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The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint?

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Abstract

The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment, in southern Portugal, was estimated during summer 1995–1997 using *n*-alkane analysis. Standing crop of herbage layer biomass was estimated between June and September 1995–1997 using the clipping quadrat method. There was a large variability between years in the availability of the herbage layer biomass. Biomass was three fold greater and availability of legumes higher in a wet than in a dry year. Live green material was available in the herbage layer in June, but not thereafter, even during a wet year. Red deer ingested a higher proportion of browse in summer during drier years (0.83–0.89) than during a wet year (0.47). In the drier years, the herbage layer was replaced in the diet by browse species that were uneaten in the wet year. Contrary to Atlantic environments, where red deer include a large proportion of browse in their diets during winter, summer is likely to be a season of nutritional constraint for red deer inhabiting Mediterranean environments.

Keywords: *Cervus elaphus*; Mediterranean; Diet composition; Browse

1. Introduction

Food is a crucial factor regulating animal populations (Klein, 1985; Begon et al., 1990). Knowing the feeding ecology of an animal species and in particular identifying periods of likely nutritional constraint is important for the management and the ecological modelling of animal populations (Begon et al., 1990).

Climate is a major determinant of plant growth and primary productivity. Because plant growth is influenced by environmental conditions and senescent plant material contains a higher ratio of cell wall to cell contents (van Soest, 1994; Iason and van Wieren, 1998), herbivores living in seasonal environments must adapt to seasonal changes in the quality and quantity of food. Herbivores can face these changes by altering the selection of their diet. ''intermediate'' or ''mixed feeders'', such as red deer, switch their diet from grasses to browse when forage plants lignify (Hofmann, 1973, 1989).

At northern latitudes, in regions of temperate climate, large mammalian herbivores face periods of nutritional constraint at the end of winter when

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availability of high quality food is low (Klein, 1985). Red deer tend to include higher proportions of browse than grass in their diets at this time (Staines and Crisp, 1978). Damage to adult trees and saplings can also be expected during this season (Edenius et al., 1993; Danell et al., 1994).

In Mediterranean environments, climate is characterised by hot and dry summers and mild and wet winters (Archibold, 1995). In summer most herbaceous plants become senescent and, before plant re-growth after first autumn rains, herbivores face low availability and quality of herbaceous food (Gutman and Seligman, 1978; Seligman, 1996). During this period browse is an important food resource for domesticated and wild ungulates (Rossiter, 1966; Rodriguez-Berrocal, 1978; Rodriguez-Berrocal et al., 1987) including red deer (Bugalho et al., 1998, 2001). Damage by wild and domesticated ungulates on trees, due to browsing, can thus be expected in summer (Zamora et al., 2001).

In Mediterranean and semi-arid environments, wide variations in amount of biomass and species composition of the herbage layer may occur both within and between years due to weather patterns (Heady, 1960; Rossiter, 1966; Pitt and Heady, 1978; Seligman, 1996), whilst availability of browse is much less variable (Illius et al., 1996; Bugalho, 1999). Date of first autumn rains and total rainfall in winter affect strongly the availability of biomass and the species composition of the herbage layer in late spring and early summer (Espigares and Peco, 1993). Variations in quantity and quality of the herbage layer are likely to affect the proportion of browse ingested by deer in summer.

Our aim in the present study was to quantify the proportion of browse in the diet of red deer in a Mediterranean environment during summer and relate it to variations in the availability and species composition of the herbage layer during three consecutive years with different levels of rainfall: a dry (1995), a wet (1996) and an intermediate year (1997).

2. Methods

2.1. Study area

The study area is an enclosed estate of approximately 300 ha located in Vila Viçosa, in southeast Portugal (38°47′N, 7°25′W). This region has a Mediterranean-type climate with mean summer temperatures of 25 °C and daytime maxima often exceeding 35 °C. Annual precipitation varies between 275 and 900 mm with at least 65% of rain falling during the winter months. Between January and September 1995, 1996 and 1997, total rainfall in the study area was 214.0, 587.2 and 337.4 mm, respectively. A high density of red deer (*Cervus elaphus*), approximately 0.7 deer/ha, was maintained in the study area by a limited culling policy. Such deer densities, generally higher than in northern Europe, are not uncommon on the Iberian Peninsula (Carranza, 1993).

The study site was a ''montado'' system with a main tree cover of cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*) and a dominant shrub cover of gum cistus (*Cistus ladanifer*). Blackberry (*Rubus ulmifolius*) and ash (*Fraxinus excelsior*) occurred along streamlines. A few olive trees (*Olea europaea*) were also present in the study area.

The herbage layer was dominated by grasses (*Vulpia bromoides*, *Bromus hordeaceus*, *Holcus lanatus*, *Agrostis poretti*, *Lolium multiflorum*, *Avena barbata*, *Poa trivialis*, *Vulpia* spp. and *Hordeum* spp.) with legumes (*Trifolium arvense*, *Trifolium angustifolium*, *Trifolium campestre*, *Ornithopus compressus* and *Vicia sativa*) occurring at lower proportions. Two species of Compositae, *Chamameleum mixtum* and *Coleostephus myconis*, were also very common.

2.2. Availability of the herbage layer

Between June and September of 1995–1997, plant biomass of the herbage layer was clipped monthly to ground level (quadrat size: 1.20 m × 0.20 m) at each of the 39 randomly selected locations in the study area. A sub-sample (a quadrat of the same shape and approximately 10% of the size of the main quadrat) was also clipped adjacent to the main quadrat and separated into dead and green plant material. In June 1995 and 1996 the same samples were also sorted into four categories of green: grasses, legumes, Compositae and other species. All samples were oven-dried at 60 °C for 48 h, and weighed.

2.3. Composition of the diet

Between July and September 1995–1997, 20 individual trees and shrubs of cork oak, holm oak, ash,

olive, gum cistus and blackberry were randomly selected. A bulked sample of 30 g (dry weight) of the current year's growth of leaf and stem, less than 0.5 cm in diameter, was collected on each species monthly. Thirty grams (dry weight) of bulked samples of the herbage layer were also clipped to ground level at 15 different locations in the study area. Fresh faeces were collected weekly along eight permanent transects of 200 m in length established in the study area (see Bugalho, 1999). Each sample consisted of all faecal pellets from a single individual found at a particular location along a transect. All faecal samples were collected between July and September. Twenty-six pellet groups were collected in 1995, 53 in 1996 and 41 in 1997. Samples were sealed in polythene bags and kept in a freezer at −15 °C. All plant and faecal samples were oven-dried at 60 °C for 48 h and ground to pass through a l mm screen mesh.

Because plant species differ in their *n*-alkane concentrations, the diet of herbivores can be estimated by relating *n*-alkane concentration available in the plants with concentrations of *n*-alkanes recovered in faeces (Dove and Mayes, 1996; Bugalho et al., 1999). The *n*-alkanes from plant cuticular wax and from faeces were extracted and quantified by gas chromatography analysis, essentially as described by Mayes et al. (1986) with the exception that C_{22}- and C_{34}-alkanes were used as internal standards. Differences in the *n*-alkane content of the individual browse species, cork oak, holm oak, gum cistus, blackberry, ash and olive, and the herbage layer occurring in the study area, had been established previously (Bugalho, 1999; Bugalho et al., 1999). Estimates of the composition of the diet, from the concentrations of C_{21}- to C_{35}-alkane in the faeces and in the plant species and categories described above, were obtained using the algorithm Eatwhat described by Dove and Moore (1995). More details of the method for estimating the composition of the diet in this study are given by Bugalho et al. (1999).

2.4. Statistical analysis

A general linear model with year and month as fixed factors and the biomass of the herbage layer as the dependent variable was used to test for differences between years and months in the availability of the herbage layer. A multivariate general linear model, with year as the fixed factor and the proportion of each dietary component (cork oak, holm oak, gum cistus, herbage layer, blackberry, olive and ash) as dependent variables, was used for testing for differences between years in the proportions of each dietary component ingested by deer. Scheffé contrast tests (Zar, 1996) were used for multiple comparisons among years in the proportion of species in the diet of red deer, and for multiple comparisons among years and among months, in the biomass of the herbage layer available to red deer. Data expressed as proportions were subjected to angular transformation to normalise their distribution (Zar, 1996). Analyses were performed in SPSS (1999).

3. Results

3.1. Availability of the herbage layer

There were significant differences among years in the availability of biomass of the herbage layer during summer ($F_{2,460} = 36.89$; $P < 0.001$) with a maximum in 1996, a minimum in 1995 and an intermediate level in 1997 (Fig. 1). In 1996, a wet year, availability of biomass in June was significantly higher than for remaining summer months (Fig. 1). Live green plant material in the herbage layer was available in June of each year and absent from July to September. The highest proportion was recorded in 1996 (0.74 ± 0.04) and the lowest in 1997 (0.19 ± 0.04) (Fig. 2). In June 1995 and 1996, grasses (0.50–0.57) and Compositae (0.22–0.27) were the dominant plant categories in the herbage layer, the remaining "other species" in 1995 (0.11) were replaced by legumes in 1996 (0.25) (see Table 1).

Table 1
Proportions of different plant categories (average and S.E.M.) in the herbage layer in June 1995 and 1996

	Grasses	Legumes	Compositae	Other species
1995	0.57	0.06	0.27	0.11
	0.070	0.020	0.050	0.040
1996	0.50	0.25	0.22	0.02
	0.062	0.020	0.032	0.005

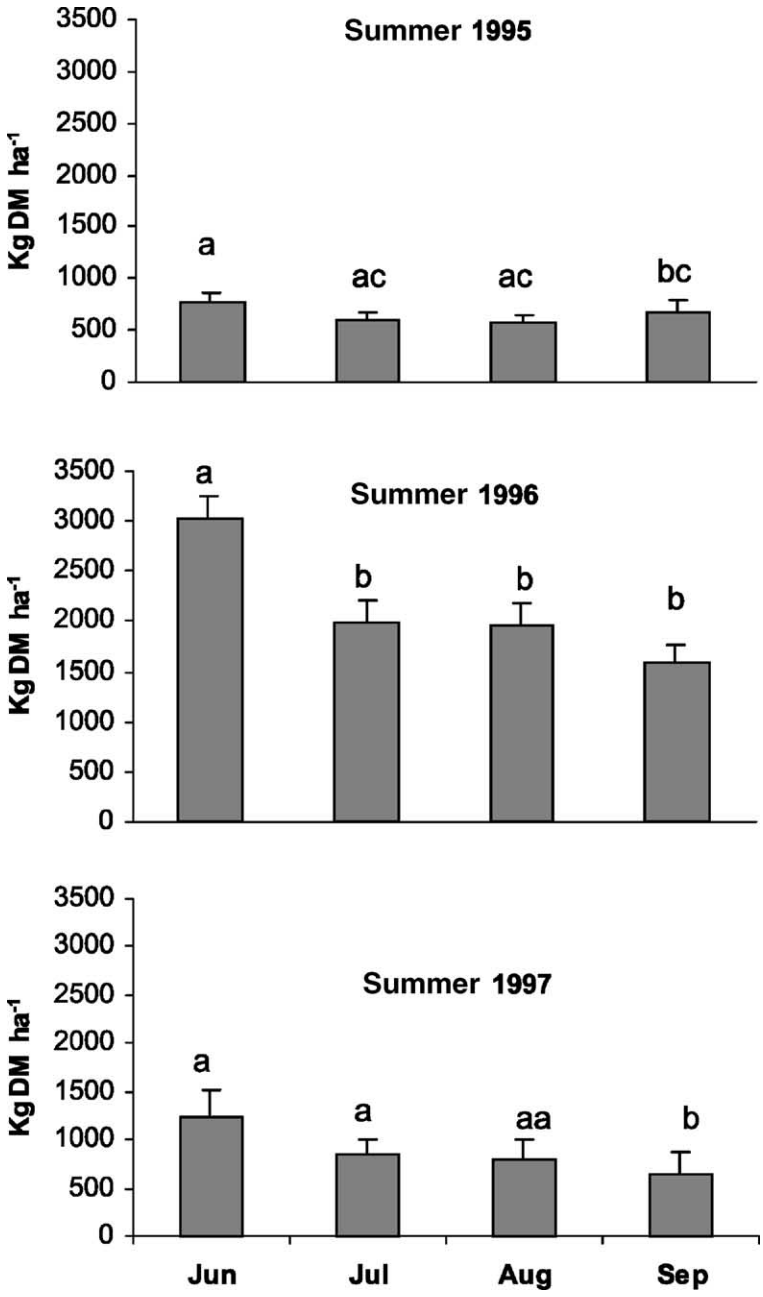

Fig. 1. Availability of biomass of the herbage layer during summer 1995–1997. Within a year, months with different letters were significantly different at $P < 0.05$ (Scheffé multiple contrast tests).

3.2. Composition of the diet

The diet of red deer contained a relative constant proportion of cork oak (approximately 0.26) and gum cistus (0.20) in summer of each year. The proportion of herbage layer in the diet was significantly higher in 1996 (0.53, $P < 0.001$) than in 1995 (0.11) and 1997 (0.20) (Fig. 3). The proportion of holm oak in the diet

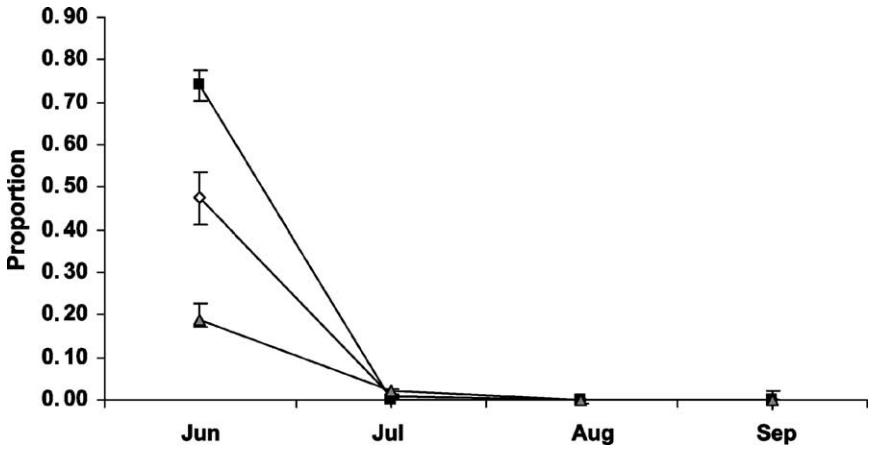

Fig. 2. Proportion of live plant material in the herbage layer during summer 1995–1997. Diamonds are used for 1995, squares for 1996 and triangles for 1997. Bars indicate 1 S.E. of mean.

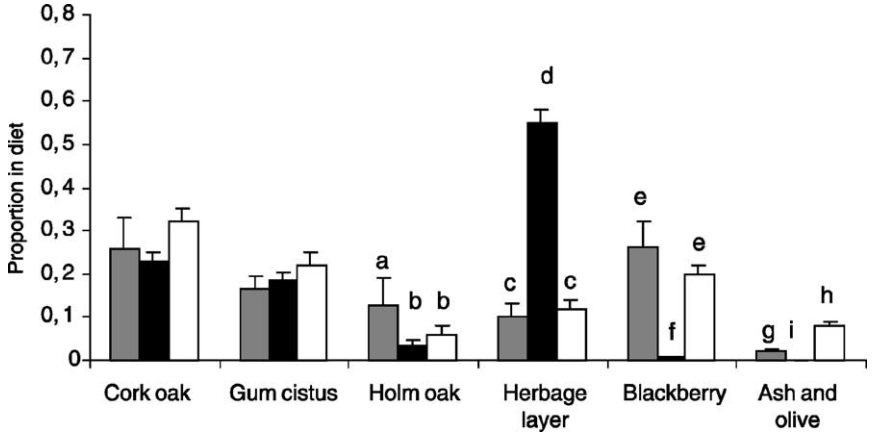

Fig. 3. Composition of the diet of red deer during summer 1995–1997. Grey bars are for 1995, dark bars for 1996 and white bars for 1997. Dietary components with different letters were significantly different across years at $P < 0.05$ (Scheffé multiple contrast tests).

increased in 1995, whilst blackberry, ash and olive were absent from the diet in 1996 (Fig. 3).

Overall, red deer had a predominantly browse diet in summer 1995 and 1997 (proportions of 0.83 and 0.89, respectively) whilst in summer 1996 only half of the diet (0.47) was browse.

4. Discussion

4.1. Availability of the herbage layer

Rainfall was low in the study area during 1995, a dry year, when availability of the herbage layer biomass was also low. Conversely, the year of 1996 was characterised by high rainfall and high herbage layer availability (approximately three times higher than in 1995). Frequently an increase in the proportion of annual grasses is accompanied by a decrease in the proportion of legumes (Pitt and Heady, 1978). In the present study legumes seemed to benefit from higher rainfall to a greater extent than grasses as they increased from 0.06 to 0.25 between June 1995 and 1996, whilst grasses remained relatively constant during the same period (Table 1).

The highest proportion of green plant material, recorded in June 1996, was probably a consequence

of the high rainfall in that year. However, the proportion of green plant material observed in the herbage layer in June 1997 was significantly lower than that recorded in June 1995, which was a drier year. This could partially be the outcome of a dilution effect of dead plant material arising from the carry-over of senescent standing biomass from the previous year. In June, lack of moisture in the soil and high temperatures, halt vegetation growth and, within an interval of few weeks, in the beginning of July, most of the herbage layer plants died back, causing a dramatic decrease in live plant material available to red deer, even during the wet year.

4.2. Composition of the diet

The proportions of cork oak and gum cistus, the most abundant browse species in the study area (Bugalho, 1999), remained relatively constant in the diet of red deer during the 3-year period of study. Jointly they comprised about 0.45 of the diet in each year. This suggests that, in spite of variability in the amount of herbage layer available, red deer had to ingest, at least, almost half of a browse diet during summer. The ingestion of browse during summer could be partially related with the requirements of red deer in crude protein, a limiting factor in the nutrition of ruminants (Jones and Wilson, 1987). Usually, concentrations of crude protein are very low in the senescent herbage layer (Fonseca, 1998) and browse is an important source of crude protein for ruminants living in a Mediterranean environment (Le Houérou, 1980; Seligman, 1996).

Other browse species, such as holm oak and ash and olive, had relatively low proportions or were absent of the diet (the case of ash and olive) in 1996, but their ingestion by red deer increased during the dry years of 1995 and 1997, when availability of the herbage layer was low. Similarly, relatively high proportions of blackberry (*Rubus* spp.) were ingested when availability of the herbage layer was low, but not included in the diet when availability was high. Availability of the herbage layer appears to have affected the ingestion of some browse species. These results are in agreement with other studies. For instance, it has been shown that Scots Pine (*Pinus sylvestris*) plantations in Sierra Nevada, southeast Spain, had signs of heavier utilisation by goats and ibex in summer, particularly during dry years when availability of grasses was low (Zamora et al., 2001).

5. Conclusions and management implications

In Mediterranean environments there is lack of high quality food during summer when most of plants of the herbage layer become senescent. Red deer, a mixed feeder (Hofmann, 1973, 1989), ingest high proportions of browse during this season. Damage to trees due to browsing is likely to occur in summer (Zamora et al., 2001). Supplementary feeding at the end of summer or, if economically viable, irrigated pastures, may mitigate damage to trees by providing alternative food to red deer. A large proportion of browse, however, should always be expected in the diet of red deer in summer. During the hot and dry Mediterranean summer, and before first autumn rains cause re-growth of the herbage layer, red deer are likely to suffer nutritional constraints.

Red deer populations may be affected differently according to season of nutritional constraint. In northern climate environments male biased mortality is likely to occur in winter (Clutton-Brock and Albon, 1989). In such regions, the low availability and quality of food in winter may not allow males to recover live weight and fat reserves that were lost during the rut. In Mediterranean environments, lack of quality food during early summer may affect the reproductive success of females namely if they are still lactating. This will be aggravated during dry years. The influence of summer nutritional constraint on the reproductive success of Mediterranean red deer populations is a subject that remains to be investigated.

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