

Diet of British Sika Deer in Contrasting Environments

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Winter diet of sika deer from 5 commercial coniferous forests in Scotland was assessed by rumen analysis. No differences were recorded in dietary composition between years or between forests. In all cases grasses composed >70% of the diet, with *Calluna* heath comprising a further 20—30%. Winter diets of sika in similar coniferous forests in southern England were broadly comparable although intake of grass tended to be lower (at 30—40%) and intake of heather higher at 40—50%. By contrast, ruminal analyses of sika deer from the more varied New Forest in Hampshire showed a lower intake of both grasses and heather, which never contributed more than 16% and 17% respectively. Intake of browse materials was far higher than that observed elsewhere, contributing >20% by volume of total ingesta. Diets of the two southerly populations (New Forest and Wareham) were compared on the basis of faecal analysis. Diet of Wareham animals changed little over the year. Intake of browse was consistently low and, throughout, the main dietary components were grasses and *Calluna*, together comprising between 75% and 90% of diet in all seasons. By contrast New Forest animals not only took a greater variety of foodstuffs in any one season, but also showed marked seasonal variation in composition of the diet. Dietary composition was considered in relation to forage availability and nutrient status. At Wareham no correlations were found between diet selected and availability of different forages; weak correlation was found with nitrogen and phosphorus content of the major forage-types. In the New Forest, dietary composition correlated well with forage availability; correlations with forage nutrient status were inconsistent, but changes in the amounts of grasses and *Calluna* in the diet in different seasons correlated with both digestibility and potassium content of these forages.

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1. INTRODUCTION

Sika deer (*Cervus nippon* Temminck) have, since their introduction at the end of the 19th century, become widely established in forest areas throughout Great Britain. Ratcliffe (1987) presents a recent review of distribution and status of the species within the U.K. For the most part, populations occur in coniferous forest; with range expansion encouraged by the presence of young conifer or new afforestations. One population in the south of England however has established itself in an area of

predominantly deciduous woodland (the New Forest of Hampshire) and sika are in fact an opportunistic species able to exploit a variety of environments (Mann & Putman, 1989). In each, their ecology is altered to match characteristics of the local environment and the available resources.

In terms of feeding strategy, Hofmann (1982) classified the sika deer on the basis of rumen morphology and physiology, as an "intermediate" or "opportunistic" feeder. Studies of the composition of sika deer diets in Japan (Takatsuki, 1980) and elsewhere (*e.g.* Askolod Island: Prisyazhnyuk & Prisyazhnyuk, 1974) support such anatomical classification, suggesting that although diet varies from place to place, the main component is always of grass. However, intermediate feeders of this type are characteristically able to alter the relative proportions in the diet of high-quality, high digestibility and bulk, high-fibre foodstuffs dependent on availability (*e.g.* Putman, 1988) and Takatsuki (1987) confirms that while the diet of sika in different Japanese populations was in most areas composed primarily of grasses, composition varied considerably between vegetation types.

Studies of the diet of sika deer in Britain have also suggested that they feed extensively on grasses (Horwood & Masters, 1970, Robinson, 1973). While analysing their material, however, most of which came from coniferous forests in Dorset, Horwood and Masters also examined the rumina of six sika deer shot in the New Forest in Hampshire; here they found significant quantities of pine needles, leading them to suggest that perhaps the sika of the New Forest fed more on browse materials than did other populations. Sample sizes were however, self-confessedly, small. Further, all analyses were carried out on rumen contents of sika shot during annual culling operations, thereby limiting analysis (as in other British studies), to that limited part of the year when deer may legally be shot.

The current paper presents a comparison of the diets of a number of populations of British sika deer living in different environments. A detailed analysis is made of the diet of New Forest sika by comparison to that of sika in Dorset (from the same populations as those studied by Horwood and Masters). In this case analyses were undertaken of faecal material as well as of rumen samples, and thus a more complete picture of dietary composition and dietary change throughout the year was obtained for the two areas. In addition, winter diet of five populations of Sika in different forests in Scotland was examined in an analysis of rumina obtained during the winter culls of 1979—80 and 1980—81; winter diet of these animals too is thus compared here with that of Dorset and New Forest animals. Finally, differences between populations

in diet, and seasonal changes in dietary composition within populations, are examined in relation to relative abundance and nutritional quality of available forage.

2. STUDY AREA, MATERIALS AND METHODS

Analysis of both faecal and ruminal materials were carried out for the sika populations of Wareham Forest (a commercial coniferous forest in Dorset) and of the predominantly deciduous New Forest in Hampshire. These areas and their characteristics are described more fully in Mann and Putman (1989). Rumen samples were obtained from animals shot during the normal culling season (November–February) during 1978–79, 1979–80, 1980–81 in both areas and in 1981–82 (New Forest only). In each case 250 ml of well mixed rumen contents were retrieved from each animal shot and fixed in 10% formalin. In addition, fresh faecal samples were collected monthly in each area from September 1979 — October 1981 (New Forest) and September 1980 — October 1981 (Wareham).

Rumen samples were also collected from animals shot during the winters 1979–80, 1980–81 from five commercial forests in Scotland: Shin, Farigaig, Knapdale, Achaglachgach, and South Kintyre.

2.1. Ruminal Analyses

Each rumen sample was washed in a 2 mm sieve until emerging water was clear and the particles remaining appeared separate and distinct. A 10 ml subsample of the residue was spread under water in a shallow plastic tray scored with parallel lines at 1.5 cm distance. All particles encountering a grid-line were identified. The procedure was then repeated with a second 10 ml sample. (Sample sizes for each study area are shown in Table 1).

In each analysis, every particle encountering a grid line was removed following identification (to avoid any risk of double-scoring). Such particles were stored in

Table 1
Numbers of rumen and faecal samples analysed.

Date	New Forest	Wareham Forest	Scottish Forests
Rumen samples			
Winter 1978–79	22	13	—
Winter 1979–80	29	35	93
Winter 1980–81	26	14	97
Winter 1981–82	35	—	—
Faecal samples			
1979–80	Monthly: 5 samples	—	—
1980–81	Monthly: 5 samples	Monthly: 5 samples	—

separate containers to build up pure samples of each dietary component. When all ruminal analyses were complete, 10 ml subsamples of each of these "monocultures" were spread onto the grid tray and the number of particles encountering a line recorded. This was repeated for each food type to provide an estimate of the number of "line-hits" which would correspond to a given volume (10 ml) of each foodstuff identified. Results from ruminal analyses could thus be converted from relative number of fragments encountered of different foodstuffs to percentage volume (Putman, 1984).

2.2. Faecal Analyses

From faecal collections made in the New Forest and Wareham, five separate faecal groups were selected in each month. Pellets were crushed with a pestle and mortar using a solution of 2% NaOH as a lubricant, and were left soaking for 12 hours. During this period the solid matter settled; the supernatant was replaced with 10% NaOH and the sample boiled for 5 minutes (method modified from London, 1979). This treatment ensured separation of all the particles and also removed gut mucus and bacteria. After cooling, the sludge was washed then centrifuged to compact the faecal matter (Putman, 1984). Washing and centrifuging were repeated a number of times.

A portion of the cleaned material was spread in water on a petri-dish which had been engraved with a 1.0 cm grid. The sample was examined under a microscope at 100 \times magnification and the first 100 particles lying across or touching grid lines were identified by comparison with a set of reference slides. Initially three replicates were examined for each sample; however it was found that the final replicate made no significant difference to results based on analysis of the first two subsamples (Mann, 1983) and thus, subsequently, two replicates only were analysed for the majority of samples.

2.3. Forage Availability and Nutrient Quality

In the New Forest and Wareham, assessments were made for the relative availability and quality of forages consumed. Availability of each foodstuff was crudely assessed in terms of its contribution to the standing crop of the community in which it occurred, multiplied by the actual area within the entire study site contributed by that vegetational community.

Forages were further analysed for digestibility and content of key nutrients, identified as nitrogen, potassium, phosphorus and calcium. Samples for nutrient analyses were collected from both Wareham Forest and the New Forest and were taken at the end of the second week in each calendar month during 1981. Digestibility and nutrient analyses were carried out using methods described in Putman and Hemmings (1986).

3. RESULTS

3.1. Ruminal Analyses

Winter diet of sika deer in Wareham forest (November-January) is summarised in Figure 1. No significant differences in diet of any month were recorded between years, and results are thus combined for analysis here. Winter diet at Wareham consisted mainly of grasses and *Calluna* (together comprising some 60% by volume of total intake) with smaller proportions of leaves, gorse and coniferous browse. Grass intake in fact declined as winter progressed, while intake of gorse increased in complement.

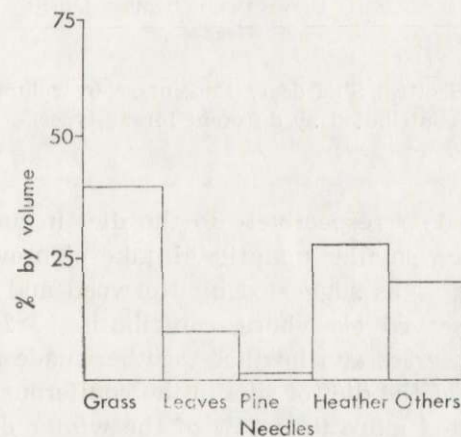


Fig. 1. Winter diet of Wareham Sika deer. (Percentage by volume of rumen contents contributed by different forage types).

Wareham forest is a commercial coniferous planting and its sika are restricted in habitat use to woodland itself and the surrounding area of heathland and farmland (Mann & Putman, 1989). The resources available are broadly similar to those of the five coniferous forests of our Scottish sample. Analyses of diet for these Scottish sika populations reflected the similarity of habitat. Diets calculated for each forest were not found to be significantly different from each other (G -test $p > 0.05$) nor were any differences recorded between years. Diet recorded (Fig. 2) was similar to that of Wareham sika (Fig. 1) except that the proportion of *Calluna* in the diet was lower in Scottish animals, with grasses comprising 70% or more of the diet.

By contrast, ruminal analyses of New Forest sika deer (Fig. 3) revealed far lower intake of both grasses and heather which never contributed

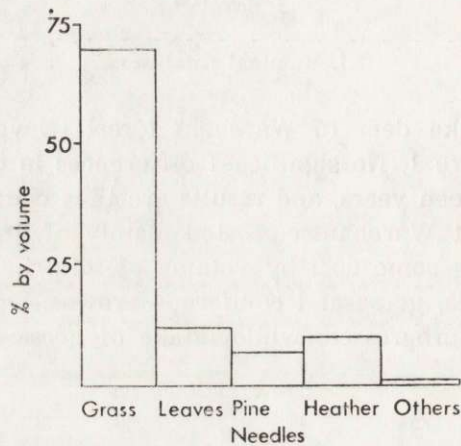


Fig. 2. Winter diet of Scottish Sika deer. (Percentage by volume of rumen contents contributed by different forage types).

more than 16% and 17% respectively to the diet in any year, and were usually taken in even smaller quantity. Intake of browse materials (needles and bark) was — as suggested by Horwood and Masters (1970) — far higher than observed elsewhere, contributing $>20\%$ by volume of the total diet. While grass and heather together made up $>60\%$ (Dorest) or $>70\%$ (Scotland) of the diet of sika in the coniferous forests examined, they never contributed more than 35% of the winter diet of New Forest animals.

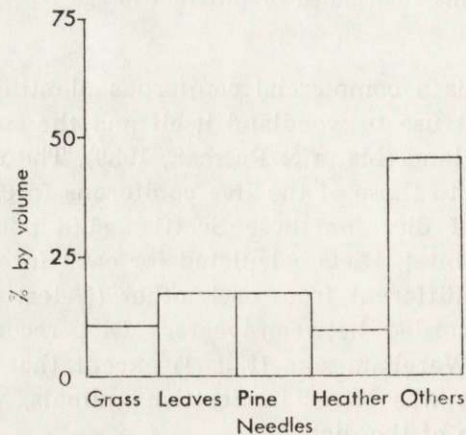


Fig. 3. Winter diet of New Forest Sika deer. (Percentage by volume of rumen contents contributed by different forage types).

3.2. Faecal Analyses

Ruminal analyses are restricted, by sampling regime, to consideration of winter diet. For the New Forest and Wareham populations therefore such analyses were complemented by examination of faecal materials. Faecal analyses were undertaken throughout the year and results are thus available from both faecal and ruminal analyses for the winter months.

The percentage occurrence of fragments of different foodstuffs in the diets of New Forest and Wareham sika are presented in Tables 2 and 3. In Wareham the diet changed little over the course of the year. Intake of browse was consistently low and throughout the main dietary components were grasses and *Calluna*, which in all seasons made up between 75% and 90% of the diet. A variety of other forage-types contributed to the remaining part of the diet, but no single item comprised more than about 8% at any time.

Table 2

Dietary composition of Dorest sika from faecal samples; September 1980—1981. Figures are % of total fragments in any month. t=trace.

	Jan	Feb	Mar/ Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Agrostis capillaris</i>	t	4	2	3	1	1	4	1	3	2	2
<i>Agrostis curtisii</i>	15	14	13	18	20	17	20	11	22	20	15
<i>Molinia caerulea</i>	t	t	3	4	3	2	4	t	3	2	t
Total grasses:	30	37	28	41	36	38	48	30	45	38	32
Forbs and deciduous leaves	1	1	1	2	3	2	1	5	5	4	3
Coniferous needles	5	6	4	1	0	t	0	1	1	1	t
<i>Calluna</i>	55	46	47	47	52	52	42	56	43	41	46
Gorse	6	7	8	7	7	8	7	5	3	10	9
Fruits	0	0	0	0	0	0	0	0	0	0	0
Others	3	3	12	2	2	0	2	3	3	6	10

By contrast once more, New Forest animals showed striking seasonality in dietary pattern. During spring and summer the diet was composed — as in the Wareham animals — of grasses (30—40%) and *Calluna* (30—35%), with lower intake of browse such as pine needles or gorse. In autumn the diet became more varied. Grasses and heather each comprised approximately 25% of total intake. The autumn leaf-fall brings leaves of a variety of deciduous trees within the animals reach and contributed a further 25% to diet at this time, while the remainder was made up of pine needles, holly, gorse and — when available — acorns.

In winter, consumption of conifer browse increased still further; intake of forbs and tree leaves from broadleaved species fell.

If analyses are carried out at the level of individual months rather than seasons it is clear that in spring and autumn, food habits changed more rapidly than they did in summer or winter. Such an observation supports an impression that the New Forest sika are opportunistic in feeding style — exploiting transient food supplies as they become available and, in consequence, exhibiting a more varied diet during seasons of rapidly changing vegetational availability and quantity (spring and autumn), a more constant dietary composition in periods of vegetational stability (summer and winter).

Table 3

Dietary composition of New Forest sika from faecal samples; October 1979—1981. Figures are % of total fragments in any month. t=trace.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Agrostis capillaris</i>	3	5	5	8	7	7	7	11	13	9	8	5
<i>Agrostis curtisii</i>	8	8	9	16	12	12	11	13	12	10	9	9
<i>Molinia caerulea</i>	t	t	1	4	6	7	5	6	5	4	t	t
Total grasses:	25	25	22	39	38	40	39	50	44	31	28	27
Forbs and deciduous leaves	12	14	11	14	15	15	17	11	21	27	15	15
Coniferous needles	20	19	23	13	2	0	0	1	0	6	8	16
<i>Calluna</i>	24	23	30	23	35	37	35	29	27	23	24	25
Gorse	7	14	8	7	6	5	6	6	7	4	7	5
Fruits	6	4	2	0	0	0	0	0	0	6	14	9
Others	6	1	4	4	4	3	3	3	1	3	4	3

3.3. Diet in Relation to Forage Availability and Quality

The flexibility in feeding behaviour of New Forest sika suggests an opportunistic use of resources so that changes in diet of these animals may reflect changes in availability and quality of different forages at different times, while lack of variation in the diet of Wareham or Scottish populations may be because food resources available do not change so markedly in either quantity or quality between seasons. Differences between the various populations in composition of the diet in any one season may also be due to differences in relative availability or quality of different forages in the different areas.

At Wareham where the diet is composed chiefly of grass and *Calluna*, no correlation was found between diet selected in any season and actual

availability of forages, suggesting that at least to some degree the deer are feeding selectively. While diet selected in any month did not optimise intake of any of the indices of forage quality considered, minor changes in dietary composition observed between months were shown to correlate with temporal changes in nitrogen and phosphorus content of deciduous browse, forbs, grasses and conifer browse ($p < 0.05$ in all cases).

In the New Forest dietary composition correlated well with forage availability in six out of eight seasons considered (Autumns 1979–1981) lacking significance only during summer and autumn of 1980. Correlations with the various measures of nutritional quality were inconsistent. Within any month, relative abundance of different foodstuffs in the diet correlated weakly with digestibility (December 1980, June 1981) and calcium (July, November 1980, September 1987) ($p < 0.01$ in all cases). However correlations were sought with six separate nutrients in 14 months and it is not improbable that, merely because of the number of tests involved, some spurious correlation might emerge. Accordingly a separate set of analyses was undertaken, as at Wareham, seeking an explanation for changes in the abundance of particular forages in the diet between months. In each analysis, changes in the quantity of grasses in the diet correlated (Spearman Rank test) with digestibility ($p < 0.01$) and with calcium potassium and magnesium ($p < 0.05$); changes in quantity of *Calluna* taken again correlated with digestibility ($p < 0.01$) and potassium ($p < 0.05$) and in this case also with phosphorus ($p < 0.05$). Amounts of broadleaved browse and forbs correlated weakly with potassium levels in 1980 and with calcium levels in 1987 ($p < 0.05$). By contrast, amounts of coniferous browse taken in different months showed negative correlations with potassium, phosphorus and nitrogen ($p < 0.05$ or higher) — an observation indubitably explained by the fact that such browse was taken predominantly in winter and thus at a time outside its own main growing season.

4. DISCUSSION

No formal analysis could be undertaken which would compare results for dietary composition derived from ruminal and faecal analyses. Even before results from ruminal analyses were converted to percentage volume and thus expressed in different units from the percentage occurrence profile provided from faecal analysis, relative fragment size of different foodstuffs in ruminal samples was so great that it would have been unreasonable to compare ruminal and faecal results on the basis of

fragment number. However, it is clear from comparison of Fig. 1 with Table 2 or Fig. 3 with Table 3 that the dietary profile for those months of the year when data are available from both sources, is broadly similar.

All data from February to October rely on faecal analyses and in the current study a relatively small sample size was taken (5 pellet groups in any month, bulked to 15 in any season). Hanson and Graybill (1956) and Anthony and Smith (1974) suggest that to describe diet effectively from faecal analyses at least 15 samples are needed. Our seasonal samples satisfy this criterion; to test the adequacy of the smaller samples used in assessing diet in any one month a number of trials were run, increasing sample size from 5 to 15 in selected months (Mann, 1983). No significant differences were revealed in relation to changing sample size ($p < 0.05$) and it is suggested that for an animal with a relatively simple diet the profile can be described with acceptable accuracy with relatively small samples.

Results from ruminal and faecal analyses combined suggest that in the primarily coniferous environment of Wareham Forest, diet was composed chiefly of grass (30–40% depending on season) and *Calluna* heath (40–50%). A variety of other foodstuffs contribute to the remaining part of the dietary intake, but no single item represented more than ca. 8% at any time. The diet was seen to be relatively constant throughout the year with only minor changes in relative proportions of heather and grass, although species of grass selected did alter. These results confirm the impressions of Horwood and Masters (1970) and it would appear from the present study that such a dietary profile is not peculiar to Wareham but is perhaps more generally characteristic of sika in commercial coniferous forest. Ruminal analyses for sika from five Scottish forests showed that at least winter diet (November to January) was extremely similar to that found at Wareham. No differences were observed between animals of the five different Scottish forests, nor between years, and in all sites, diet was once again comprised chiefly of grasses and heather (Fig. 2), although we would note that Scottish animals take less heather than was found for Wareham deer, with grasses making up 70% or more of the winter diet (cf. 30% grass, 70% heather and grass, in Wareham).

In a preliminary analysis of the ecology of sika deer in the vegetationally more varied New Forest, Horwood and Masters (1970) noted that "In spite of the fact that sedges and grasses are undoubtedly available, and apparently in sufficient quantity, the sika appear to be browsers and furthermore, they browse to a large extent on conifers, at least during February when six stomachs were examined." This conclusion

is not entirely supported by the larger sample available from the present study. That the Hampshire animals do feed on coniferous browse is certain, but there was clear seasonal variation in diet (with coniferous browse at its most important during the winter period) and also marked variation between successive years. (Thus in some years the intake of pine needles was falling by February (*e.g.* 1980—1981); in others it was still high (1979—80). The degree of variation in dietary composition observed between years and the fact that, unlike the Dorset sika, New Forest deer showed pronounced seasonal variation in diet suggest that New Forest animals were not so much the committed "browsers" suggested by Horwood and Masters but rather opportunists. At the end of the autumn the New Forest animals exploited transiently abundant foods (acorns, beech mast, fallen leaves); when these are depleted they switched to a more browsing habit and fed more extensively on dwarf shrubs (*Calluna*, *Ulex europaeus*) and trees, while also maintaining a steady if reduced intake of grasses. Areas of felling operations were also heavily exploited and here feeding site inspection revealed extensive feeding from cut branches. As winter progressed, intake of leaves and grasses declined and the intake of heather and coniferous browse rose (this in direct contrast to Wareham where only a slight decrease in grass intake was observed and consumption of coniferous browse remained low) but as soon as new growth recommenced in spring the New Forest animals stopped taking coniferous browse and relied heavily on grasses. Intake of *Calluna* remained steady — although there is some indication of a decrease in consumption in late summer (coinciding with flowering which, it is thought, makes the heather less palatable to deer: *cf.* red deer, van de Veen, 1979).

Such opportunism in feeding strategy may be most apparent in the relatively diverse and variable environment offered by the New Forest — but may well be a characteristic of sika in general (and just not expressed in the relatively limited environment offered by commercial coniferous forest) While sika in Japan are primarily grazers or intermediate-feeders (*e.g.* Miura, 1974; Furubayashi & Maruyama, 1977; Takatsuki, 1980) dietary composition is reported to change quite markedly in different vegetational communities (Takatsuki, 1980, 1987). Further evidence for this may be taken from the fact that in the more variable New Forest, sika diet is shown to be rather closely correlated with availability of different forages.

In both Wareham and New Forest populations, however, some evidence of selectivity is shown as, despite the high availability of coniferous browse in the Dorset forest, needles scarcely feature in the diet (while they occur as a prominent feature of the winter diet of animals

in the New Forest — where in practice such browse is of lower availability overall). Further in both areas there is some suggestion that within the overall constraints imposed by absolute availability, animals selected foods of particular nutrient status. Sika in Wareham selected foods relatively higher in nitrogen and phosphorus; those in the New Forest appeared to be selecting for highly digestible forages, high in calcium and potassium. In the same area, fallow deer (Parfitt, in Putman, 1986) were shown to be selecting for digestible nitrogen, and diet of freeranging ponies was also found to correlate with productivity and digestible nitrogen (Putman, 1986; Putman *et al.*, 1987). The negative correlations observed between amount of use of coniferous browse by New Forest sika and its nutritional status also parallels a negative correlation reported by Putman *et al.* (1987) for use of the grass *Agrostis curtisii* by New Forest ponies; as in that case, the negative correlation doubtless reflects the fact that New Forest sika mainly feed on such browse outside its main growing season.

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POKARM JELENI SIKA W RÓŻNYCH TYPACH LASU W WIELKIEJ BRYTANII

Streszczenie

Badano skład zimowego pokarmu jeleni sika zamieszkujących lasy zagospodarowane w Szkocji. Trawy stanowiły ponad 70% pobranego pokarmu a wrzos 20—30% (Ryc. 2). Zimowy skład pokarmu jeleni sika w lasach iglastych południowej Anglii był podobny: trawy stanowiły 30—40%, a wrzos 40—50% objętości zjadanych roślin (Ryc. 1). Pokarm jeleni żyjących w bardziej zróżnicowanym lesie New Forest w Hampshire wyraźnie różnił się od dwu poprzednich sytuacji: trawy stanowiły najwyżej 16%, wrzos 17%, natomiast pędy drzew i krzewów ponad 20% zawartości żołądków (Ryc. 3).

Skład pokarmu dwu najbardziej południowych populacji jeleni sika (w New Forest i Wareham) porównano w ciągu całego roku metodą analizy odchodów. Zwierzęta z Wareham przez cały rok żywiły się głównie trawami i wrzosem (75—90%). Nie wykryto korelacji między dostępnością określonych typów żeru a ich udziałem w pokarmie. Stwierdzono natomiast słabą korelację między zawartością azotu i fosforu w różnych rodzajach żeru a ich udziałem w pokarmie jeleni. Pokarm jeleni z New Forest był znacznie bardziej zróżnicowany i wykazywał zmiany sezonowe. Skład pokarmu skorelowany był z jego dostępnością w środowisku. Udział traw i wrzosu w pokarmie odzwierciedlał zarówno sezonowe różnice strawności tych roślin, jak i zawartości w nich potasu.