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# Estimation of the chemical composition of black grouse *Tetrao tetrix* diets in the eastern Italian Alps

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In a study area situated in the eastern Italian Alps, samples of the main ingredients in the diet of male black grouse were collected nine times between September 1993 and December 1994 and analysed for crude protein (CP) content and cell wall components (NDF, ADF, ADL). The mean monthly chemical composition of the diet was calculated on the basis of the percentage of dry matter (DM) weight of the main ingredients in the crop or gizzard, estimated in a previous experiment with 100 male birds shot in the same region in the periods April-June and September-December. Dietary CP reached its maximum value in spring (17.4 and 14.5% DM in May and June respectively), and its minimum in autumn (8.4% DM). Non-protein cellular solubles (NPS) were particularly high (66.7% DM) in September. The NDF content was highest in May (52.5% DM) and lowest in autumn, when it increased linearly from September (24.7% DM) to November (35.3% DM). The variability of the diets could be described by two principal factors, the first of which was correlated with the level of fibrous constituents and the second with the protein level and an ingredient diversity index (DI). In the plane defined by these two factors, five different types of diets were identified by cluster analysis; one diet distributed over all months was associated with two 'spring' and two 'autumn' diets. The first, 'basal' diet had intermediate chemical characteristics (CP 10.2% DM; NDF 37.1% DM) and a relatively high DI (3.3). The two spring diets had very high (CP 18.1% DM; NDF 64.7% DM) or high (CP 11.9% DM; NDF 46.7% DM) protein and fibre levels, due to the selection of beech *Fagus sylvatica* buds or bilberry *Vaccinium myrtillus* or larch *Larix decidua* shoots and needles. The two autumn diets had a high concentration of NPS (70.5% DM and 61.2% DM) due to the presence of fruits, particularly from bilberry and cowberry *Vaccinium vitis-idaea*; they differed in their DI (2.6 vs 3.5) and the partial substitution of bilberries by bilberry shoots and *Rhododendron* spp. buds and leaves in the second diet.

*Key words: black grouse, chemical composition, diet, eastern Italian Alps, Tetrao tetrix*

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The black grouse *Tetrao tetrix* L. is distributed throughout the alpine region in the Italian Alps between 1,400 and 2,200 m a.s.l. (de Franceschi 1994). Most of the research on the diet of this species has been conducted in environments which differ from those on the Italian side of the Alps. The integration of knowledge of the diet composition with the chemical content is necessary to understand the feeding ecology and the nutrient requirements of this species. Crop and gizzard contents have been used to estimate the diet composition of black grouse (Ponce 1987) and chemical composition of other galliform diets (Moss 1972, Gasaway 1976, Servello & Kirkpatrick 1987).

In a study carried out in the Central Carnian Alps (de Franceschi 1978, 1981) the diet composition of male black grouse was estimated by analysing the contents of 100 crops and gizzards of birds shot during the hunting seasons in 1969-1976 (Table 1). The chemical composition of the main plant species reported in the study of de Franceschi (1978, 1981) was determined in spring and autumn to estimate the chemical contents and ingredient diversity in the diet of black grouse in the alpine environment, in particular during the breeding and the moulting periods. To obtain this objective, chemical analyses were performed on hand-clipped dietary ingredients to allow a more accurate evaluation of the soluble components of the diet, which disappear rapidly from the gizzard and are quickly digested (Jayne-Williams & Fuller 1971).

## Material and methods

The study area was located in the Central Carnian region, in the eastern Italian Alps, at an altitude of 1,400-1,800 m a.s.l.. It included woodland dominated by beech *Fagus sylvatica* interspersed with Norway spruce *Picea abies* up to 1,500 m a.s.l. and open mixed conifer woods composed of spruce and larch *Larix decidua* at higher altitudes. Above 1,700 m green alder *Alnus viridis*, *Vaccinium* spp., rubigenous rhododendron *Rhododendron ferrugineum*, heather *Calluna vulgaris* and common juniper *Juniperus communis* dominate.

Along a 3,000 m transect, leaves, buds, shoots, twigs, catkins, berries, fruits and seeds of 10 species,

Table 1. Mean abundance (%DM) of the main ingredients of black grouse diets in the central Carnian Alps (de Franceschi, 1978, 1981).

| | Apr. | May | Jun. | Sep. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|
| Number of birds | 7 | 10 | 5 | 21 | 35 | 18 | 4 |
| Ingredients | | | | | | | |
| Buds, leaves, twigs and shoots | | | | | | | |
| *Vaccinium myrtillus* (*) | 17.5 | 10.2 | 23.2 | 8.4 | 18.8 | 17.4 | 23.3 |
| *V. vitis-idaea* (*) | 0.0 | 0.0 | 0.0 | 0.2 | 1.1 | 0.5 | 0.0 |
| *Rhododendron* spp. (*) | 12.4 | 7.1 | 6.7 | 3.7 | 5.1 | 13.4 | 33.1 |
| *Calluna vulgaris* (*) | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 | 5.6 | 0.0 |
| *Juniperus communis* (*) | 0.0 | 0.0 | 0.0 | 0.5 | 1.3 | 0.1 | 0.0 |
| *Alnus viridis*[1] (*) | 24.6 | 5.0 | 0.0 | 0.0 | 4.1 | 8.8 | 7.4 |
| *Larix decidua* (*) | 2.6 | 12.6 | 27.7 | 1.3 | 0.8 | 1.5 | 0.0 |
| *Fagus sylvatica* (*) | 0.1 | 20.2 | 6.3 | 0.0 | 0.0 | 0.0 | 17.6 |
| *Sorbus* spp. (*) | 0.2 | 0.0 | 10.8 | 0.0 | 0.0 | 3.1 | 0.0 |
| *Salix* spp. | 0.0 | 0.0 | 3.1 | 0.0 | 0.2 | 0.0 | 0.0 |
| *Picea* spp. | 12.1 | 2.7 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 |
| *Pinus mugo* | 7.9 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Other | 3.1 | 9.7 | 2.4 | 16.3 | 16.3 | 5.8 | 5.0 |
| Flowers and catkins | | | | | | | |
| *Salix* spp. | 0.0 | 6.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pinus mugo* | 0.0 | 9.1 | 17.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Other | 7.1 | 8.7 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| Fruits and seeds | | | | | | | |
| *V. myrtillus* (*) | 0.0 | 0.0 | 0.0 | 42.4 | 25.2 | 4.3 | 0.0 |
| *V. vitis-idaea* (*) | 0.0 | 0.0 | 0.0 | 5.9 | 7.4 | 11.8 | 9.6 |
| *R. ferrugineum* (*) | 0.0 | 0.0 | 0.0 | 0.4 | 0.6 | 4.8 | 0.0 |
| *Sorbus* spp (*) | 7.1 | 0.0 | 0.0 | 1.4 | 8.1 | 14.2 | 4.0 |
| *Robus* spp. | 0.0 | 0.0 | 0.0 | 6.0 | 1.7 | 0.0 | 0.0 |
| *Rosa* spp. | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.4 | 0.0 |
| Other | 5.3 | 0.8 | 0.0 | 2.5 | 4.0 | 4.4 | 0.0 |
| Arthropods | 0.0 | 6.8 | 1.8 | 11.0 | 4.1 | 0.0 | 0.0 |

(*) Ingredient hand-clipped and chemically analysed
[1] Buds and catkins

Table 2. Chemical composition of the main ingredients of black grouse diets.

| Ingredient | | Apr. | May | Jun. | Sep.* | Oct. | Nov.* | Dec. |
|---|---|---|---|---|---|---|---|---|
| **Buds, leaves, twigs and shoots** | | | | | | | | |
| *V. myrtillus* | CP | 9.2 | 13.1 | 15.7 | 11.2 | 10.3 | 7.8 | 9.5 |
| | NDF | 44.7 | 51.2 | 47.9 | 38.2 | 43.8 | 44.3 | 42.2 |
| | ADF | 43.0 | 45.9 | 38.7 | 30.0 | 40.1 | 42.9 | 40.7 |
| | ADL | 24.9 | 30.5 | 26.6 | 14.2 | 23.5 | 25.9 | 23.5 |
| *V. vitis-idaea* | CP | | | 14.2 | 7.0 | 7.1 | 7.6 | 7.0 |
| | NDF | | | 38.0 | 42.3 | 42.1 | 40.6 | 41.7 |
| | ADF | | | 28.9 | 38.0 | 34.0 | 37.9 | 33.5 |
| | ADL | | | 22.9 | 25.7 | 18.4 | 23.5 | 20.9 |
| *R. ferrugineum* | CP | 9.7 | 10.4 | 10.2 | 10.1 | 10.2 | 9.8 | 9.1 |
| | NDF | 34.6 | 45.6 | 46.7 | 36.0 | 36.4 | 33.9 | 31.8 |
| | ADF | 32.8 | 37.6 | 39.2 | 29.8 | 34.2 | 33.1 | 31.1 |
| | ADL | 20.6 | 28.2 | 27.0 | 17.2 | 22.9 | 23.7 | 22.6 |
| *R. hirsutum* | CP | 10.2 | | 11.5 | 11.2 | 11.2 | 10.2 | 9.5 |
| | NDF | 39.5 | | 48.5 | 44.8 | 36.7 | 36.2 | 32.8 |
| | ADF | 38.5 | | 40.4 | 38.6 | 34.6 | 36.0 | 31.2 |
| | ADL | 25.2 | | 27.5 | 24.2 | 23.4 | 23.1 | 19.0 |
| *C. vulgaris* | CP | 9.4 | | 11.0 | 9.3 | 8.2 | 7.7 | 8.0 |
| | NDF | 52.7 | | 48.0 | 47.2 | 41.6 | 43.9 | 37.5 |
| | ADF | 42.8 | | 40.1 | 33.9 | 34.0 | 36.8 | 28.2 |
| | ADL | 26.6 | | 25.6 | 20.0 | 19.0 | 21.8 | 15.4 |
| *J. communis* | CP | 8.1 | 7.9 | 10.9 | 9.8 | 9.5 | 8.3 | 8.0 |
| | NDF | 32.3 | 38.6 | 29.2 | 42.0 | 31.5 | 32.6 | 31.9 |
| | ADF | 29.4 | 37.4 | 24.6 | 36.6 | 28.9 | 30.7 | 30.1 |
| | ADL | 13.6 | 21.6 | 12.3 | 16.8 | 11.6 | 12.9 | 13.9 |
| *A. viridis* | CP | 11.9 | 15.9 | 16.1 | 12.6 | 11.0 | 10.1 | 11.6 |
| | NDF | 25.6 | 27.6 | 23.9 | 35.1 | 34.6 | 32.5 | 28.5 |
| | ADF | 21.5 | 25.2 | 18.5 | 26.2 | 32.4 | 31.3 | 28.2 |
| | ADL | 13.9 | 16.4 | 10.0 | 15.1 | 19.1 | 19.4 | 17.3 |
| *L. decidua* | CP | 9.8 | 15.4 | 14.5 | 11.7 | 8.3 | 8.6 | 8.5 |
| | NDF | 44.4 | 45.1 | 35.6 | 43.9 | 43.7 | 49.4 | 51.2 |
| | ADF | 37.1 | 38.0 | 28.4 | 39.7 | 42.0 | 46.8 | 46.6 |
| | ADL | 26.0 | 22.4 | 16.3 | 22.0 | 24.3 | 27.8 | 29.0 |
| *F. sylvatica* | CP | 12.5 | 23.9 | | | 9.8 | 8.7 | 9.3 |
| | NDF | 66.3 | 65.2 | | | 72.0 | 73.6 | 68.2 |
| | ADF | 52.6 | 48.4 | | | 59.4 | 58.9 | 48.8 |
| | ADL | 18.3 | 20.9 | | | 19.9 | 17.9 | 11.8 |
| *Sorbus* spp. | CP | | | 18.1 | | | | |
| | NDF | | | 35.9 | | | | |
| | ADF | | | 32.4 | | | | |
| | ADL | | | 22.4 | | | | |
| **Flowers and catkins** | | | | | | | | |
| *A. viridis* | CP | | | | 15.0 | 13.1 | 12.5 | 11.9 |
| | NDF | | | | 37.5 | 30.7 | 30.2 | 32.1 |
| | ADF | | | | 31.6 | 24.5 | 24.9 | 26.0 |
| | ADL | | | | 14.9 | 11.9 | 13.3 | 14.5 |
| **Fruits and seeds** | | | | | | | | |
| *V. myrtillus* | CP | | | | 8.0 | 8.8 | | |
| | NDF | | | | 17.9 | 22.2 | | |
| | ADF | | | | 14.6 | 20.4 | | |
| | ADL | | | | 5.8 | 10.2 | | |
| *V. vitis-idaea* | CP | | | | 6.2 | 4.6 | 4.7 | |
| | NDF | | | | 19.9 | 13.1 | 13.0 | |
| | ADF | | | | 15.2 | 11.9 | 12.3 | |
| | ADL | | | | 7.6 | 7.8 | 6.9 | |
| *R. ferrugineum* | CP | | | | 12.4 | 11.1 | 7.3 | 10.7 |
| | NDF | | | | 66.2 | 74.6 | 77.8 | 75.2 |
| | ADF | | | | 56.7 | 67.3 | 69.2 | 68.7 |
| | ADL | | | | 31.3 | 34.2 | 35.8 | 33.5 |
| *Sorbus* spp. | CP | | | | 9.3 | 6.7 | | |
| | NDF | | | | 30.7 | 29.2 | | |
| | ADF | | | | 25.6 | 21.8 | | |
| | ADL | | | | 12.2 | 17.8 | | |

* Mean of two samples collected in 1993 and 1994.

found to be the main ingredients of black grouse diet (see Table 1) in the Central Carnian Alps (de Franceschi 1978, 1981) were sampled. The plant species sampled were: cowberry *Vaccinium vitis-idae* and bilberry *V. myrtillus*, rubigenous rhododendron and hirsute rhododendron *R. hirsutum*, rowan *Sorbus chamaemespilus*, whitebeam *Sorbus aria*, heather, common juniper, beech, larch and green alder. Samples were hand-clipped nine times from September 1993 to December 1994 (Table 2) to simulate the browsing of black grouse; the green parts, fruits, flowers and catkins were sampled randomly from different plants. The green parts of ericaceus plants, larch and common juniper were obtained as the outermost two cm of shoots, twigs, buds and stems.

Each sample was oven-dried at 60-65°C, milled (1 mm), and analysed for the content of: crude protein (CP, N*6.25, Kjeldahl procedure, AOAC 1990), neutral detergent fibre (NDF) acid detergent fibre (ADF) and acid detergent lignin (ADL, Goering & van Soest 1970). Other chemical components were calculated as follows: hemicellulose, HEM = NDF-ADF; cellulose, CEL = ADF-ADL; neutral detergent solubles, NDS = 100-NDF(%); non-protein cellular solubles, NPS = NDS-N*6.25.

For each plant component, the percent dry matter (DM) content of each crop and gizzard examined in the study of de Franceschi (1978, 1981) was multiplied by the chemical content corresponding to the month in which the gut tract samples were obtained. The contributions from the different plant components were thus summed to calculate the chemical composition of the DM in each gut tract.

Monthly data were grouped into the following three seasons, identified on the basis of the average climate: spring including samples from May and June, autumn from September to November, and winter from December to April.

The chemical components (CP, NDF, ADF, ADL, HEM, CEL, NPS) and the Shannon-Waimer ingredient diversity index (DI) (Ricklefs 1979) of the crops and gizzards were submitted to the following statistical procedures:

1) Analysis of variance (PROC GLM, SAS 1988) to study the effect of the $i^{th}$ gut tract (G), the effect of the $j^{th}$ season (S), the effect of $k^{th}$ month (M) within the season, and the interaction between gut tract and season ($GS_{ij}$) using the following model:

$$Y_{ijkl} = m + G_i + S_j + GS_{ij} + M(S)_k + e_{ijkl}.$$

2) Factor analysis (PROC FACTOR, rotate = promax, SAS 1988) to select factors for explaining the interrelationships among the chemical components and DI.
3) Cluster analysis (PROC CLUSTER, method = average, SAS 1988) for grouping the gut tract contents into different groups of homogeneous chemical composition and DI, each of which was assumed to correspond to a different type of diet selected by the black grouse.

## Results

Chemical analysis was performed on the plant components identified in the crops and gizzards examined in the original study of de Franceschi (1978, 1981). These chemically analysed dietary ingredients contributed an average of 55% in May to 85% in December (see Table 1) of the total DM.

The food items with the highest level of CP were beech buds in May (23.9% DM), green alder buds (16.1% DM) and shoots and leaves of bilberry (15.7% DM) in June, and young needles of larch in May (15.4% DM) (Table 2). The level of CP fell in the autumn for all ingredients, apart from the leaves and buds of *Rhododendron* spp., which had a constant level throughout the year. In autumn, the berries of *Vaccinium* spp., especially cowberry, and the fruits of *Sorbus* spp. had the lowest CP level (4.6-8.8% DM). The rubigenous rhododendron seeds (77.8% DM) and beech buds (73.6% DM) in November had the highest content of NDF whereas bilberries (17.9% DM in September) and cowberries (13.0% DM in November) had the lowest. The ingredients with the highest level of ADL were seeds of *Rhododendron* spp. (35.8% DM in November) and bilberry shoots in May (30.5% DM), whereas bilberries in September had the lowest ADL (5.8% DM).

The estimation of the chemical composition of the diet was not dependent on the type of digestive tract considered (crop vs gizzard, Table 3). Dietary CP was highest in spring (15.9% DM), and lowest in autumn (8.4% DM). The NPS reached a particularly high level (66.7% DM) in September.

The effect of season on cell wall constituents was not significant, probably due to the high month-within-season variability. The NDF content was highest in May (52.5% DM) and lowest in autumn, when it increased linearly from September (24.7% DM) to November (35.3% DM). The annual trend of the

Table 3. Mean chemical composition (% DM) and ingredient diversity index (DI) of black grouse diets. Means in the same column with different superscripts differ within the season ($P < 0.05$)

| | No | CP | NPS | NDF | ADF | ADL | HEM | CEL | DI |
|---|---|---|---|---|---|---|---|---|---|
| Crop | 82 | 9.6 | 56.7 | 33.6 | 29.4 | 16.8 | 4.2 | 12.6 | 2.9 |
| Gizzard | 18 | 10.8 | 54.9 | 34.4 | 29.7 | 17.1 | 4.5 | 12.7 | 3.1 |
| May | 10 | 17.4$^{a}$ | 30.1$^{b}$ | 52.5$^{a}$ | 42.6 | 24.0 | 9.9$^{a}$ | 18.6$^{a}$ | 2.4 |
| June | 5 | 14.5$^{b}$ | 41.7$^{a}$ | 43.8$^{b}$ | 35.5 | 23.4 | 8.3$^{b}$ | 12.1$^{b}$ | 2.6 |
| Spring | 15 | 15.9 | 35.9 | 48.2 | 39.1 | 23.7 | 9.1 | 15.4 | 2.5 |
| September | 21 | 8.7 | 66.7$^{a}$ | 24.7$^{a}$ | 20.1$^{c}$ | 9.2$^{c}$ | 4.6$^{a}$ | 10.9 | 2.4$^{b}$ |
| October | 35 | 8.7 | 61.1$^{b}$ | 30.2$^{b}$ | 27.2$^{b}$ | 15.9$^{b}$ | 3.0$^{b}$ | 11.3 | 3.3$^{a}$ |
| November | 18 | 7.8 | 57.0$^{b}$ | 35.3$^{c}$ | 33.0$^{a}$ | 20.2$^{a}$ | 2.2$^{b}$ | 12.8 | 3.3$^{a}$ |
| Autumn | 74 | 8.4 | 61.6 | 30.1 | 26.8 | 15.1 | 3.3 | 11.7 | 3.0 |
| December | 4 | 9.5 | 46.9 | 43.6 | 38.0 | 19.8 | 5.6 | 18.3 | 2.6 |
| April | 7 | 10.5 | 54.2 | 35.3 | 31.9 | 19.9 | 3.5 | 11.9 | 3.6 |
| Winter | 11 | 10.0 | 50.6 | 39.5 | 35.0 | 19.9 | 4.6 | 15.1 | 3.1 |
| Significance of the effect: | | | | | | | | | |
| Gut tract | | 0.5914 | 0.6055 | 0.6614 | 0.8589 | 0.9912 | 0.3199 | 0.6574 | 0.3485 |
| Season | | 0.0271 | 0.1101 | 0.2241 | 0.4428 | 0.4652 | 0.1483 | 0.6525 | 0.3980 |
| Gut*Season | | 0.5101 | 0.7112 | 0.7904 | 0.9313 | 0.9588 | 0.4470 | 0.7225 | 0.3375 |
| Month(Season) | | 0.0014 | 0.0036 | 0.0014 | 0.0001 | 0.0001 | 0.0202 | 0.0087 | 0.0372 |
| MSE model | | 3.0 | 100.2 | 79.6 | 464.7 | 19.9 | 6.8 | 16.7 | 1.2 |
| MSE month | | 14.5 | 422.2 | 386.6 | 54.7 | 302.3 | 21.0 | 71.5 | 3.2 |

dietary ADF content was different from that of NDF, especially during spring, when the HEM concentrations were the highest in the year (9.9% DM in May and 8.3% DM in June). As for NDF, the dietary ADL level increased linearly from September (9.2% DM) to November (20.2% DM), when its values were comparable to those of the winter months (19.9% DM) and slightly lower than those of spring (23.7% DM).

The DI (see Table 3) had a value lower in September than those of the last two autumn months (2.4 vs 3.3 ). The same lower index was observed in the diets of May and December. The interrelationships among the chemical components and DI could be described by two factors (Fig. 1), with an eigenvalue higher than 1, which together explained 86% of the variability of the dietary composition. The first factor (F1), which explained 68% of the total variability, was positively correlated with the cell wall components and especially with the NDF content ($r = 0.90$). The second factor (F2), which explained 21% of the variability, was negatively correlated with the CP ($r = -0.52$) and HEM ($r = -0.61$) and positively correlated with DI ($r = 0.73$).

The cluster analysis allowed the identification of five different homogeneous types of diets. Figure 1 also shows the distribution of the dietary types in the F1 × F2 plane. Of the two types of diet that were located along the positive half of F1 (diets 1 and 2), diet 1 was located further from the ori-

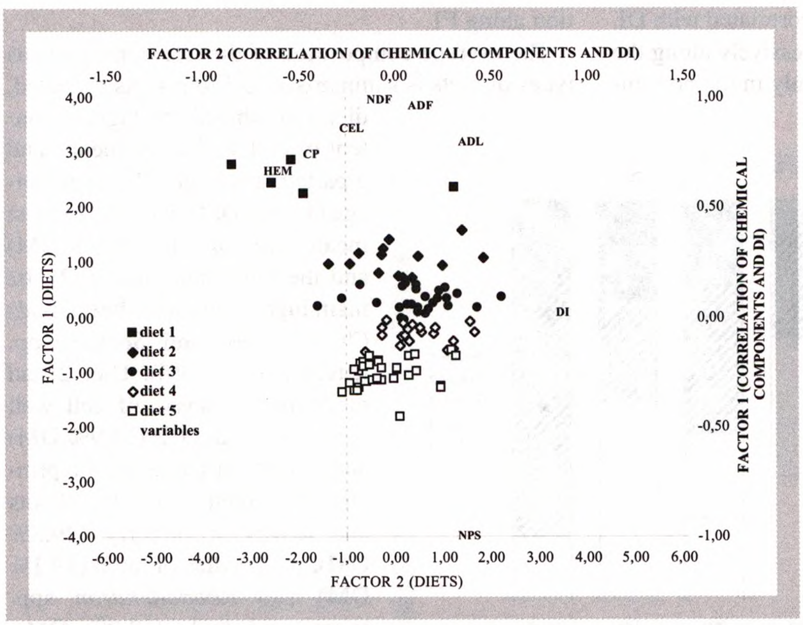


Figure 1. Correlations among the chemical components (CP, NPS, NDF, ADF, ADL, HEM, CEL), ingredient diversity index (DI) and the selected factors (Factor 1 and 2) explaining the diet composition. Distribution of the black grouse diets with homogeneous composition in the Factor 1 × Factor 2 plane.

Table 4. Mean composition of the homogeneous types of black grouse diet obtained by cluster analysis. 1: spring-high CP diet; 2: spring-middle CP diet; 3: basal diet; 4: autumn-middle NPS diet; 5: autumn-high NPS diet.

| Diet | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| Number of birds | 6 | 14 | 28 | 20 | 32 |
| Proportion of known chemical composition (% DM content of gut tract) | 65.6 | 68.1 | 71.5 | 74.6 | 71.1 |
| Chemical composition (% DM) | | | | | |
| CP | 18.1 | 11.9 | 10.2 | 8.7 | 7.9 |
| NPS | 17.3 | 41.4 | 52.7 | 61.2 | 70.5 |
| NDF | 64.7 | 46.7 | 37.1 | 30.1 | 21.7 |
| ADF | 49.9 | 40.8 | 33.8 | 27.0 | 18.6 |
| ADL | 21.8 | 25.8 | 20.3 | 16.3 | 9.4 |
| HEM | 14.8 | 5.9 | 3.4 | 3.2 | 3.1 |
| CEL | 28.1 | 14.9 | 13.5 | 10.7 | 9.2 |
| Ingredient diversity index (DI) | 2.2 | 2.6 | 3.3 | 3.5 | 2.6 |
| Ingredients (% DM of known chemical composition) | | | | | |
| Buds, leaves, twigs and shoots | | | | | |
| *V. myrtillus* | 2.9 | 49.3 | 31.8 | 19.4 | 7.4 |
| *V. vitis-idaea* | 0.0 | 1.3 | 0.5 | 0.9 | 0.1 |
| *Rhododendron* spp. | 2.2 | 12.0 | 20.2 | 14.4 | 3.2 |
| *C. vulgaris* | 0.0 | 0.7 | 3.5 | 3.6 | 0.5 |
| *J. communis* | 0.0 | 0.1 | 2.7 | 0.0 | 0.0 |
| *A. viridis*[1] | 0.0 | 3.1 | 16.9 | 11.6 | 0.9 |
| *L. decidua* | 0.0 | 19.1 | 7.7 | 0.3 | 1.2 |
| *F. sylvatica* | 70.8 | 0.1 | 1.4 | 0.0 | 0.0 |
| *Sorbus* spp. | 11.8 | 5.8 | 0.0 | 0.5 | 0.1 |
| Fruits and seeds | | | | | |
| *V. myrtillus* | 0.1 | 0.6 | 4.9 | 24.6 | 59.3 |
| *V. vitis-idaea* | 0.3 | 1.5 | 3.5 | 12.2 | 15.8 |
| *R. ferrugineum* | 7.1 | 6.4 | 0.6 | 0.9 | 0.0 |
| *Sorbus* spp. | 4.8 | 0.0 | 6.2 | 11.6 | 11.4 |

[1] Buds and catkins

gin and was also mainly dispersed in the top-left quadrant of the F1 × F2 plane, i.e. positively correlated with CP level and negatively correlated with DI. Diets 4 and 5 were distributed successively along the negative half of F1. Diet 4 was mainly in the bottom-right quadrant of the F1 × F2 plane, i.e. positively correlated with DI. Diet 3 had an intermediate position along F1.

The average composition of the five homogeneous types of diets is summarised in Table 4. As expected, diet 1 combined the highest content of cell wall constituents, and a particularly high HEM percentage (14.8% DM), with the highest mean level of CP (18.1% DM) and the lower DI value (2.2). Its main ingredients were beech buds (70.8% DM) and *Sorbus* spp. leaves (11.8% DM). Diet 2 had medium-high levels of cell wall components and CP (11.9% DM) and a medium DI value; the principal ingredients were the shoots and leaves of bilberry (49.3% DM), the needles of larch (19.1% DM) and *Rhododendron* spp. leaves and buds (12.0% DM). Diet 3 was intermediate in the chemical composition and had a high DI (3.3), with the shoots and

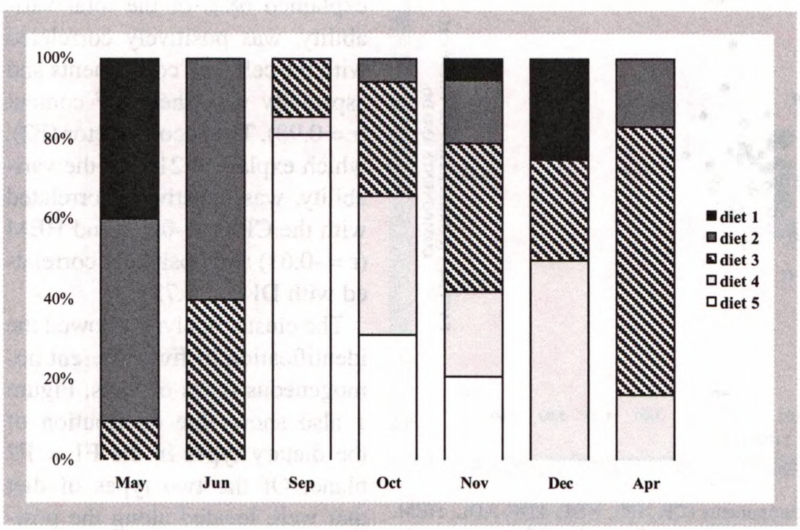


Figure 2. Distribution of the monthly frequency (%) of black grouse diets with homogeneous composition.

leaves of bilberry (31.8% DM), buds and leaves of *Rhododendron* spp. (20.2% DM) and buds and catkins of green alder (16.9% DM) as the main ingredients. Diet 4 was rich in NPS (69.9% DM) but low in CP (8.7% DM); its ingredients were the most diversified (DI 3.5) and included mainly bilberries (24.6% DM) and cowberries (12.2% DM) in addition to bilberry stems (19.4% DM) and buds and leaves of *Rhododendron* spp. (14.4% DM) and buds and catkins of green alder (11.6% DM). Diet 5 had the lowest level of NDF and CP (21.7 and 7.9% DM) and a medium DI (2.6). It was composed mainly of bilberries (59.3% DM), cowberries (15.8% DM) and *Sorbus* spp. fruits (11.4% DM).

Figure 2 shows the distribution of frequency of the diets through the months. Diet 1 was most commonly found in May (40% of cases for the month), whereas diet 2 was more frequent in both the spring months. The intermediate diet was distributed over all months but was most frequent in April. Diet 4 was observed throughout the autumn and winter months whereas diet 5, found only in autumn, was most frequent in September and then decreased until November.

## Discussion

The proportion of the ingredients analysed, averaging 70% of the diet, did not allow an absolute measure of its dietary composition. However, the relative constancy of the proportion of these ingredients throughout the diet types allowed an estimation of the chemical characteristics of the diet, which was useful in terms of describing the nutrient requirements and the food selection of the species.

The dietary composition of wild birds is generated by the interaction between the supply of nutrients and nutrient requirements. In the eastern Italian Alps, snow cover extends from December to April and part of May, so the month of May can be considered the first month of spring. In this period, male black grouse are present on the leks, with a maximum concentration in the first 10 days of the month (de Franceschi 1978), and the protein requirements are high (Robbins 1983). At the same time the supply of protein is high because of the presence of beech, *Rhododendron* spp. and green alder buds and the appearance of bilberry stems and shoots and young leaves of larch. This highest level of protein corresponds to the highest level of cell wall constituents, which accompanies the rapid rate of spring growth (Strasburger 1982).

The diets of the spring months had high values of protein and a low diversity index, especially in May. This was due to a combination of snow cover, vegetative growth pattern and protein requirements for the display activity. In the first part of May the highest level of protein was mainly due to selection of beech buds, as these are above the snow cover and have the highest level of protein. Then, during the month of May, with the development of beech buds into leaves and the rapidly increasing supply of young larch leaves, bilberry shoots and *Rhododendron* spp. buds, the composition changed to contain less protein and fibre. In these two spring months, the level of protein appeared to be an important factor of selection. It is likely that caecal fermentation could improve the digestive utilisation of the spring foods, which were rich not only in protein but also in fibre (McBee 1977, Goldstein 1989).

In September the diet composition changed due to the presence and selection by the birds of bilberries and cowberries which increased non-protein cellular solubles. In this period, the composition of the black grouse diet decreased in protein content, in spite of the requirements to complete the moult. This low level of protein content could be compensated for by refluxes of urine into the cloaca and recycling of nitrogen from uric acid (Karasawa & Maeda 1992, 1994, Mortenson & Tindall 1981a, 1981b) and, in young birds, the consumption of insects. As autumn advances, the supply of berries decreases, and the vegetative parts of bilberry and *Rhododendron* spp. increase to maintain a moderate level of cellular contents, with a slight increase in protein. In autumn, the cellular contents appear to be the most important selective factor. These components, rich in energy, can be used to build the adipose reserves for winter (de Franceschi 1978). The intermediate diet is obtained throughout the year with different amounts of different species, probably according to their availability. In conclusion, nitrogen recycling and microbial activity in the caecum could play an important role in terms of the interaction between nutrient supply and nutrient requirements.

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