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# Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*

**David Storms, Philippe Aubry, Jean-Luc Hamann, Sonia Saïd, Hervé Fritz, Christine Saint-Andrieux & François Klein**

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Use of food resources by herbivores depends on intrinsic constraints, essentially body size and morpho-physiological characteristics, which determine the range of foods they tolerate and environmental constraints, such as seasonality and interspecific interactions, which determine the availability of resources. We analysed a collection of rumen contents samples from sympatric populations of red deer *Cervus elaphus* and roe deer *Capreolus capreolus* and tested several theoretical predictions relating to the impact of intrinsic and environmental constraints on diet composition, diversity and similarity. Red deer consumed more slowly digestible, fibrous forage than roe deer and had a more diverse diet throughout the year, which supports predictions deriving from specific body size and morpho-physiological characteristics. In conformity with the optimal foraging theory, both species consumed more slowly digestible forage in times of low food availability (i.e. during winter) than during the rest of the year. An increase in diet similarity in winter, along with predictions from the theory on competitive interaction processes, led us to assume that food resources were not limiting and that exploitative competition between red and roe deer was unlikely in our study area. We underline the importance of studies of the use of food resources by sympatric herbivores in answering applied ecological questions at the local scale, and we suggest that the Euclidean geometrical approach we used is particularly well suited for the analysis of resource matrices, a common end-product of long-term field data gathering on the feeding habits of animals.

*Key words: Capreolus capreolus, Cervus elaphus, diet overlap, diet similarity, Principal Component Analysis, red deer, resource partitioning, roe deer, seasonal variation*

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An animal's diet is the product of intrinsic constraints (essentially its body size and morpho-physiology) that determine the range of foods it tolerates, and environmental constraints that determine the availability of food resources. On evolutionary time scales, natural selection shapes the species' morphological and physiological adaptations to environmental constraints and defines the limits of their fundamental feeding niches (Hutchinson 1957, Hanley 1982, Chase & Leibold 2003). The role interspecific competition plays in setting limits to feeding niches is a matter of controversy (Wiens 1977, Diamond 1978, Connell 1980, Schoener 1982), but it is admitted that in order to coexist in the long term, populations of sympatric species have to segregate on at least one dimension of their niche space (the competitive exclusion principle; Gause 1934, Hardin 1960), which often appears to be food (Schoener 1974, 1983). In ruminant ungulate assemblages, food resource partitioning is facilitated by body size differences between the species (Bell 1971, Jarman 1974). Besides evolutionary-shaped specific body size and morpho-physiological characteristics, use of food resources by individuals of a population (i.e. the population's realised feeding niche) also depends on variations in food availability occurring over shorter time scales (Schwartz & Ellis 1981). Seasonality and interspecific interactions are two environmental constraints likely to influence food availability, and hence the use of food resources by individuals of sympatric populations.

By contrasting diet composition and temporal variability among sympatric populations of species of a same guild (*sensu* Root 1967), comparative nutritional ecology studies allow testing predictions on the way sympatric populations cope with seasonal variations in food availability. We tested such predictions on sympatric populations of red deer *Cervus elaphus* and roe deer *Capreolus capreolus*, two ruminant ungulates that frequently occur together in European forests and differ markedly in body size (average weight in kg: for red deer ♂ 160.0 and ♀ 107.5 and for roe deer ♂ 27.7 and ♀ 26.7; Loison et al. 1999). Food resources available to ungulates consist of plant species that differ in nutritional quality, particularly because cells that constitute plant tissues vary in their ratio of slowly digestible cell walls to easily assimilated cell constituents, and therefore differ in their rate of digestion by ungulates (Demment & van Soest 1985). Fibres are structural cells with particularly thick walls (Raven & al. 1992) that form slowly digestible tissues (sclerenchyma). Among the plants available to ungulates, forbs present the lowest proportion of fibre, grasses, sedges, heathers and ferns contain high proportions of fibre and are therefore slowly digestible, and leaves of trees and shrubs are in the medium-high range (Gonzalez-Hernandez & Silva-Pando 1999). In ruminants, body size, and hence gut capacity, determine the retention time of the ingesta in the gastrointestinal tract and thereby the extent to which individuals are able to utilise slowly digestible, fibrous forage (Demment & van Soest 1985, Gordon & Illius 1994, Robbins et al. 1995, van Soest 1996). Tolerance to fibrous forage has also been attributed to interspecific differences in morpho-physiology (Hofmann & Stewart 1972, Hofmann 1989, Clauss & Lechner-Doll 2001, Clauss et al. 2003), on the basis of which Hofmann (1989) set up a classification of ruminants according to their feeding selectivity. Red and roe deer appear in this classification as an intermediate feeder (opportunistic forager having a mixed diet of grasses and roughage and concentrate food items) and a concentrate selector (selective feeder choosing forage rich in accessible plant cell contents, i.e. 'browser'; *sensu* Clauss et al. 2003), respectively. Many studies have been carried out in order to describe the



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botanical composition of their diets (see reviews by Tixier & Duncan 1996, Cornelis et al. 1999, Gebert & Verheyden-Tixier 2001), mostly in relation to their impact on commercial forests. However, data on seasonal variation in the composition and similarity of the diets of red and roe deer when populations occur sympatrically are still rare. Only a few studies produced data on diet similarity (Schröder & Schröder 1984, Putman 1996, Latham et al. 1999, Mysterud 2000), and differences in measures of food use and calculation of similarity indices make results difficult to compare across studies. In the present context of an increase in range and numbers of red and roe deer across Europe (Gill 1990), and the subsequent increase in situations where these species coexist, comparative studies of their nutritional ecology will prove an essential basis for the sound management of their populations and habitats.

We analysed food resource use by sympatric populations of red and roe deer using an Euclidean geometrical approach that allows for the multivariate and compositional nature of the data. Our aim was to confront measures of diet composition, diversity and similarity to several theoretical predictions and see 1) if diet composition and diversity conform to predictions deriving from specific body size and morpho-physiological characteristics, 2) if seasonal variation in diet composition conforms to predictions of the optimal foraging theory and 3) if seasonal variation in food resource partitioning among populations conforms to predictions from the theory on competitive interactions processes.

According to differences in body size and morpho-physiological feeding types (Hofmann 1989, Gordon & Illius 1994) and following the hypothesis that browsers are 'obligatory non-grazers' (van Wieren 1996, Clauss et al. 2003) and avoid grasses to a much higher degree than grazers avoid browse (forbs and leaves of shrubs and trees, i.e. less fibrous plants), we 1) expected the diet of red deer to include a higher proportion of fibrous forage, especially grasses, and be more diverse than that of roe deer. Then, under the optimal foraging theory-related hypothesis that individuals become less selective when food abundance decreases (Schoener 1971, Owen-Smith & Novellie 1982) and knowing that the fibre content of plants is lowest in the growing season and increases from spring through summer to fall-winter (Gonzalez-Hernandez & Silva-Pando 1999), we 2) predicted that the diets of both species would include more fibrous forage in winter, when forage abundance and quality are at their lowest (Dzieciolowski 1969, Bobek 1977). Finally, under the hypothesis that during times of low resource abundance competing species pull back to the more or less exclusive set of resources to which each is best adapted (Schoener 1982), we 3) expected values of diet similarity to be minimal in winter if red and roe deer compete for limited food resources.

## Study area

Our study was carried out in la Petite-Pierre National Hunting and Wildlife Reserve (NHWR), a 2,800-ha unfenced forest area located in the Vosges mountain range, in northeastern France (48.5°N, 7°E), at a mean elevation of 300 m a.s.l. The climate is continental with oceanic influence, leading to mild winters and cool summers (mean January and July temperatures are 0.6 and 18.4°C, respectively; Bonenfant et al. 2005). Snow accumulation is rare. The sandstone substrate in la Petite-Pierre NHWR produces acidic and poor soils, resulting in a poorly diversified vegetation of low nutritive quality (*sensu* Gonzalez-Hernandez & Silva-Pando 1999) for herbivores. The forest is structured in even-aged clusters of trees, and comprises roughly equal proportions of broadleaved, mainly beech *Fagus sylvatica*, and coniferous trees, mainly silver fir *Abies alba*, Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* (Hamann et al. 1997). Red deer, roe deer, wild boar *Sus scrofa* and brown hare *Lepus europaeus* are present within the Reserve. The area is free of big game predators, and ungulate populations are managed through hunting, either with (deer) or without quota (wild boar). Red and roe deer population densities have been maintained at relatively constant levels since 1984 (Bonenfant et al. 2002), and in the past 10 years an average of 40 red deer and 50 roe deer have been hunted annually in la Petite-Pierre NHWR.

## Material and methods

Samples of red and roe deer rumen contents were taken from animals shot by Office National de la Chasse et de la Faune Sauvage and Office National des Forêts staff or killed in traffic collisions in la Petite-Pierre NHWR. During 1986-1997, a total of 127 red deer and 157 roe deer rumen content sam-



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ples were collected throughout the Reserve. For the purpose of the analyses, we aggregated data across years and samples were grouped into seasons according to plant phenology and biology of both deer species (winter: 1 November-15 April; spring: 16 April-30 June, including calving; summer/autumn: 1 July-31 October, including breeding; the vegetation period was 15 April-31 October).

**Rumen contents analysis**

Samples of 500 g of rumen contents were frozen and later washed in a sieve with a mesh size of 5.0 mm. The retained material was sampled and sorted macroscopically using a method adapted from the point-frame technique developed by Chamrad & Box (1964). Sieved items were mixed with water and spread over a rectangular tank on the bottom of which a grid formed 100 intersection points, allowing the selection of 100 items. This process was repeated three times to obtain a sample of 300 items per rumen contents, from which the occurrence proportion of each type of food item could be calculated. A former study based on a subset of the data we used here demonstrated that occurrence proportions estimated from a sample of 300 items were not statistically significantly different from those measured from the entirety of the sieved items, neither were they different from the weight proportions obtained after drying and weighing the 300 items (Dubois 1992). Each plant fragment found was separated and identified to the lowest possible taxon using reference collections. For the purpose of the analyses, the original 99 different types of identified items were grouped into 29 food categories (detailed in Appendix I). Our data set therefore consisted in a $n \times p$ 'resource matrix' (*sensu* Colwell & Futuyma 1971) with n individuals as rows and p food categories as columns, each row total being equal to 1. Two additional columns described the species (i.e. red or roe deer) and the sampling season (i.e. winter, spring or summer/autumn).

**Statistical methodology**

***Geometrical representation of the resource matrix***

Let $P = [p_{ij}]$ the $n \times p$ resource matrix for one deer species with $p_{ij}$ the proportion $(0 \leq p_{ij} \leq 1)$ of $j^{th}$ food category (columns, $1 \leq j \leq p$) in the $i^{th}$ rumen (rows, $1 \leq i \leq n$) so that $\sum_{j=1}^{p} p_{ij} = 1$ (i.e. 100%); such data are known as compositional data (see Aitchison 1986, Billheimer 2002, Titterington 2006). When $p = 3$, compositional data may be depicted using the so-called triangular or ternary diagram (Gower 1967, Aitchison 1986, de Crespin de Billy et al. 2000). A ternary diagram is a triangle, with each of the three apexes representing a composition of 100% for the corresponding food category. Thus, one rumen lies somewhere within the triangle, according to the proportion of each of the $p = 3$ food categories. When $p > 3$, the entire data set cannot be displayed in a plane without using a dimension reduction technique, such as Principal Component Analysis (PCA; see Legendre & Legendre 1998, Jackson 2003). Initiated by Gower (1967), the link between PCA and the triangular diagram was further investigated by ter Braak (1983), who established that the result of a column-centred PCA is a geometrical generalisation of a ternary diagram. Note that, in the Euclidean geometrical framework of multivariate analysis (e.g. Gower 1967, Pontier et al. 1990), multivariate normality is not required for PCA, and the issue of estimating a population covariance matrix from a moderate size sample is irrelevant.

The very key plot from a PCA is an approximated biplot (or simply, a biplot), that is, a graphical display approximation of a matrix in a single plot by means of markers for both rows and columns (Gabriel 1971, Gower & Hand 1996, Gabriel 2006). In the context of diet composition analysis, the application of PCA involves the distance biplot (ter Braak 1983) established on column-centred matrix data (de Crespin de Billy et al. 2000). In the distance biplot, the data matrix centred by columns $P_0$ of rank $r \leq p$ is factorised as the product $AB^T$ into a $n \times r$ matrix A and a $p \times r$ matrix B, with A the matrix of the principal components (scaled to variances $\lambda_1, \ldots \lambda_k, \ldots \lambda_r$, with $\lambda_k$ the $k^{th}$ eigenvalue) and B the matrix of the eigenvectors of unit norm. In practice, the matrix $P_0$ is approximated in the least square sense using the first k dominant eigenvalues and eigenvectors, typically with $k = 2$. In terms of graphical display, the distance biplot is the plot of the row and column markers whose coordinates are in matrices A and B; row markers are points, and column markers are displayed as arrows from the origin. The distance biplot is said to be row isometric or row metric preserving (RMP), which means that Euclidean distances among rows in the biplot are approximations of their Euclidean distances in multidimensional space but the angles among column vectors are meaningless (Legendre & Legendre 1998, Gabriel 2006).



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### *Diet composition analysis*

We analysed diet composition by examining the first two principal components of PCA on distance biplots ($k = 2$). Specific interpretation rules arise from the compositional nature of the resource matrix (de Crespin de Billy et al. 2000). Each food category is linked to the rumen centroid, here the origin of the axes since $P_0$ was column-centred, by an arrow whose length is proportional to the overall abundance of this food category. Furthermore, the length of an arrow depends on the variation of the relative abundance of the corresponding food category among rumens. Consequently, dominant food categories are dispersed on the first factorial plane of PCA, whereas rare food categories are concentrated around the origin (de Crespin de Billy et al. 2000). Each rumen is at the centroid of the food categories, with each food category being given a weight equal to its proportion in the rumen (de Crespin de Billy et al. 2000). The higher the proportion of a given food category in a rumen, the closer the rumen is to the food category's position (i.e. the head of the arrow).

We first performed separate PCAs for red and roe deer on annual data. Then, after testing for seasonal variation in diet composition, we distinguished between winter and aggregated spring and summer/autumn data and performed PCAs first on the data set including both red and roe deer samples, then separately for each species. Computations were performed using the 'ade4' package for R (Chessel et al. 2004).

### *Effects of sampling season and species on diet composition*

We used between-class PCA (Dolédec & Chessel 1987, Chessel et al. 2004) to test the null hypotheses ($H_0$) of an absence of sampling season and species effects on diet composition. Testing for the effect of a descriptor on diet composition involves the ratio of the trace of the diagonalised matrix to the total variance as a test statistic (Kazi-Aoual et al. 1995), that is, the ratio of the sum of the eigenvalues of the between-class PCA to the sum of the eigenvalues of the classical PCA (inter-inertia to total-inertia ratio). Statistical significance was evaluated by using a randomisation test (see Edgington 1987, Manly 1997, Edgington 2006). In order to obtain accurate results, we estimated the P-value of the test statistic by randomising the rumens among descriptor states $10^6$ times, and the minimum attainable P-value is thus $P = 0.000001$. We do not rely on an arbitrary $\alpha$-level of statistical significance and strictly interpret P-value as the strength of the evidence against $H_0$, conditionally to the data at hand (Edgington 1987, Yoccoz 1991, Johnson 1999, Anderson et al. 2000).

We first tested for the absence of any sampling season effect on diet composition ($H_{0\ season}$) and removed one season at a time to check whether seasonal variation in diet was due to any particular season. Then, we tested for the absence of any species ($H_{0\ species}$) effect on diet composition for each season (i.e. winter and aggregated spring/summer/autumn). Computations were performed using the 'ade4' package for R (Chessel et al. 2004).

### *Diet diversity*

Diet composition is said to be diverse if all proportions of food categories are close to $1/p$, and is described as even if all proportions are equal to $1/p$ (Solow 2002). Diet diversity was measured by calculating Simpson's index of diversity ($S'_i$; Solow 2002) for each rumen as $S'_i = 1 - S_i$, with Simpson's index ($S_i$; Simpson 1949) as:

$$S_i = \sum_{j=1}^{p} p_{ij}^2.$$

$S_i$ can be interpreted as the probability that two items chosen from the rumen i, at random and independently, will be found to belong to the same food category. Thus, $S'_i$ lies between 0 when the composition is concentrated on only one food category (one probability equal to 1, the others equal to 0) and $1 - 1/p$ when the probabilities are all equal to $1/p$. It is worth noting that Simpson's index is closely related to the distance biplot we used to perform the diet composition analysis (see ter Braak 1983).

We studied variation in diet diversity using the ANOVA framework, with deer species and season as factors. We used the measure of unbalancedness for one-way design $\gamma = \tilde{n}/\bar{n} \leq 1$ where $\bar{n}$ and $\tilde{n}$ denote the arithmetic and harmonic means of the group sizes, respectively (Ahrens & Pincus 1981, Ahrens & Sanchez 2006). $\gamma = 1$ if the design is balanced; the closer $\gamma$ is to 0, the more unbalanced is the design. We found that all the one-way designs were only slightly unbalanced ($\gamma > 0.98$). Nevertheless, in agreement with Shaw & Mitchell-Olds (1993), when computing the two-way ANOVA with deer species and season as factors we used the so-called Type III



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sum of squares for performing the tests. We tested the null hypotheses of an absence of species ($H_{0\ species}$), sampling season ($H_{0\ season}$) or interaction ($H_{0\ species \times season}$) effects on diet diversity and used correlation ratio squared ($\eta^2$) for one-way ANOVA and partial $\eta^2$ for two-way ANOVA to assess the strength of the effects (Tabachnick & Fidell 2001:52). ANOVA computations were performed using the 'car' package for R (Fox 2002).

### *Diet similarity*

Similarity in diet composition between red and roe deer can be measured by a similarity coefficient for proportion data. One widely used similarity coefficient is the symmetric niche overlap coefficient (Pianka 1973). Let $\bar{p}_j = 1/n \sum_{i=1}^{n} p_{ij}$ the mean proportion of the $j^{th}$ food item for roe deer and $\bar{q}_j = 1/n \sum_{i=1}^{n} q_{ij}$ the mean proportion of the $j^{th}$ food item for red deer. The symmetric niche overlap coefficient (Pianka 1973) is:

$$\phi = \frac{\sum_{j=1}^{p} \bar{p}_j \bar{q}_j}{\sqrt{\sum_{j=1}^{p} \bar{p}_j^2 \sum_{j=1}^{p} \bar{q}_j^2}}.$$

Diet similarity lies between 0 (maximal dissimilarity) and 1 (maximal similarity).

We evaluated the statistical significance of the observed values of diet similarity by using a randomisation test. We considered zeros as sampling rather than structural zeros. Thus, according to the terminology of Lawlor (1980), the randomisation test we used was the RA3 randomisation algorithm (Winemiller & Pianka 1990). Computations were performed using EcoSim (Ellison 2000, Gotelli & Entsminger 2006) with 30,000 random permutations, which is the maximum allowed by the program, and the minimum attainable P-value is thus approximately P = 0.000033.

## Results

### Effects of sampling season and species on diet composition

After performing separate PCAs on red and roe deer annual data, we found evidence against the absence of any sampling season effect on diet composition ($H_{0\ season}$) for both species (ratio = 0.090, P = 0.000001 for red deer, and ratio = 0.050, P < 0.001 for roe deer). When we performed the randomisation test on data sets from which winter data were removed, there was no longer evidence against $H_{0\ season}$ (ratio = 0.020, P = 0.28 and ratio = 0.017, P = 0.23, respectively). When spring or summer/autumn data were removed, evidence against $H_{0\ season}$ remained for both species (ratio = 0.076, P = 0.000001 and ratio = 0.046, P < 0.001 without spring data; ratio = 0.072, P < 0.00001 and ratio = 0.033, P = 0.016 without summer/autumn data). Spring and summer/autumn data were therefore aggregated for further analyses.

Then, after winter and aggregated spring and summer/autumn data were distinguished and PCAs performed on the data set including both red and roe deer samples, we found strong evidence against the absence of any species effect on diet composition ($H_{0\ species}$) for both seasons (ratio = 0.178, P = 0.000001 for winter, and ratio = 0.280, P = 0.000001 in spring/summer/autumn).

### Diet composition

Annual diet was composed mainly of grasses, bramble and conifers in red deer, and bramble, silver fir and forbs in roe deer. These results are based on the examination of the first two principal components of PCA on distance biplots showing sim-

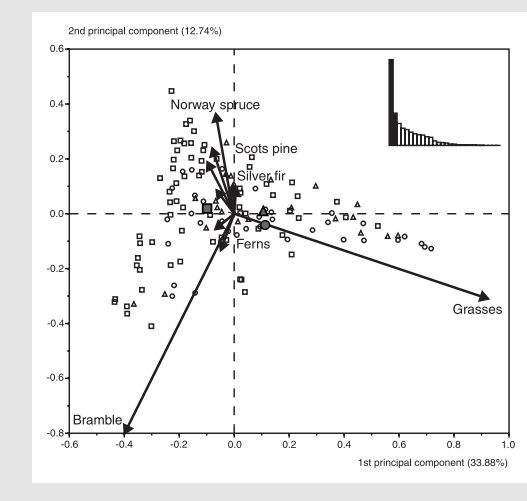



Figure 1. Column-centred PCA screeplot and distance biplot of individual red deer rumens (□, △, ○) and season's centroids (filled symbols: ■ = winter, ▲ = spring, ● = summer/autumn) on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.



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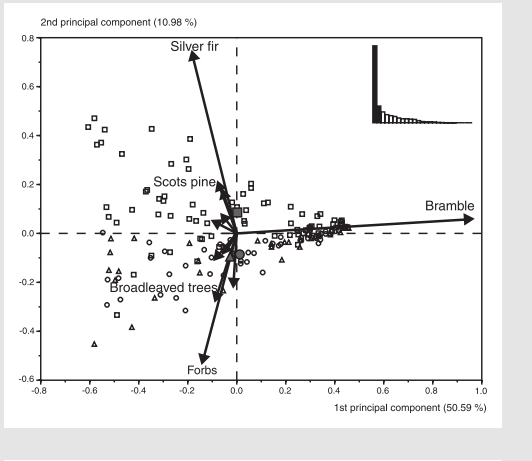



Figure 2. Column-centred PCA screeplot and distance biplot of individual roe deer rumens (□, △, ○) and season's centroids (filled symbols: ■ = winter, ▲ = spring, ● = summer/autumn) on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.

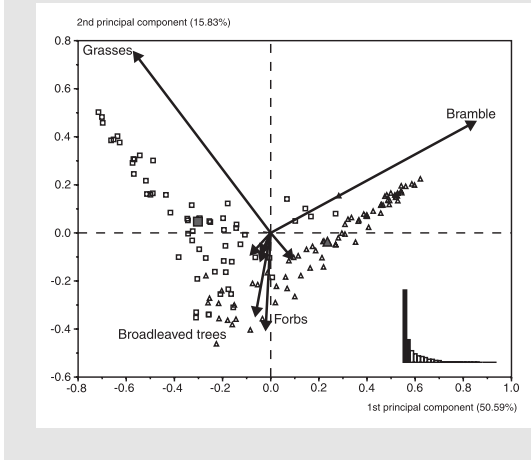



Figure 4. Column-centred PCA screeplot and distance biplot of individual red and roe deer rumens (□, △, ○) collected in spring and summer/autumn and species' centroids (filled symbols: ■ = red deer, ▲ = roe deer) on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.

ultaneously food categories, individual rumens and season's centroids (Figs. 1 & 2). For clarity, extremely minor food categories were not labelled. These biplots display seasonal variation in diet composition, with an opposition between the centroid of rumens collected in winter and centroids of rumens collected in other seasons.

Seasonal diet composition differed between red and roe deer, with grasses and bramble categories accounting for most of the interspecific segregation in winter and spring/summer/autumn (Figs. 3 & 4). Winter diet was composed mainly of grasses, bramble and conifers (Norway spruce, silver fir and Scots pine) in red deer (Fig. 5), and bramble,

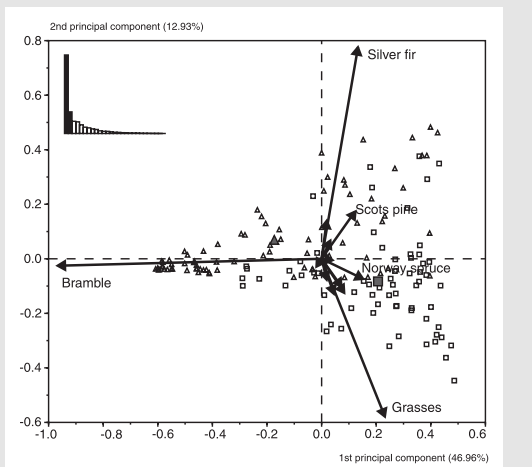



Figure 3. Column-centred PCA screeplot and distance biplot of individual red and roe deer rumens (□, △, ○) collected in winter and species' centroids (filled symbols: ■ = red deer, ▲ = roe deer) on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.

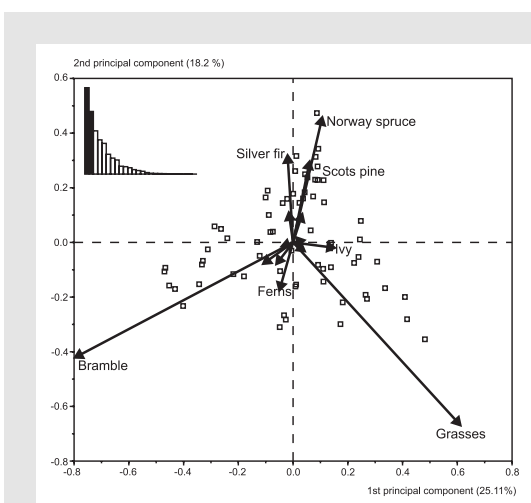



Figure 5. Column-centred PCA screeplot and distance biplot of individual red deer rumens collected in winter on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.



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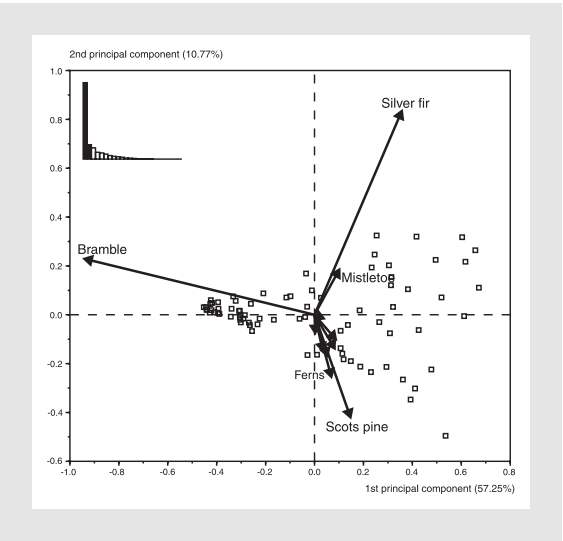



Figure 6. Column-centred PCA screeplot and distance biplot of individual roe deer rumens collected in winter on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.

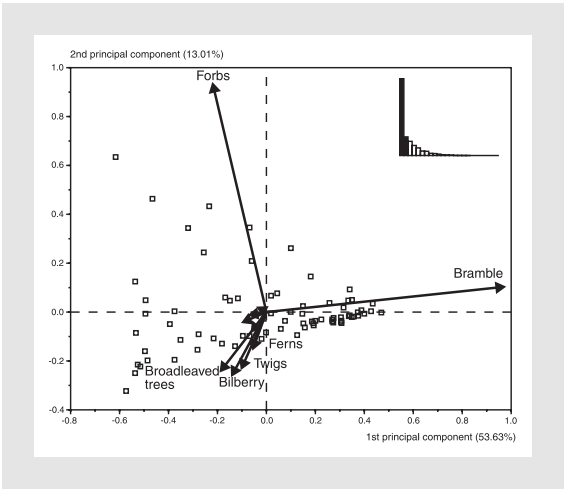



Figure 8. Column-centred PCA screeplot and distance biplot of individual roe deer rumens collected in spring and summer/autumn on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.

silver fir and Scots pine in roe deer (Fig. 6). During the rest of the year, the diet was composed mainly of grasses, leaves of broadleaved trees, bramble, twigs and forbs in red deer (Fig. 7), and bramble, forbs, leaves of broadleaved trees, bilberry, twigs and ferns in roe deer (Fig. 8).

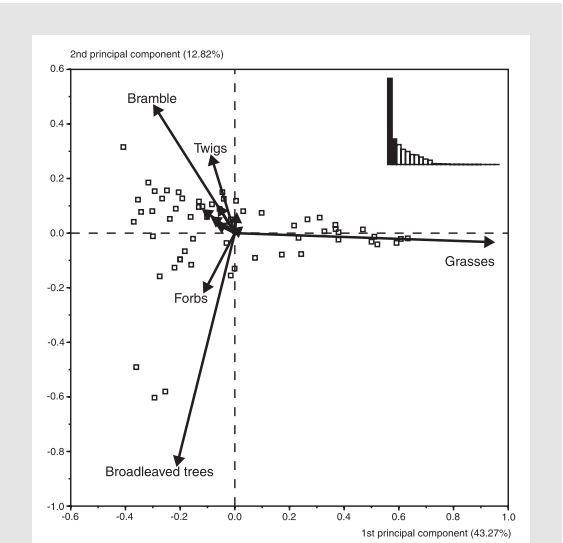



Figure 7. Column-centred PCA screeplot and distance biplot of individual red deer rumens collected in spring and summer/autumn on 1st factorial plane according to food categories (arrows), with the percentage of total variance accounted for by the first two principal components.

## Diet diversity

Simpson's index of diversity ($S'_i$) was 0.70 for red deer and 0.48 for roe deer in winter, and 0.62 for red deer and 0.51 for roe deer during the rest of the year. The ANOVA framework allowed us to test for the absence of species ($H_{0\ species}$), sampling season ($H_{0\ season}$) or interaction ($H_{0\ species \times season}$) effects on diet diversity. Analysis of associations between sampling season, species and diet diversity revealed no evidence against $H_{0\ season}$ ($P = 0.28$, partial $\eta^2 = 0.004$), strong evidence against $H_{0\ species}$ ($P < 0.000001$, partial $\eta^2 = 0.154$), and comparatively weak evidence against $H_{0\ species \times season}$ ($P = 0.017$, partial $\eta^2 = 0.020$). The interaction effect, which accounted for a significant but much smaller proportion of the variance in diet diversity than the species effect, was further investigated through within-season analyses of associations between species and diet diversity. This revealed that red deer had a more diverse diet than roe deer all year long, and that this species effect on diet diversity was more pronounced in winter ($P < 0.0001$, $\eta^2 = 0.36$) than during the rest of the year ($P = 0.002$, $\eta^2 = 0.07$).

## Diet similarity

Diet similarity was maximal in winter ($\phi \approx 0.70$ in winter and $\phi \approx 0.41$ for the rest of the year). Randomisation tests revealed that in winter the symmetric niche overlap coefficient was significantly higher than what would be expected by chance alone





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(P = 0.003). This was also true, but to a lesser extent, for the coefficient calculated for the rest of the year (P = 0.042). The category 'bramble' accounted for 81% of the symmetric niche overlap coefficient in winter and 67% during the rest of the year.

## Discussion

In temperate deciduous forests, seasonal variation in the quantity and quality of available food resources (Dzieciolowski 1969, Bobek 1977) is likely to represent a strong determinant of ungulate diet composition and affect resource partitioning among species. In roe deer, Cornelis et al. (1999) showed that variation in diet composition relates more to the research method and location than to season, and they therefore suggest that in order to study seasonal variation in diet composition, one should use the same research method and the same location, including the same habitat. This is equally true if one wants to contrast diet composition and its seasonal variability among sympatric species. Theses conditions were met in our study and our analyses drew a clear distinction in diet composition between winter (1 November-15 April) and the rest of the year for both red and roe deer.

Analysis of diet composition confirms the predictions based on differences in body size and morpho-physiological type between red and roe deer, and results conform to what is known from reviews of the diets of these species across Europe (Tixier & Duncan 1996, Cornelis et al. 1999, Gebert & Verheyden-Tixier 2001). Red and roe deer have distinct diets in all seasons, with most of the segregation in diet composition resulting from red deer having a grasses-based diet and roe deer having a bramble-based diet (see Figs. 3 & 4). This confirms that red deer tend to consume forage richer in fibre than do roe deer, as grasses have higher fibre content than bramble (Gonzalez-Hernandez & Silva-Pando 1999). In spring, summer and autumn, red deer had a mixed diet of slowly digestible grasses and the less fibrous bramble and leaves of broadleaved trees, along with substantial proportions of twigs and forbs (see Fig. 7). In winter, they supplemented their diet of grasses and bramble with Norway spruce, silver fir and Scots pine (see Fig. 5). This agrees with their intermediate feeder type (Hofmann 1989): opportunistic foragers having a mixed diet of grasses and roughage and concentrate food items. Roe deer had a diet composed of forbs, bramble and the more fibrous leaves of broadleaved trees, bilberry, twigs and ferns in spring, summer and autumn (see Fig. 8). In winter, they supplemented their diet of bramble with silver fir and Scots pine (see Fig. 6). This agrees with roe deer being selective feeders able to switch diets between seasons (Tixier & Duncan 1996). Red and roe deer diets as documented here share characteristics of diets that have been described as typical of either broadleaved or conifer forests in reviews by Gebert & Verheyden-Tixier (2001) and Tixier & Duncan (1996). In our mixed broadleaved-conifer forest, deer consume leaves of broadleaved trees in spring, summer and autumn, conifers in winter, and bramble all year long. Additionally, red deer consume grasses all year long and roe deer consume forbs in spring, summer and autumn.

Red and roe deer winter diets contained substantial proportions of conifers, a food resource that is widely available in winter but is rich in fibre (Raven & al. 1992) and relatively unpalatable to both species (Hosey 1981, Dumont et al. 2005). This supports the optimal foraging-related hypothesis that deer are less selective and consume more fibrous forage in winter, when forage abundance and quality are at their lowest.

Throughout the year, and especially in winter, red deer had a more diverse diet than roe deer. This, along with the fact that red deer used all food items eaten by roe deer, whereas grasses were virtually absent from roe deer diet, supports the hypothesis that browsers are 'obligatory non-grazers' and avoid grasses to a higher degree than grazers avoid browse (van Wieren 1996, Clauss & Lechner-Doll 2001, Clauss et al. 2003).

Several studies produced data on red and roe deer diet similarity. Schröder & Schröder (1984) used rumen contents samples collected in summer to calculate Schoener's (1970) index of overlap and suggested that its low value (0.25) was the result of differential habitat use by red and roe deer. Putman (1996) used roe deer rumen contents samples and feeding observations made on red deer to calculate Pianka's (1973) index of overlap in the four seasons (0.47, 0.42, 0.39 and 0.32 for winter, spring, summer and autumn, respectively). These values decreased sharply (to 0.12, 0.01, 0.03 and 0.07, respectively) after he took habitat use into account and calculated multidimensional overlap by combining food and habitat niche overlap indices. Latham et al. (1999) used rumen contents samples to calculate Schoener's (1970) index of overlap in five study sites in



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summer (range: 0.18-0.43) and winter (range: 0.51-0.65) and suggested that, whereas much of the winter overlap was for widespread heath species, higher values of overlap in winter when food is limited may indicate the existence of competition. Mysterud (2000) used data from allopatric populations to calculate Schoener's (1970) index of overlap in summer (0.20). All these results are difficult to compare or interpret across studies, either because different indices of diet similarity were used or because of differences in the definition of food categories (Abrams 1980). In our study, comparisons with values from null models proved useful in revealing that similarity coefficients were higher than what would be expected by chance alone, especially in winter. Yet, a high similarity in food resource use can be evidence either for or against the existence of exploitative competition (Colwell & Futuyma 1971, Sale 1974, Abrams 1980), depending on available resources being, or not being, in short supply (de Boer & Prins 1990, Putman 1996). Here, the most informative result about diet similarity is the fact that it was highest during times of low resource availability, namely in winter. Under Schoener's (1982) hypothesis, species competing for limited resources should demonstrate a lower similarity of resource use during times of low resource availability, and Smith et al. (1978) and Gordon & Illius (1989) suggested that a higher similarity of the diets of sympatric species when resources are scarce is likely to occur only if those resources are not in short supply. This is probably the case in our study area, a production forest where populations of red and roe deer are regulated through hunting and are maintained at densities sufficiently low to avoid major damage to forest regeneration. Even though the variety and the quality of plants available to red and roe deer decrease in winter, abundance of food resources, especially grasses, conifers and bramble, is likely to be sufficient to sustain both populations.

One of the main problems facing forest managers in the Vosges mountain range concerns the natural regeneration of commercial tree species, particularly silver fir. Silver fir saplings often suffer from competition with Norway spruce, and selective browsing by deer in winter may worsen this situation (Ammer 1996, Heuzé et al. 2005a,b). Our results showed that in winter red deer diet contained about equal proportions of spruce and fir, and roe deer diet contained much fir but only a very small proportion of spruce. This suggests that when browsing in regeneration patches where both fir and spruce occur, roe deer might be more selective towards fir and therefore more inclined to hamper fir regeneration than red deer. In our study area, bramble most probably plays a key role in relieving regeneration of commercial trees of the browsing pressure by red and roe deer, as it constitutes a substantial proportion of the diets of both species all year long and accounts for 81% of the symmetric niche overlap coefficient in winter. However, bramble availability is likely to vary from year to year (Storms et al. 2006), and browsing pressure will therefore depend on annual variations in the availability of such a key alternate food resource. Other factors, such as the type of silvicultural system (Reimoser & Gossow 1996, Partl et al. 2002, Reimoser 2003) or the presence of other herbivores such as mountain hares *Lepus timidus* (Hulbert & Andersen 2001), may also influence the impact of deer browsing on forest regeneration.

Reviews of studies of red and roe deer feeding habits (Tixier & Duncan 1996, Cornelis et al. 1999, Gebert & Verheyden-Tixier 2001) revealed that diet composition is mainly explained by the habitat in which they forage, implying that food availability in selected habitat is a key determinant of the diet (Duncan et al. 1998). Conclusions about diet composition drawn in a particular study area will therefore rarely be relevant to other areas, and interspecific comparisons of diets are likely to be biased if use of food resources is not measured in the same study site for all species. While single-species diet descriptions may appear overabundant in the literature (O'Connor 2000), studies of feeding habits of sympatric herbivores are still rare, and we underline the importance of such studies in answering applied ecological questions at the local scale, such as how sympatric species share available resources, what impact their coexistence may have on the vegetation, and in which conditions these impacts are the most susceptible to hamper forest management.

In our comparative nutritional ecology study, we used the method of the distance biplot of column-centred PCA (%PCA, *sensu* de Crespin de Billy et al. 2000), identified earlier in ecology by Green (1979) as particularly effective for compositional data analysis. We believe that this method is too rarely used for analysing resource matrices, despite its appropriateness to such analyses (see Dolédec 1986, Baubet 1998, de Crespin de Billy et al. 2000, Pontier et al. 2002 for applications of %PCA to resource



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matrices). Resource matrices are common end products of long-term field data gathering on the feeding habits of animals, but their analysis is made difficult by the multivariate and compositional nature of the data. We believe that the %PCA technique is well suited for the analysis of resource matrices, produces results that are easy to interpret, and could therefore benefit many researchers and managers in making hard-won data profitable.

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Software availability - the R system for statistical computing and its packages are available at http://cran.r-project.org, and the 'ade4' and 'car' packages for R are available at http://pbil.univ-lyon1.fr/ADE-4 and http://socserv.socsci.mcmaster.ca/jfox, respectively.

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Appendix I. Mean percentage of each food category in rumen samples (%quant) and percentage of the samples in which it was found (%occur), for red deer and roe deer in winter and during the rest of the year (spring/summer/autumn), with the number of samples in each season × species combination (N).

| | Red deer | | | | Roe deer | | | |
|---|---|---|---|---|---|---|---|---|
| | Winter | | Rest of year | | Winter | | Rest of year | |
| | %quant | %occur | %quant | %occur | %quant | %occur | %quant | %occur |
| Grasses (Herbaceous monocots) | 18.64 | 92.54 | 37.12 | 98.33 | 0.63 | 45.00 | 1.75 | 59.74 |
| Sedges *Carex* sp. | 0.14 | 7.46 | 0.01 | 1.67 | 0.00 | 0.00 | 0.11 | 1.30 |
| Forbs (Herbaceous dicots) | 0.18 | 22.39 | 6.21 | 63.33 | 2.87 | 42.5 | 9.66 | 80.52 |
| Heather *Calluna vulgaris* | 1.99 | 28.36 | 0.22 | 15.00 | 0.62 | 7.50 | 0.57 | 9.09 |
| Honeysuckle *Lonicera periclymenum* | 0.00 | 0.00 | 0.08 | 10.00 | 0.02 | 3.75 | 0.00 | 1.30 |
| Broom *Cytisus scoparius* | 0.39 | 13.43 | 0.85 | 28.33 | 0.01 | 2.50 | 0.36 | 18.18 |
| Bilberry *Vaccinium myrtillus* | 1.77 | 26.87 | 2.01 | 35.00 | 1.83 | 25.00 | 3.04 | 20.78 |
| Mistletoe *Viscum album* | 0.05 | 7.46 | 0.00 | 0.00 | 3.31 | 27.50 | 0.14 | 7.79 |
| Ivy *Hedera helix* | 0.03 | 4.48 | 0.07 | 8.33 | 0.90 | 11.25 | 0.17 | 10.39 |
| Bramble *Rubus* sp. | 19.57 | 95.52 | 12.38 | 85.00 | 54.42 | 98.75 | 52.79 | 96.10 |
| Broadleaved trees | 0.12 | 16.42 | 9.5 | 78.33 | 1.05 | 25.00 | 7.42 | 89.61 |
| Buds | 0.42 | 25.37 | 0.27 | 25.00 | 0.11 | 12.50 | 0.57 | 16.88 |
| Twigs | 8.76 | 89.55 | 10.84 | 86.67 | 4.53 | 70.00 | 6.37 | 84.42 |
| Bark | 0.62 | 28.36 | 0.78 | 25.00 | 0.05 | 3.75 | 0.12 | 1.30 |
| Norway spruce *Picea abies* | 8.82 | 76.12 | 2.98 | 35.00 | 2.10 | 38.75 | 0.25 | 10.39 |
| Scots pine *Pinus sylvestris* | 7.02 | 67.16 | 0.54 | 21.67 | 4.63 | 30.00 | 0.04 | 3.90 |
| Weymouth pine *Pinus strobus* | 0.39 | 7.46 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Silver fir *Abies alba* | 7.22 | 76.12 | 0.18 | 11.67 | 12.75 | 80.00 | 0.29 | 18.18 |
| Douglas fir *Pseudotsuga menziesii* | 0.59 | 17.91 | 0.00 | 0.00 | 0.02 | 3.75 | 0.16 | 1.30 |
| European larch *Larix decidua* | 0.00 | 0.00 | 0.01 | 1.67 | 0.00 | 0.00 | 0.00 | 0.00 |
| Unidentified conifer needles | 1.79 | 47.76 | 0.31 | 21.67 | 0.73 | 22.5 | 0.24 | 10.39 |
| Dead leaves | 3.31 | 52.24 | 2.87 | 58.33 | 0.57 | 25.00 | 1.25 | 45.45 |
| Ferns | 7.42 | 91.04 | 6.19 | 73.33 | 5.83 | 82.50 | 3.15 | 67.53 |
| Roots & bulbs | 4.69 | 40.30 | 0.04 | 8.33 | 0.01 | 3.75 | 0.02 | 3.90 |
| Pulpy fruits | 0.46 | 11.94 | 1.43 | 18.33 | 0.88 | 21.25 | 7.78 | 64.94 |
| Dry fruits | 3.08 | 19.40 | 4.36 | 36.67 | 1.31 | 10.00 | 1.90 | 10.39 |
| Agricultural crops | 1.21 | 8.96 | 0.13 | 3.33 | 0.00 | 0.00 | 0.00 | 0.00 |
| Mushrooms | 0.75 | 5.97 | 0.37 | 8.33 | 0.75 | 25.00 | 1.77 | 24.68 |
| Others | 0.58 | 22.39 | 0.27 | 5.00 | 0.07 | 12.50 | 0.06 | 9.09 |
| N (Fawns, ♀, ♂) | 67 (32, 21, 14) | | 60 (7, 23, 30) | | 80 (25, 53, 2) | | 77 (9, 27, 41) | |



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