan-Mar | 30 |
| | 82 | Siuda *et al.* (1969) | 22 Dec--21 Mar | 21 |
| | 83 | Tixier *et al.* (1997) | Jan-Mar | 7 |

As a first step, following the traditional approach (e.g. Siuda, Zurowski & Siuda, 1969), we summarized the reviewed information for each season. The differences in diet composition during the year are influenced both by the changes in food item availability and by the changing food requirements of the animals during the year (lactation, mating, etc.) (van Wieren *et al.*, 1997). In order to arrange the data of the selected studies for each season according to their similarity a two-way indicator species analysis was applied, using 6 cut levels (0, 2, 5, 10, 20, 50) (TWINSPAN; **Hill**, 1979a). The other parameters, being the minimum group size for division, the maximum number of indicators per division, the maximum number of species in the final tabulation and the maximum level of divisions, were set default.

To identify the main sources of variation in the food selection of roe deer (habitat, season, research method, geographical location), we submitted the data set to a detrended correspondence analysis (DCA), using DECORANA (**Hill**, 1979h). For this purpose we generalized the locations of the different study areas, expressed as longitude and latitude, by rounding the degrees of latitude and longitude to the nearest 5 ° parallel or meridian. The 29 studies used in the data analysis include 20 rumen analyses, 8 faecal analyses and one direct observation transformed into consumed dry weight. Twenty-four studies were carried out in

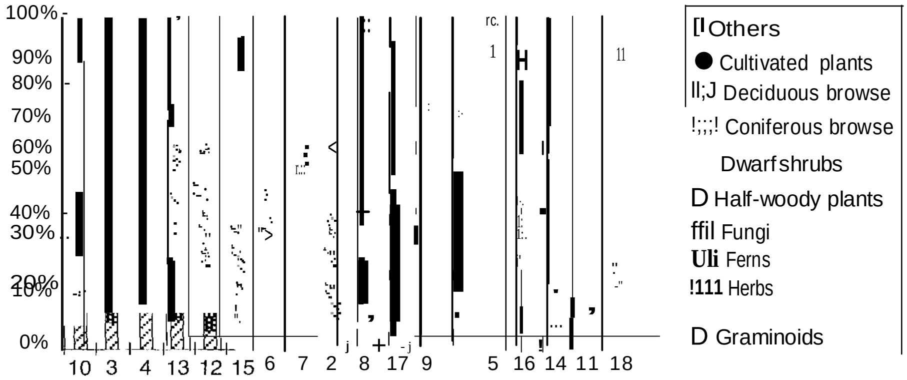

**Fig. 1.** Spring diet of roe deer per study (studies numbered as in Table 3). The order and subdivision is determined by TWINSPAN.

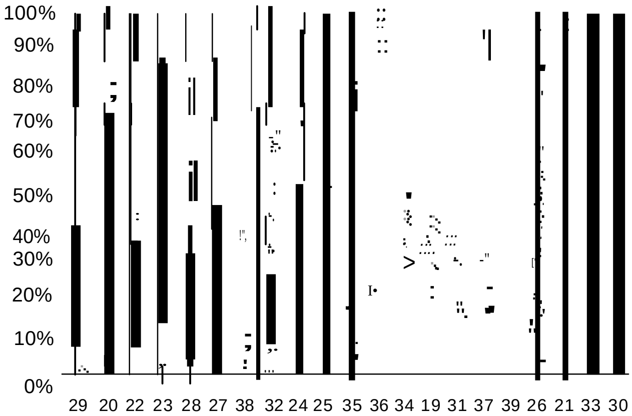

**Fig.** 2. Summer diet of roe deer per study (studies numbered as in Table 3; key as in Fig. 1). The order and subdivision is determined by TWINSPAN.

forests (4 in coniferous forest, 8 in deciduous forest and 12 in mixed forest) and 5 studies in agricultural areas (see Table 2). Some studies include more than 1 season; there are 18 studies in spring, 21 in summer, 20 in autumn and 24 in winter (see Table 3). Therefore the DCA includes 83 cases and 10 food groups. This matrix of 83 cases was also submitted to a TWINSPAN analysis to discover the main factors subdividing the observations. To confirm statistically the observed differences (DCA, TWINSPAN) we applied a Kruskall--Wallis test, using the coordinates on the I and II axes as input scores and the different factors (season, habitat, geographical location and method) as grouping factors.

To obtain a general overview of the diet composition a weighted average contribution of each of the 10 food items was calculated for each season, each habitat and each method and for the cross-products of habitat and season, method and season, and habitat and method. The weighted average was calculated by multiplying the percentage contribution of a food group in the total amount of food intake in a study by the number of samples in that study (sec Table 3) and divided by the total number of samples occurring in that specific subclass (e.g. diet composition in the winter in conifer habitats). For the data of de Jong *et al.* (1995) we used the minimum number of samples each time. To integrate the relationship between diet composition and other variables, the matrices containing the weighted averages were subjected to Multivariate Ratio Analysis (MRA) (Lewi, 1989; Hermy & Lewi, 1991). MRA produces biplots of bath rows (season, habitat, method or a combination of two factors) and columns (food groups). It provides direct insight into the interaction and discriminating power of columns and rows of the data matrix.

## RESULTS

### Seasonal summaries

Roe deer diet varies greatly in all seasons (Figs 1-4). In spring the observed diet variation is divided by TWINSPAN into four groups (Fig. 1): three studies (nos. 14, 11, 18) where cultivated plants partly compose the roe deer diet; three studies with a large amount of coniferous browse (10, 3, 4); two central clusters with relatively small differences in diet, except that the half-woody plants are a much more important constituent of the diet in the left group (13, 12, 15, 6, 7, 2).

For the summer diet TWINSPAN divided the sample into four major groups of studies (Fig. 2). In two studies the diet mainly consists of cultivated plants (33, 30). A second group, of *fout* studies, is characterized by a large amount of coniferous browse in the diet (29, 20, 22, 23). The large central group of studies may be divided on the basis of the combined presence (28, 27, 38, 32, 24, 25, 35, 36) or absence of dwarf shrubs and fungi in the diet (except study 21).

In autumn, studies are divided into five groups (Fig. 3). Three studies feature considerable amount of cultivated plants in the diet (54, 51, 56). On the other side of the figure three studies (50, 43, 44) are characterized by the considerable amount of coniferous browse and ferns, large amounts of dwarf shrubs and, particularly, the absence of deciduous browse and near absence of half-woody plants. The central part is divided into three groups: one with a large amount of dwarf shrubs in the diet (58, 48, 41, 57) and two groups less clearly separated by differences in the food groups 'others', coniferous browse and half-woody plants.

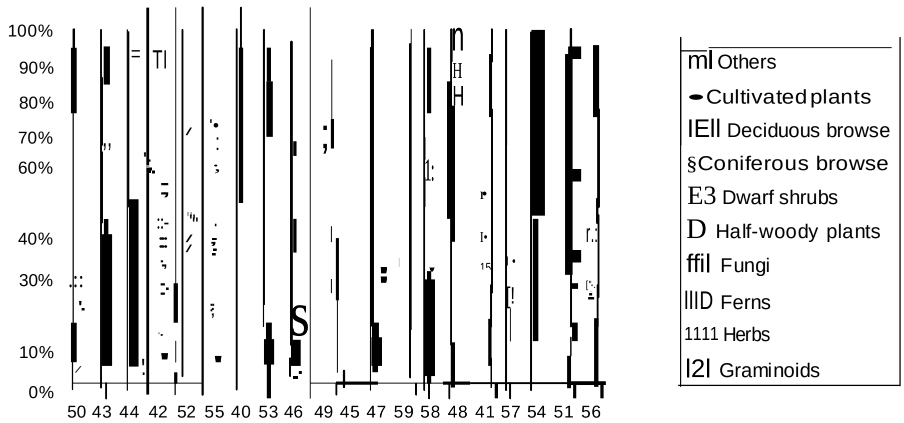

Fig. 3. Autumn diet of roe deer per study (studies numbered as in Table 3). The order and subdivision is determined by TWINSPAN.

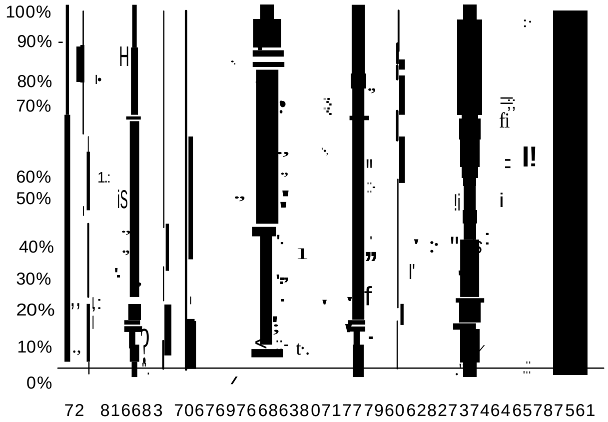

Fig. 4. Winter diet of roe deer per study (studies numbered as in Table 3; key as in Fig. 3). The order and subdivision is determined by TWINSPAN.

In winter, TWINSPAN divides the spectrum into four clearly defined groups (Fig. 4). In three studies the diet is composed almost entirely of cultivated plants (78, 75, 61). The next six studies (62, 82, 73, 74, 64, 65) show a high contribution of coniferous browse and dwarf shrubs. A third cluster (76, 68, 63, 80, 71, 77, 79, 60) differentiates from the other through high amounts of half-woody plants and the presence of fungi. The remainder are differentiated only by deciduous browse and 'others'.

## DCA and TWINSPAN

The results of the DCA on all observations are visualized in Figs 5 & 6. Figure 5 shows that cultivated plants have high scores on axis I. Axis II separates half-woody plants and deciduous browse from dwarf shrubs and coniferous browse. Figure 6a shows clearly that axis I divides the studies into those that took place in agricultural areas, and the other studies. The same division is found in the TWINSPAN table where all the studies that took place in agricultural areas are located in group *1 (Figs 6f & 7). The Kruskall-Wallis test revealed a marginally significant difference $(P = 0.066)$ in the mean ranks of the scores on axis I between the studies in agricultural areas and the other habitat types. Axis II separates deciduous from coniferous forests, with mixed forests in between them. This subdivision is also apparent in the TWINSPAN table where all the coniferous habitats are found in group *00, which also includes two observations in mixed habitats. All the observations in deciduous forest ecotypes are grouped in group *01. This group also includes the rest of the observations in mixed habitat types. The difference in mean ranks of the scores on axis II of the studies in coniferous forests and those in deciduous or mixed forest is highly significant $(P < 0.001)$.

The research technique used partly explains the variation in diet (Fig. 6b). There is a significant difference $(P < 0.05)$ between the mean ranks of scores on the first axis of the DCA of those studies using faecal analysis expressed as percentage of the total number of fragments and the scores of studies based on rumen content analysis. The second axis of the DCA separates the two types of rumen content analysis and the two types of faecal analysis. However, the TWINSPAN table does not reveal any clear major divisions based on research method. The TWINSPAN technique can only find subdivisions based on the research method, on the lower levels.

Besides the habitat and the research technique, the variation is also explained by the geographical location. The different degrees of longitude and latitude are grouped together, although there is no clear transition from low to high values (Fig. 6d, e). The differences in the mean ranks of the different groups do show some significant scores though no clear pattern can be found.

Season is not an explanatory factor for the variation in diet composition (Fig. 6c), since the difference between the mean ranks of the scores on the first and second axis of the DCA is not significant $(P = 0.61$ and $P = 0.80$, respectively).

### Weighted averages

Following the traditional approach, which emphasizes the seasonal variation in the diet, and the results of the TWINSPAN and DCA approaches, which strongly suggest the overall importance of habitat differences, we calculated the weighted averages of those two factors. Tables 4 and 5 allow us to make a general comparison between the four seasons and the four habitats.

### *Season (Table 4)*

From the yearly weighted averages it is clear that half-woody plants, deciduous browse, dwarf shrubs and cultivated plants are the most important food items for roe deer. In combination they form more than two-thirds of the diet. Half-woody plants, such as bramble and ivy, are eaten in approximately the same proportion during each season. More graminoids are eaten during spring than during the other seasons. Herbs are much more important in spring and summer than in autumn and winter, when more dwarf shrubs are eaten to compensate. During summer, consumption of broad-leaved trees and shrubs reaches its maximum. When broad-leaved trees and shrubs have dropped their leaves, roe deer switch to coniferous browse, where it is available. Fungi are practically only available during the autumn, as is reflected in the diet.

### *Habitat (Table 5)*

Cultivated plants are of course most important in agricultural areas. Nor is it surprising that the highest proportion of deciduous browse and coniferous browse was found in deciduous and coniferous forests, respectively. Dwarf shrubs are mostly eaten in coniferous forests, while half-woody plants were almost always found in mixed and deciduous forests. Finally, herbs are more eaten in coniferous and deciduous forests, although their proportion is considerable in the other habitats as well.

### MRA

For the same reason as the weighted averages, we combined only season and habitat in a MRA (Fig. 8). The bi-plot clearly shows the grouping effect of the habitat type, rather than the season, and indicates the relations between the different groups of food items and the two factors. 'Cultivated plants' is closely aggregated with agricultural areas, coniferous browse with coniferous forest and deciduous browse with deciduous and mixed forest ecotypes. The graminoids and herbs seem to occur together with cultivated plants and coniferous forest rather than with mixed or deciduous forest types.

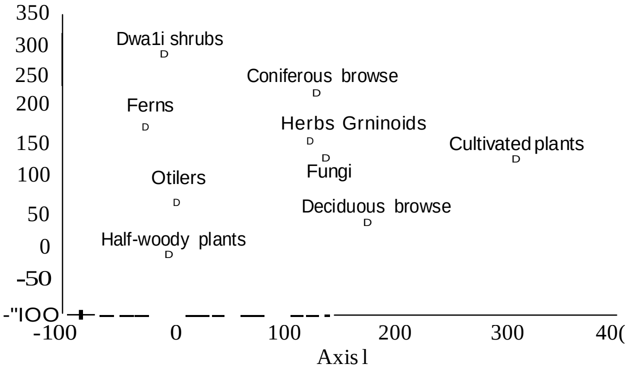

Fig. 5. DCA-plot of all observations ($n = 83$) showing the position of food items.

## DISCUSSION

Drawing conclusions from the DCA and the TWINSPAN table as well as the interpretation of the Kruskall-Wallis tests and the subsequent multiple comparisons was complicated by the fact that most of the factors were highly correlated. The Cramers measure of association for categorical data and the associated significance tests revealed highly significant associations between the geographical location and the habitat ($V = 0.95$ for casting and 1 for northing), the latitude and the longitude ($V = 1$) and even, though to a far lesser extent, between the method and the habitat type ($V = 0.54$).

The results of our research on the impact of the different factors influencing roe deer diet composition reported in the literature, made us question the decision of Tixier & Duncan (1996) not to include the results from faecal analysis since 'the species composition of the fragments in faecal samples differs considerably from stomach samples'. They are surely right that the various research techniques return different results when applied on the same animal, or even on the same population, since each technique has a bias towards certain food item groups (see Research techniques). However, our results clearly reveal that whenever comparing the diet composition of roe deer populations spread over different habitats, the influence of habitat (the available food items) is more important than the research method used. These findings argue in favour of using all available studies, rather than limiting the number of studies to those that used the same research method. The following discussion therefore takes all the reviewed studies into account.

Our conclusion, that the variation in food intake of roe deer is mainly explained by the habitat in which they live (see Figs 6a & 7), is confirmed by other authors (e.g. Jackson, 1980; Holisova *et al.*, 1986b; Tixier & Duncan, 1996). This tendency is here even more clear than in the review of Tixier & Duncan (1996). The habitat is responsible for food availability, but major differences in food availability are still possible in the same type of habitat. For example, when comparing the composition of roe deer's diet in two Polish forests,

Table 4. Weighted averages of the food selection of roe deer per season (%)

| Season | Graminoids | Herbs | Ferns | Fungi | Half-woody plants | Dwarf shrubs | Coniferous browse | Deciduous browse | Cultivated plants | Others |
|---|---|---|---|---|---|---|---|---|---|---|
| Spring | 10.12 | 14.50 | 0.57 | 0.51 | 19.56 | 12.59 | 3.95 | 16.48 | 11.66 | 10.06 |
| Summer | 2.97 | 16.80 | 1.60 | 1.04 | 20.26 | 10.51 | 1.27 | 24.23 | 10.24 | 11.07 |
| Autumn | 3.74 | 7.86 | 1.29 | 3.94 | 22.58 | 17.93 | 3.40 | 20.39 | 8.62 | 10.24 |
| Winter | 5.22 | 4.80 | 0.96 | 0.54 | 19.57 | 17.01 | 11.60 | 12.64 | 20.94 | 6.71 |
| Yearly weighted average | 5.32 | 9.34 | 1.08 | 1.41 | 20.38 | 15.29 | 6.54 | 17.17 | 14.58 | 8.88 |

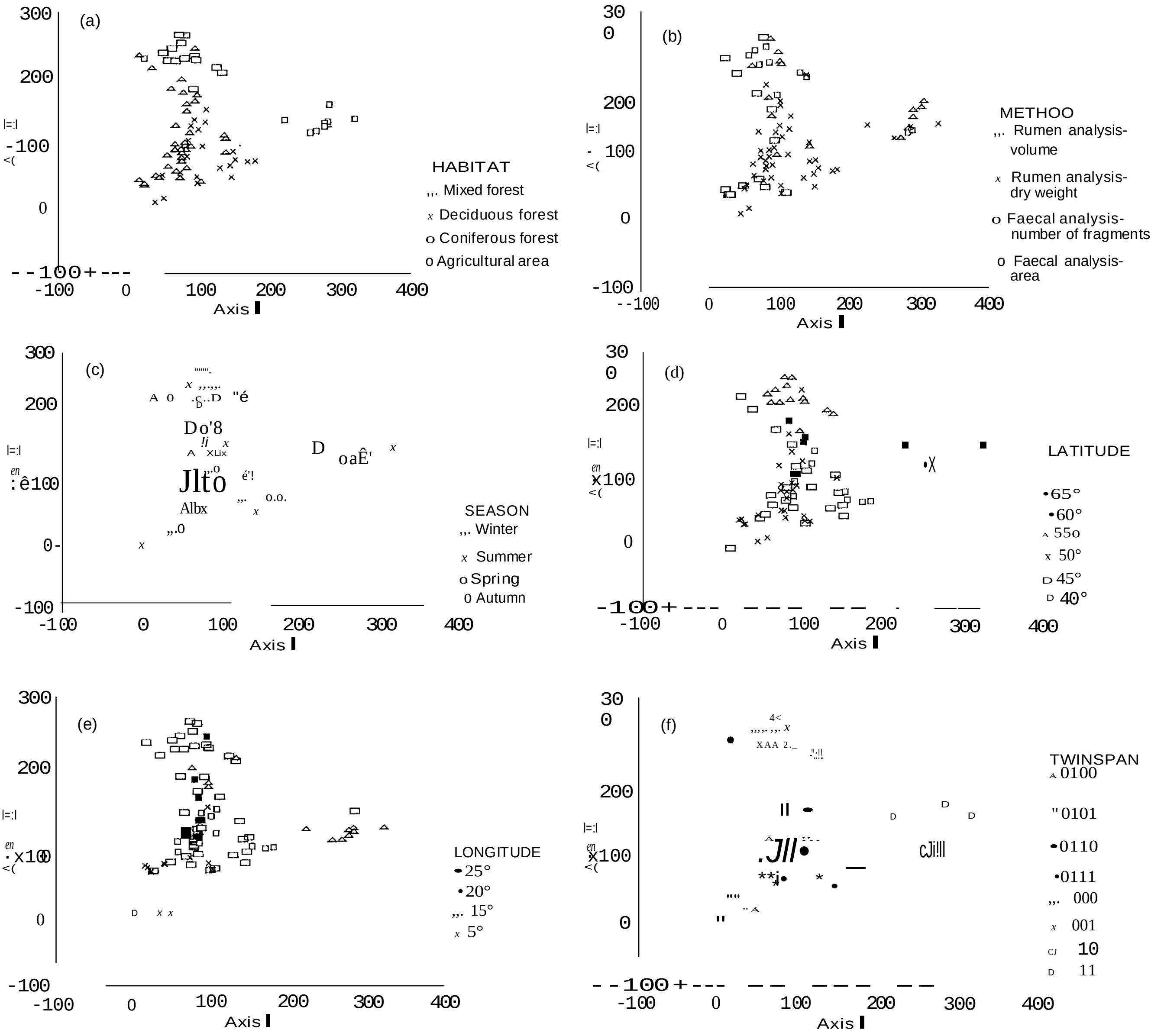

Fig. 6. DCA-plot of diet cases labelled by (a) habitat type, (b) research method, (c) season, (d) latitude, (e) longitude, (f) TWINSPAN group.

namely the Pisz Forest (Siuda *et al.*, 1969) and the Bialowieza Primeval Forest (Gebczynska, 1980), significant differences were apparent between them, although both forests are classified as mixed forests and both studies used the same method of analysing rumen contents. The fundamental difference arises because in the first case it was concluded that the basic food of roe deer consists of leaves and twigs of trees, shrubs and dwarf shrubs, and that herb layer plants were of secondary importance. In the second case it was found

**Table 5.** Weighted averages of the food selection of roe deer per habitat (in %)

| Habitat | Graminoids | Herbs | Ferns | Fungi | Half-woody plants | Dwarf shrubs | Coniferous browse | Deciduous browse | Cultivated plants | Others |
|---|---|---|---|---|---|---|---|---|---|---|
| Agricultural area | 4.59 | 7.41 | 0.00 | 0.17 | 0.84 | 0.00 | 1.86 | 16.25 | 68.51 | 0.37 |
| Coniferous forest | 15.59 | 11.29 | 4.66 | 0.42 | 1.50 | 44.07 | 20.57 | 0.00 | 0.00 | 1.90 |
| Deciduous forest | 2.26 | 12.79 | 1.00 | 0.91 | 37.72 | 3.06 | 5.04 | 30.26 | 0.05 | 6.91 |
| Mixed forest | 3.91 | 8.38 | 0.59 | 2.36 | 27.46 | 18.05 | 5.17 | 17.62 | 1.48 | 14.98 |

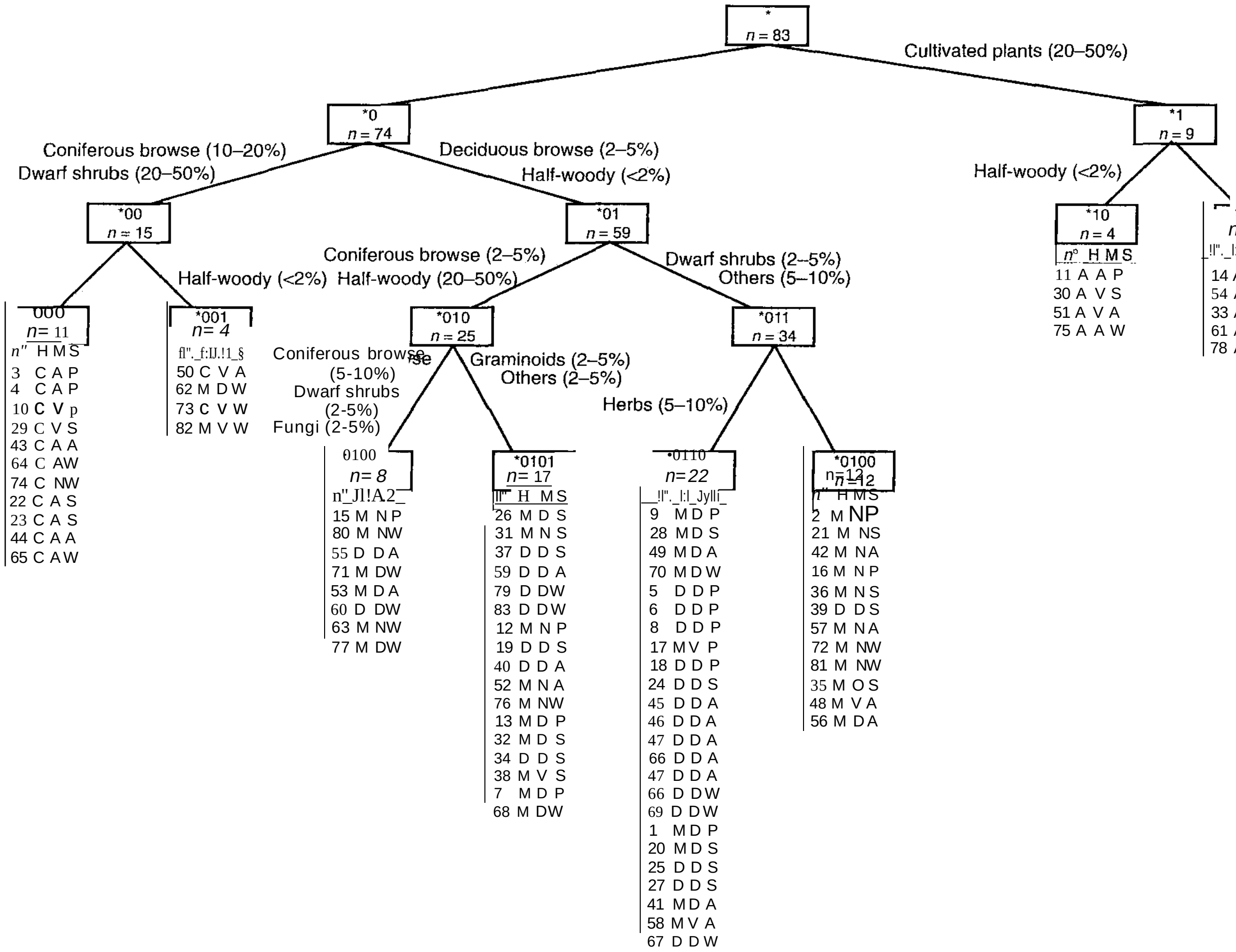

**Fig.** 7. TWINSPAN classification of roe deer diet cases (*n* = 83). *n*, number of cases; *n*°, number of each case (see Table 3); H, habitat (A, agricultural area; C, coniferous forest; D, deciduous forest; M, mixed forest); M, research method (A, faecal analysis – area; D, rumen analysis -- dry weight; N, faecal analysis - number of fragments; V, rumen analysis – volume); S, season (A, autumn; P, spring; S, summer; W, winter).

that roe deer feed chiefly on herb layer plants, and although the percentage of trees and shrubs consumed increases in autumn and winter, herb layer plants continue to form the basic food in these seasons. The reason for these differences is the different food availability.

The quantity and quality of the available food can undergo some major changes during the seasons (see Table 4), but variation in the annual diet relates more to research method and location than to season. So, to compare the diet composition of different seasons, one should use the same research method and the same location, including the same habitat.

The results of this review also justify the statement that the food supply of roe deer living in a forest habitat is composed of trees, shrubs, dwarf shrubs and herbs (see Table 5). As a rule, the representation of tree and shrub sprouts in the diet is higher than 30% through the year, often amounting to more than 60% of the diet (Homolka, 1991). A lower representation of woody plants in the roe deer diet is found in field habitats (Holisova *et al.*, 1982, 1984, 1986b; Kaluzinski, 1982), which is easily understood considering the scarcely wooded agrocoenoses.

The use of clearcutting in forest exploitation and nitrogen deposition have enabled *Rubus fruticosus* and

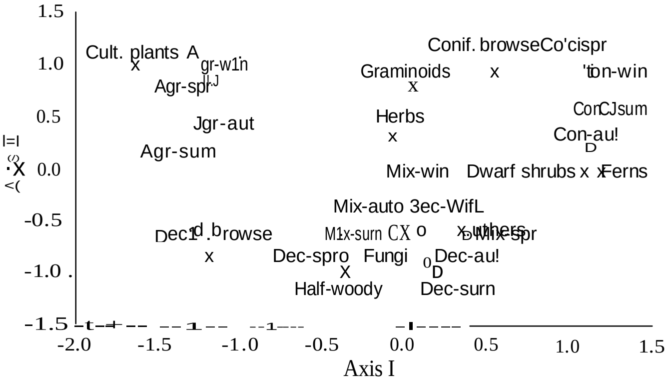

Fig_ 8. Multivariate ratio analysis of the weighted averages for habitat (Dec, deciduous forest; Mix, mixed forest; Con, coniferous forest; Agr, agricultural area and season; Spr, spring; Surn, summer; Aut, autumn; Win, winter). Boxes represent the scores of the diet cornposition in each season-habitat combination relative to the scores of the food groups (crosses).

*R. idaeus* to spread considerably in forests. This fact has increased the food supply for deer not only in the growing season, but also in winter (Homolka, 1991). The considerable importance of *Rubus* spp. as a food source is indicated by their representation in the roe deer's diet in various parts of Europe: in France (Maillard & Picard, 1987; Birkenstock & Maillard, 1989; Ballon *et al.*, 1991), England (Hosey, 1981; Hearney & Jennings, 1983), Belgium (Fichant, 1974; Degrez & Libois, 1991), the Netherlands (Poutsma, 1977), the Czech Republic (Homolka, 1991), Bulgaria (Grigorov, 1976), Poland (Siuda *et al.*, 1969), etc.

Coniferous browse constitutes a considerable part of the roe deer diet in winter (Fig. 4), especially in periods with snow (Siuda *et al.*, 1969; Henry, 1978a, *b;* Cederlund *et al.*, 1980; Birkenstock & Maillard, 1989). In the growing season this component is shunned, except when no deciduous browse is available (Henry, 1978a; de Jong *et al.*, 1995). The high proportion of coniferous browse in the winter diet may reflect the fact that it is the only food of high quality that is still available in large amounts. It has a high content of proteins, water and sugars (Matrai & Kabai, 1989). In the northern part of its range roe deer eat arboreal lichens as well as dwarf shrubs and twigs of trees and shrubs (Helle, 1980). Foods such as fruit and fungi are available only strictly seasonally, which is reflected in the analyses of the diet (Fichant, 1974; Jackson, 1980; Maizeret & Tran Manh Sung, 1984). Forest fruits and seeds are fairly heavily eaten, but there is a large variation of fruits in the diet, related to the irregularity of fruit production (e.g. acorns).

Cultivatcd plants are the most important in open fields (see Table 5), though there is no direct unfavourable effect on plant production (Kaluzinski, 1982; Holisova *et al.*, 1984). However, whcn possible, field roe deer, will supplement their diet by browsing in pockets of woodland such as windbreak beits and small copses (Holisova *et al.*, 1982, 1984; Putman, 1986).

Considering the high percentage of woody plants in the roe deer diet, it is ohvious that the deer may be of considerable importance in forest management by damaging shoots of broad-leaved and coniferous woody plants (Gill, 1992; Picard *et al.*, 1994). Roe deer may suppress, distort or kil! economically important species in a variety of ways. Some, such as fraying and trashing, are associated with the buck's territoria! behaviour whereas browsing results directly from the animal's feeding activities (Hoolboom, 1976).

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