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**The Food Habits of Deer in the Białowieża Primeval Forest\***

[With 6 Tables &amp; 10 Figs.]

Observations were made twice every month over a period of three years, in 6 different forest associations, of the traces left by roe deer *Capreolus capreolus* and red deer *Cervus elaphus* in visiting and feeding in 60 experimental areas (3 ha). The extent of feeding of the animals on different species of plants was examined and also variations in food preferences depending on the ecosystem, age class of the tree stand, phenological season and abundance of the various species of plants. The food of deer includes all species of trees, and dwarf-shrubs, and 63% of the species of dicotyledonous forbs, grasses and sedges occurring in the experimental areas. Trees included in the basic food of deer are *Carpinus betulus*, *Fraxinus excelsior*, *Quercus robur* and *Salix caprea*, while the dicotyledonous forbs most commonly eaten are *Ranunculus repens*, *Caltha palustris*, *Filipendula ulmaria*, *Aegopodium podagraria* and *Impatiens noli-tangere*. There is a relation between the abundance of a given plant in the area and the intensity with which the deer feed on it; the greater the coefficient of abundance of a plant, the greater the percentage it forms in the animals' diet. The deer's intensity of feeding varies over the course of the year, with distinct intensification in summer and winter, and depressions in spring and autumn. Summer intensification of feeding is connected with the greater variety of species in the animals' diet, while the winter intensification affects only a small number of species, chiefly trees. During the winter trees form 85—95% of the animals' food. Deer feed chiefly on the younger age classes of tree stands, that is, plantations and thickets. Preferences for the different age classes varies, however, over the course of the year and is characteristic of the different ecosystems. Dicotyledonous forbs are particularly preferred in the generative stage. One of the ways in which deer obtain food is by stripping the bark from trees and shrubs, the species most frequently barked being *Picea excelsa*, *Tilia cordata*, *Quercus robur* and *Fraxinus excelsior*. Examination was made of the connections between the animals' activity and intensity of feeding in winter. It was found that there are only slight differences in the penetration of ecosystems by roe deer and red deer, but considerable differences in the amount of food consumed in them by these two species. Examination was also made of the effect of the depth of the snow cover on the activity of deer. Snow cover deeper than 50 cm limits the roe deer's activity, and deeper than 80 cm that of the red deer.

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## 1. INTRODUCTION

The role of wild ungulates in man's management of nature is generally known. It is only really comprehensive studies, taking into consideration the biology of ungulates on the one hand, and on the other the habitat in which these animals live, which can form a basis for rational management. The Białowieża Primeval Forest forms a particularly valuable object for such studies, as in the first place, despite the forest management activities carried out in it, it has retained its character of a relatively primeval forest, and in the second it harbours the three largest European species of ungulates, the European bison, the moose and the red deer. Roe deer and wild boar also occur there in large numbers. These conditions provide an opportunity for making complex studies on the role of these animals in forest ecosystems. A basis for rational management of ungulate populations is obtained by, *inter alia*, ascertaining the food requirements of the various species and defining the habitat's capacity for supplying such food. The present paper is concerned with two species of ungulates: the roe deer and the red deer. The food preferences of the European bison have been discussed separately (Borowski & Kossak, 1972), while the moose, on account

of the small numbers in which it occurs in the Białowieża Forest, has not been included in such studies.

The purpose of this study was to make an exhaustive examination of the food habits of *Cervidae* in relation to the habitat. There can be no doubt that these relations are formed by a large number of as yet uninvestigated factors. It is sufficient to mention such factors as: seasonal variations in accessible food, type of habitat in which the given animals live, abundance and accessibility of plants which can form their food, the animals' food requirements and preferences, depending, *inter alia*, on the individual's age and physiological state, and competitive inter- and intraspecific relations. It is for this reason that in dealing with the food preferences of deer attention has been paid to the following aspects: the degree to which deer make use of the plants species occurring in the area, taking into account their abundance, variations in food preferences depending on the type of biotope and age of the tree stand and also the season, the relation between food preferences and the structure of phytocenoses and seasonal rhythm of the development of plants. Examination has been made of differences between roe deer and red deer in respect of preferences for different ecosystems, treating this as an introduction to studies on the competition between these species.

## 2. STUDY AREA

The results of studies presented in this paper are concerned with the food relations of deer within the forest complex of the Białowieża Primeval Forest, which occupies an area of approximately 1.250 km<sup>2</sup>. It lies between 23°31' and 24°21' E and 52°20' and 52°57' N. The climate of the Forest is defined as a subcontinental forest climate of the cool temperature zone. The flora of the Forest is composed of 990 species of plants, 26 of which are trees and 55 shrubs and dwarf shrubs. Subcontinental oak-hornbeam forests predominate in the Forest (47.2% of forest area) and mixed coniferous forest (26.4% of forest area).

The Białowieża Forest has been subject to human activities for many centuries and consequently (with the exception of the National Park 4,747 ha in area) has the character of a cultivated forest, and can thus be regarded as an only relatively natural forest complex (Faliński, 1968).

Ungulates in the Forest includes wild boar *Sus scrofa* Linnaeus, 1758; red deer *Cervus elaphus* Linnaeus, 1758; roe deer *Capreolus capreolus* (Linnaeus, 1758); and since 1952 — European bison *Bison bonasus* (Linnaeus, 1758). Since 1969 the moose *Alces alces* (Linnaeus, 1758) has occurred in the Forest.

## 3. MATERIAL AND METHODS

Studies on the food relations of roe deer and red deer were carried out for three full years (1968—1971). The composition of the animals' food was examined on the basis of analysis of the traces left by wild animals feeding in an open area included in normal forest management.

A total 60 experimental areas were set up, in the following 6 forest associations: *P—P* — continental pine forest (*Peucedano-Pinetum* Mat. 1962); *P—Q* — continental pine-oak mixed forest (*Pino-Quercetum* Kozl. 1925); *C—Q* — mixed pine and oak forest (*Calamagrostio-Quercetum* (Hart. 1934) Scam. 1959); *T—C<sub>1</sub>* — typical subcontinental oak-hornbeam forest (*Tilio-Carpinetum typicum* Tracz. 1962); *T—C<sub>2</sub>* — a lowland subcontinental oak-hornbeam forest (*Tilio-Carpinetum stachyetosum* Tracz. 1962); and in *C—A* — an alder-ash alluvial forest (*Ciraeo-Alnetum* Oberd. 1953) (Table 1), allocating of 60 experimental areas of the 10 of such to each association (Fig. 1).

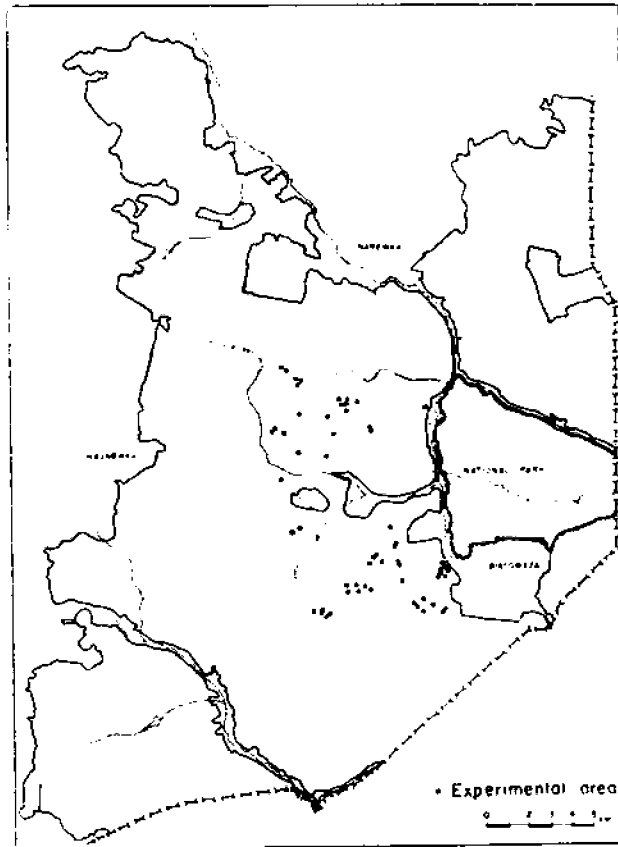


Fig. 1. Map of the Białowieża Forest illustrating the distribution of the study areas.

The dimensions of one area were 10×50 m in the first year, but in the subsequent years, on account of the excessive amount of labour involved in the studies, these areas were reduced in size to 2×50 m. In the various forest associations the experimental areas were situated in tree stands in four age classes: a plantation (age of tree stand 2—6 years), thicket (8—15 years), pole-sized stand (40—60 years) and timber stand (80 years and over).

In order to define the abundance of occurrence of the different plant species in the experimental areas, an exact botanical record was made twice (October—

November 1968 and June 1969) for the area, together with lists of plants. The coefficient of abundance of occurrence for the different plant species ( $D$ ) was obtained by means of the phytosociological surveys made in June 1969, calculation being made (using the Braun-Blanquet scale) of the percentages formed by the different species in each experimental plot. The data obtained in this way were referred to Braun-Blanquet's equation (1946, 1951) giving the value of the abundance coefficient  $D$  (Deckungswert):

$$D = \frac{\text{Sum total of average percentages of cover in all surveys}}{\text{Number of surveys}} \times 100$$

The areas were inspected twice a month, giving a total of 4,320 inspections from December 1968 to November 1971. Lasting traces of feeding by deer and European bison were marked on various individual plants (cropping of leaves and shoots, strapping of bark). One unit of feeding was held to be cropping or eating the leaves from 1 shoot of a tree, shrub or dwarf-shrub, cropping 1 tuft of grass or sedge, grazing 1 dcm<sup>2</sup> of grass or sedge on the ground, consumption of 1 individual (whole or part) of a dicotyledonous forb. Barking was calculated in cm<sup>2</sup> of bark stripped from the trunk.

Table 1

Types of forest associations in which studies were made on the food relations of deer.

Phytosociological terminology of ecosystems after Matuszkiewicz, 1967	Abbreviation
<i>Peucedano-Pinetum</i> (Mat. 1962)	P—P
<i>Pino-Quercetum</i> (Kozł. 1925)	P—Q
<i>Calamagrostio-Quercetum</i> (Hartm. 1934) (Scam. 1959)	C—Q
<i>Tilio-Carpinetum typicum</i> (Tracz. 1962)	T—C <sub>t</sub>
<i>Tilio-Carpinetum stachyetosum</i> (Tracz. 1962)	T—C <sub>s</sub>
<i>Circaeo-Alnetum</i> (Oberd. 1953)	C—A

As units of feeding recorded in this way differed markedly from each other in respect of mass, endeavour was made to render them more uniform. For this purpose, samples were taken near the experimental areas, composed of parts of plants approximately corresponding to units of feeding by ungulates. The samples consisted of plants most often eaten by ungulates, dividing them into four groups: (1) shoots of trees, shrubs and dwarf-shrubs, (2) bark, (3) grasses and sedges, (4) dicotyledonous forbs. By comparing the dry mass of samples, means of conversion were obtained making it possible to compare cropping and bark stripping by deer in comparable units of their mass. In further discussions the term «contact» has been used to define this smallest unit of feeding by ungulates. A more detailed explanation of this method is to be found in an earlier study (Borowski & Kossak, 1972).

The presence of ungulates in the areas was established by means of their tracks and traces of their feeding. In summer traces of feeding by roe deer and red deer were treated jointly, as feeding by deer. Cases in which traces of visits by both deer and European bison were observed were not taken into account, in view of the fact that the authors were unable to determine what part of the food consumed in such cases had been eaten by bison and what by deer. This made it

possible to avoid errors connected with incorrect interpretation of results. The material obtained over the course of three years has been treated jointly.

During the whole study period a record was kept of all traces of animals on the experimental areas, also meteorological data, and in winter additionally the depth of the snow cover. These data made it possible to define the activities of roe deer and red deer in winter.

#### 4. FOOD PREFERENCES OF CERVIDAE

In the author's opinion the composition of the diet of deer depends on three factors: (1) number of plant species in the area, the accessibility of which provides the possibility of the animal's making use of them, (2) likelihood of the animal's encountering the given species of plant capable of forming its food. This easiness of access is largely dependent on the abundance of the plant in the area, (3) the animal's preferences

Table 2

Comparison of the number of plant species occurring in the diet of deer ( $n^2$ ) with the number of plant species found in the study areas ( $n^1$ ).

Ecosystem	Trees, shrubs and dwarf-shrubs		Dicotyledonous forbs and grasses		
	$n^1$	$n^2$	$n^1$	$n^2$	$n^2/n^1 \times 100, \%$
P—P	19	23	64	16	25
P—Q	26	27	104	58	56
C—Q	21	24	85	71	83
T—C <sub>1</sub>	18	20	82	64	78
T—C <sub>2</sub>	21	26	82	55	67
C—A	22	25	81	49	60
Total	37	36	217	137	63

connected with, e.g. the taste values of plants, the animal's requirements for given components etc.

An attempt was made at tracing the influence of these factors on the food preferences of deer.

##### 4.1. Number of Plant Species in the Area and Composition of the Animals' Diet

In order to obtain an idea of the extent of the food preferences of deer comparison was made of the number of plant species growing in the experimental areas in the various ecosystems, with the number of species recorded in the animals' diet (Table 2). In the case of trees, shrubs and dwarf-shrubs a combined number of 37 species grew in the areas, 36 species of which were found in the animals' diet. When considering the various ecosystems separately, the number of species record-

Table with columns: Ecosystem, Species, n, %, D, P-P, P-Q, C-Q, T-C1, T-C2, C-A, Total. Rows include species like Carpinus betulus, Quercus robur, Picea excelsa, etc.

DICOTYLEDONOUS FORBS

Table with columns: Species, n, %, D, P-P, P-Q, C-Q, T-C1, T-C2, C-A, Total. Rows include species like Ranunculus repens, Galium palustre, etc.

GRASSES, SEDGES AND RUSHES

Table with columns: Species, n, %, D, P-P, P-Q, C-Q, T-C1, T-C2, C-A, Total. Rows include species like Milium effusum, Carex silvatica, etc.





ed in the animals' diet is always slightly higher than the number occurring in the area. This is presumably due on the one hand to the appearance of seedlings (three-year study period), and on the other of omission of very small individual plants from phytosociological surveys. The list shows that deer feed on all species of plants from this group except *Crataegus oxyantha*. The lack of contacts of deer with this plant may be due to the fact that only one example of this plant was found on the experimental areas.

In the group of dicotyledonous forbs, grasses, sedges and rushes a total number of 217 species were recorded as occurring in the experimental areas. The deer cropped 137 species, which forms 63% of all species. This percentage varies in different ecosystems, for instance the smallest number of species eaten is in *P—P* (25%), the most in *C—Q* (83%) and in *T—C<sub>1</sub>* (78%), and in the remaining ecosystems this percentage comes within limits of 56—67. Thus slightly more than half the species growing there were observed to be used as food by deer.

#### 4.2. Abundance of Plants and Their Participation in the Animals' Diet

In order to grasp the relation between abundance of plants in the area and their participation in the food of deer the whole of the data obtained in the experimental areas were arranged in a floristic list of trees, shrubs and dwarf-shrubs, and dicotyledonous forbs, grasses, sedges and rushes, occurring in the diet of deer. The plants were arranged in order of their decreasing participation in the whole of the animals' food (Table 3). The above list was compared with the coefficient of abundance (*D*) of the various plant species in ecosystems.

##### 4.2.1. Trees, Shrubs and Dwarf-shrubs

A total of 424,215 contacts with 36 species of plants was recorded. The animals were observed to feed particularly intensively on two species of trees: *Carpinus betulus*, which forms 25.7% of the whole of browse, and *Fraxinus excelsior*, which forms 12.7%. The next two species of trees are: *Quercus robur* — 8.9% and *Salix caprea* — 7.4%. The above four species thus form 54.7% of the browse eaten by deer, while the percentage formed by none of the remaining 32 species exceeds 5% (Table 3).

The order of percentage formed by ligneous plants in the animals' food differs in different types of tree stands, for instance: in *P—P* the order is as follows: *Pinus silvestris* (27.6%), *Vaccinium myrtillus* (22.3%), *Calluna vulgaris* (19.2%), *Cytisus nigricans* (14.6%). There is a direct relation between the considerable amount of these species eaten as food and their abundance of occurrence. All are characteristic of plant com-

munities of fresh coniferous forest, all occur in large numbers and in the case of *Vaccinium myrtillus* — occurrence is very high indeed ( $D = 1.825$ ).

In P—Q the basis of the deer's food is formed by 5 species differing in abundance of their occurrence. *Pinus silvestris* (14% of food), *Vaccinium myrtillus* (8.6%) and *Quercus robur* (8.2%) are common in this ecosystem. Their coefficient of abundance is high, being respectively 150, 1,085 and 125. *Salix caprea* (26.7% of food) and *Carpinus betulus* (13.5%) occur less frequently ( $D = 30$ ).

In C—Q *Carpinus betulus* (39.1% of browse) and *Quercus robur* (19.7%) are the species dominating in the animals' food. Both these species are characterized by a high coefficient of abundance (respectively 135 and 115).

The basis of the food consumed by deer in T—C<sub>1</sub> is formed by three plant species. *Carpinus betulus* decidedly dominates (44.8% of the whole of the browse eaten in this ecosystem) and occurs very numerously ( $D = 370$ ). *Salix caprea* (13.1% with  $D = 105$ ) occurs frequently in the animals' food, while *Quercus robur*, forming 11.2% of food, occurs less often ( $D = 50$ ).

The food consumed in T—C<sub>2</sub> consists mainly of common species, but which even occur in very great numbers. For instance: *Fraxinus excelsior* ( $D = 345$ ) forms 45.4% of the whole of the browse eaten in this ecosystem, *Carpinus betulus*, with  $D = 260$ , forms 19.9%, while the numerously occurring *Rubus ideus* ( $D = 195$ ) forms 8.1%.

In C—A four species from the basis of the food of deer. Two of them — *Fraxinus excelsior* ( $D = 290$ ) and *Corylus avellana* ( $D = 225$ ) form respectively 36.4% and 11.5% of the browse consumed in this ecosystem, while the following two species — less numerous in the area *Picea excelsa* ( $D = 90$ ) and *Carpinus betulus* ( $D = 25$ ) forms respectively 12.4% and 8.8% of the food of deer.

It is clear from the above that plants occurring numerously or even in very great numbers there dominate in the food of deer eaten in the various ecosystems. At the same time, however, a certain number of cases are observed of species with a low coefficient of abundance of occurrence forming a high percentage of the diet of both roe deer and red deer.

#### 4.2.2. Dicotyledonous Forbs, Grasses, Sedges and Rushes

A total number of 84,480 contacts with 137 species of plants was recorded in this group of plants (Table 3). The majority of them form only a low percentage of the food of deer (below 5%). It is only in the

case of 7 species that a considerable number of contacts was recorded. These are: *Ranunculus repens* (16.2%) of the whole of the animals' food in this group of plants), *Caltha palustris* (12.8%), *Filipendula ulmaria* (8.4%), *Aegopodium podagraria* (8.1%), *Impatiens noli-tangere* (7.1%), *Ranunculus lanuginosus* (5.7%) and *Urtica dioica* (5.1%). Taken together they form almost  $\frac{3}{4}$  of the animals' diet.

The domination of the different species of plants in food consumed by deer in different ecosystems is as follows:

In P—P 66.4% of the diet is formed by *Genista tinctoria* ( $D = 55$ ). than two species occurring less numerously in the areas: *Rumex acetosella* ( $D = 15$ ) forming 10.1% of food and *Senecio vernalis* (9.1% of food), not recorded in phytosociological surveys. It must be emphasised that the high percentage formed by the above species of plants was partly due to the small number of species found in the diet of deer in this ecosystem (16) and the small joint number of contacts (939). The above species formed only a negligible percentage of the total diet of deer.

In P—Q, 5 of the 58 species found in the diet of deer formed 56.5% of the food. Two of them: *Solidago virga-aurea* (13.0%) and *Cirsium arvense* (10.2%) are common in this association ( $D$  respectively 70 and 40), while two occur less often: *Aegopodium podagraria* (12.3% with  $D = 10$ ) and *Genista tinctoria* (10.0% with  $D = 25$ ). *Hieracium umbellatum* (10.0% of food) occurred in such extremely small numbers in the areas that it was not included in the phytosociological surveys.

The above plants formed a fairly high percentage of the whole of the food consumed by deer in all ecosystems (13.6%).

Of the 71 species of plants occurring in the diet of deer in C—Q, the largest number of contacts was found for *Centaurea jacea* (21.2%), although this species does not occur very numerously ( $D = 15$ ). The next two species predominating in the animals' diet occur in extremely great numbers, i.e. *Ranunculus lanuginosus* — 16.5% ( $D = 100$ ) and *Urtica dioica* — 11.0% ( $D = 110$ ). *Filipendula ulmaria* ( $D = 5$ ), occurring rarely in the areas, was very readily eaten by deer (8.8%).

The above species of plants are eaten by deer in all the ecosystems in which they occur, and the percentage they form in the whole diet was 21.6%.

The plant species occurring most frequently in T—C<sub>1</sub> is *Aegopodium podagraria* ( $D = 290$ ), and it also dominates in the food of deer (25.5%). *Ranunculus lanuginosus* (11.9% of food with  $D = 150$ ) is also often eaten. The situation is different in the case of the next two species, readily eaten by deer, i.e. *Ficaria verna* (16.3% of food) and *Cirsium arvense* (10.4%), since they occur in far smaller amounts than those

mentioned previously ( $D =$  respectively 35 and 65). The species mentioned form 19.5% of the diet.

In  $T-C_2$  the three species dominating in the diet of deer occur numerously, even in great numbers. These are: *Caltha palustris* ( $D = 130$ ), *Impatiens noli-tangere* ( $D = 860$ ) and *Cirsium oleraceum* ( $D = 160$ ). The percentages they form of the animals' diet are as follows: 30.0%, 13.0%, 8.9%. The percentage of these species in the whole of the succulent food eaten by deer is 23.6%.

In  $C-A$ , as in the preceding ecosystem, species occurring in very great numbers dominate in the food of these deer. They are: *Ranunculus repens* ( $D = 340$ ), forming 36.4% of the animals' diet, *Filipendula ulmaria* ( $D = 380$ ), forming 13.7% and *Caltha palustris* ( $D = 130$ ), forming 10.9%. It must be emphasised that the greatest number of the animals' contacts with herbaceous plants was noted in  $C-A$  (28,959) and consequently the food eaten in this ecosystem decidedly influenced the percentage of the different species of plants in the whole diet, of which the above three species form 37.4%.

In general it may be said that as in the case of trees, shrubs and dwarf-shrubs a large part of herbs eaten depends on their abundance. There are, however, cases in which the number of contacts is greater than it would appear to result from the value of the coefficient of abundance. Such plants can be treated as those specially preferred by deer.

#### 4.3. Food Preferences of Cervidae

The food preferences of deer are indicated, *inter alia*, by cases of intensive cropping by the deer of rare plants in the area (see section 4.2), and avoidance during feeding of certain numerously occurring plants.

In the group of herbaceous plants a certain number of species were characterized by a high coefficient of abundance, although no cases were found of their having been cropped by deer. These are, *e.g.* *Molinia coerulea* (in  $P-P$   $D=400$ ), *Trientalis europaea* (in  $P-P$   $D=185$ ) (in  $P-Q$   $D=145$ ), *Polytrichum communis* (in  $P-P$   $D=185$ , in  $P-Q$   $D = 170$ ). These plants were treated as being clearly avoided by deer.

Both in the group of ligneous and herbaceous plants a certain number of cases were observed of the deer avoiding in certain ecosystems plants commonly occurring in them. In respect of the group of ligneous plants this phenomenon took place *e.g.* in  $P-Q$ , where *Picea excelsa* ( $D = 710$ ) and *Betula verrucosa* ( $D = 400$ ) occur abundantly but were only sporadically cropped (respectively 1.6% and 5.6% of food), in  $C-Q$  *Tilia cordata* ( $D = 420$ , 4.4% in diet), *Betula verrucosa* ( $D = 395$ , 7.7% in

diet). Similar cases were observed in the other ecosystems. In the group of herbaceous plants cases of the deer avoiding plants commonly occurring in the area took place, *inter alia*, in C—Q, where the animals sporadically cropped *Stellaria holostea* ( $D = 810$ ), *Fragaria vesca* ( $D = 295$ ) and *Oralis acetosella* ( $D = 250$ ), and in T—C<sub>1</sub> where a small number of contacts were observed with the commonly occurring *Urtica dioica* ( $D = 535$ ), *Anemone nemorosa* ( $D = 460$ ), *Galeobdolon luteum* ( $D = 380$ ).

Cases in which one and the same species of plant is eaten in greater quantities in one ecosystem than in others, regardless of abundance of occurrence (a phenomenon particularly frequent in the group of trees, shrubs and dwarf-shrubs), is evidence of the variations in the food preferences of deer in relation to the different species of plants. The above question has been discussed in detail in the study dealing with the hypothesis that there are food clusters in the diet of deer (K o s s a k, 1976).

## 5. ANNUAL CYCLE OF THE ANIMALS' FEEDING IN DIFFERENT ECOSYSTEMS

Intensity of feeding and the species composition of the diet of deer over the yearly cycle were examined on the basis of totalled data for the three study years. The two main categories of food: ligneous and succulent, were considered separately.

### 5.1. Trees Shrubs and Dwarf-shrubs

The intensity with which deer feed on the shoots of trees, shrubs and dwarf-shrubs varies over the course of the year (Fig. 2A), this being particularly intensive in the winter months (December and January), and summer months (June and July). The smallest number of contacts was observed in May and September—October. Certain differences can be observed in the distribution of feeding in different ecosystems, for instance: P—P and C—A are characterized by faintly marked summer intensification of feeding (less than 6000 contacts). The winter feeding peak in these ecosystems is clearly evident and occurs in P—P in December (approx. 13,000), but in C—A in January (about 12,000 contacts). In T—C<sub>1</sub> and T—C<sub>2</sub> the distribution of feeding over the year is similar. There is a marked summer peak of feeding (in both ecosystems over 12,000 contacts) and slightly less distinct winter peak (in T—C<sub>1</sub> less than 12,000, in T—C<sub>2</sub> less than 9,000 contacts). In P—Q both peaks of feeding are faintly marked (below 8,000 contacts). The winter peak of feeding is most strongly marked in C—Q, where 19,000 contacts were observed in December and 31,000 in January. There is, however, no summer peak of

feeding in this ecosystem. The number of contacts observed in June (about 6,000) is lower than that recorded for September—October.

Additionally in *P—P* and *C—A* the summer intensification of the animals' feeding is shifted in time, namely it is about one month later than in the other ecosystems, and occurs in July.

The species composition of the animals' diet in different months did not include all species of ligneous plants eaten by deer in the Białowieża Forest in any of the ecosystems examined (cf. Table 3). The largest

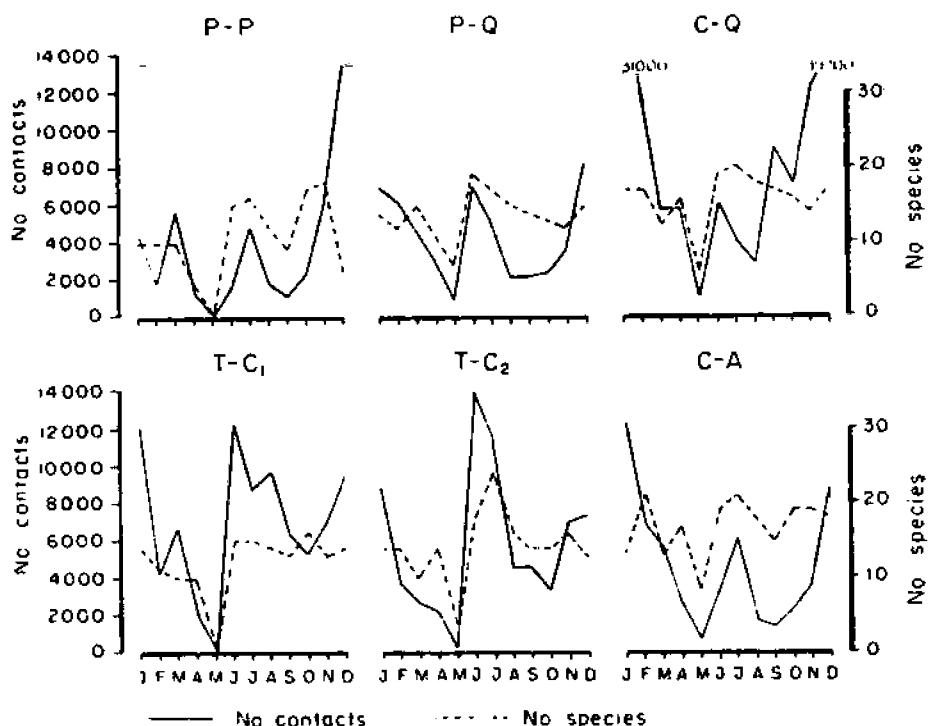


Fig. 2. Yearly cycle of feeding by deer in different ecosystems, taking into account the number of contacts and number of species of plants in the animals' diet in successive month.

A. Shoots of trees, shrubs and dwarf-shrubs.

number of species in the animals' diet (24) was observed in *T—C<sub>2</sub>* in July, and in *C—A* (21) in July and February.

In all the ecosystems examined the summer (June and July) peak of feeding included a larger number of species than was the case with the winter peak (December and January). The differences in favour of the summer diet were from 1 species (*T—C<sub>1</sub>* in June and July — 15, in De-

ember and January — 14) to 11 species ( $T-C_2$  in July — 24, in December 13).

### 5.2. Dicotyledonous Forbs, Grasses and Sedges

There is a strongly marked increase in the number of contacts from the spring to summer months in this group of plants, followed by a decrease in the autumn months (Fig. 2B). Peak feeding by deer occurs in  $P-Q$ ,  $T-C_2$  in June, in  $C-Q$  in May—June, and in  $T-C_1$  and  $C-A$

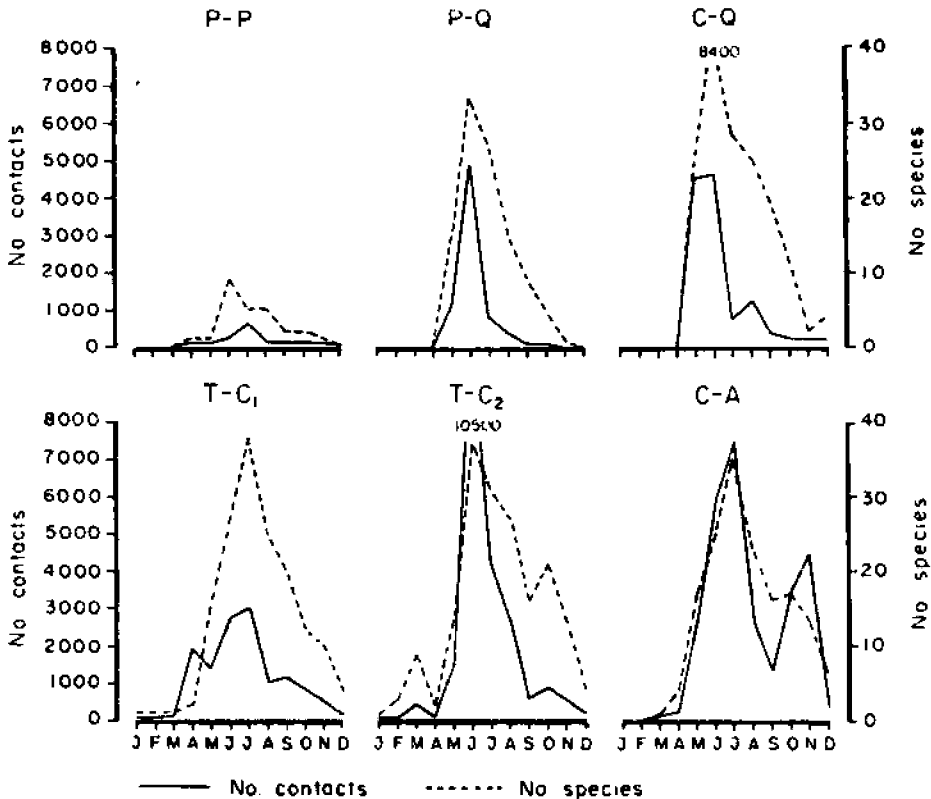


Fig. 2B. Dicotyledonous forbs, grasses sedges and rushes.

in June—July, and in  $P-P$  in July. In the case of  $C-A$  there is an increase in the number of contacts in November due chiefly to intensive cropping of *Ranunculus repens* by deer.

When comparing intensity of feeding by deer with the variety of species in their diet it can be seen that these two features are connected with each other. In each of the ecosystems examined the largest number

of species cropped occurred during the time, when there was a peak of feeding.

**5.3. Percentages Formed by Trees and Herbs in the Animals' Food over the Course of a Year**

We have limited ourselves here to discussing differences in the percentages formed in the animals' diet by the two basic groups of plant food they eat, namely, trees, shrubs and dwarf-shrubs, and dicotyledo-

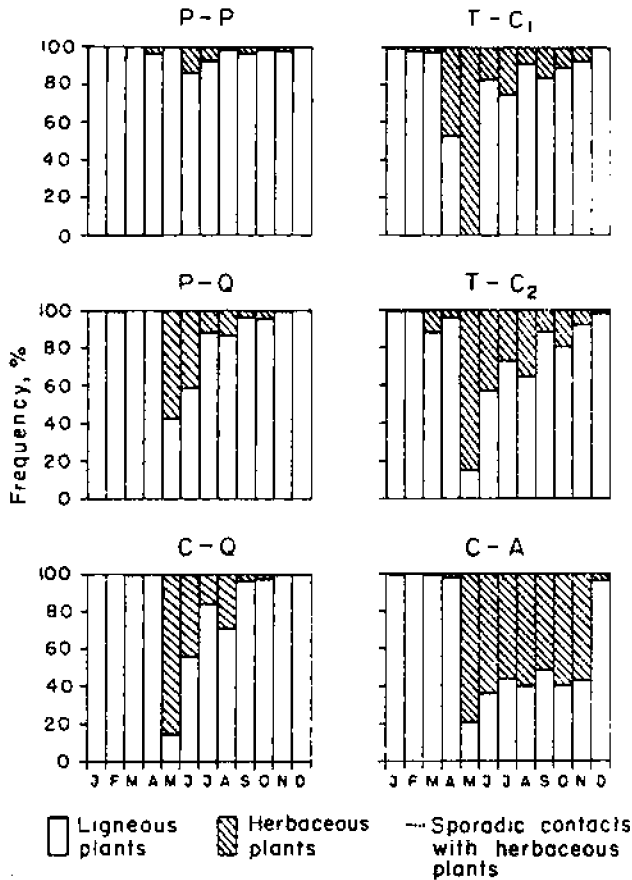


Fig. 3. Percentages formed by trees, shrubs and dwarf-shrubs (open), and dicotyledonous forbs and grasses (hatched) in the diet of deer over the yearly cycle in six ecosystems studied.

nous forbs, grasses, edges and rushes, over the yearly cycle and in all the ecosystems examined. No analysis has, however, been made of the percentages formed by these groups of plants in the whole of the animals' food since it was assumed that the fairly large number of contacts



between the animals and dicotyledonous forbs and grasses could not be grasped during the course of collecting material.

It can be seen from Fig. 3 that the lowest percentage of herbaceous plants was observed in  $P-P$  and  $P-Q$ , and the highest in  $C-A$ . Omitting cases in which single contacts were observed during the course of a month, deer fed longest in  $T-C_1$  and  $T-C_2$ , in which the interval in feeding on this group of plants was only two months. In the other ecosystems the corresponding interval was: in  $P-P$  from December to March inclusive, in  $P-Q$  and  $C-Q$  from November to April inclusive and in  $C-A$  from January to March inclusive.

In the associations examined (except for  $C-A$ ) a decrease is observed in successive summer months of the percentage formed in the animals' food by herbaceous plants. In  $C-A$  from June to November inclusive the percentage formed by this group of plants is maintained on a similar level. In May herbaceous plant food dominates in all the ecosystems from the aspect of the percentage it forms (Fig. 3). This is partly due to both roe deer and red deer almost completely ceasing to feed on ligneous plants at this time. This in turn is due, *inter alia*, to the animals changing from winter to summer food.

#### 6. ANNUAL CYCLE OF THE ANIMALS' FEEDING ON TREE STANDS OF DIFFERENT AGE

Observations were made of which age classes of tree stand deer prefer during the course of the year and whether such preferences differ in different ecosystems by examining four groups of tree stands of different age. It was only in  $T-C_2$  and  $C-A$  that the youngest age class was not taken into consideration (plantations), on account of their absence in the area (cf. Material and methods). As a different number of study areas were chosen in the different age classes (from 1 to 5), calculation was made of the average number of contacts per 1 area of the given age class in the given ecosystem. Average numbers of contacts in each age class of 6 ecosystems have been set out distributed over the course of a year. On account of the considerable differences in preferences for different age classes a separate description has been given of successive ecosystems.

##### 6.1. Trees, Shrubs and Dwarf-shrubs

*Peucedano — Pinetum (P-P)*. In this ecosystem (Fig. 4A) the food consumed by deer in the plantation dominates in March and November, in July — food in the thickets and in December in the timber stand. Intensity of feeding by both roe deer and red deer is only slight in the

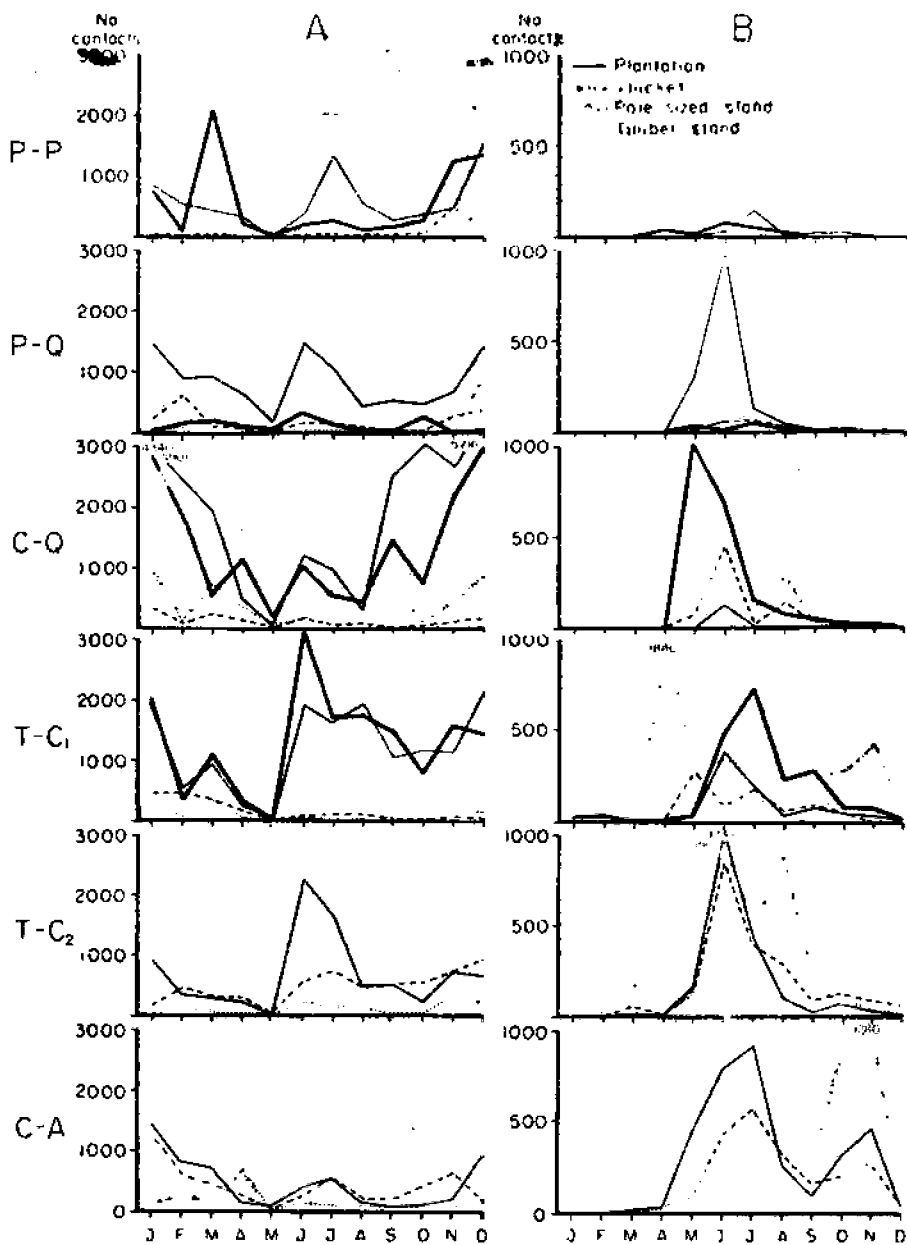


Fig. 4. Yearly cycle of feeding by deer in tree stands of 4 different age classes in 6 different ecosystems in the Białowieża Forest.

A. Trees, shrubs and dwarf-shrubs, B. Dicotyledonous forbs, grasses sedges and rushes.

timber stand (except in December). This also applies to pole-sized stands, in which there was a slight increase in the number of contacts in November. Peak feeding by deer occurred in December, during which time the greatest number of contacts was found in the timber stands thickets and plantations.

*Pino — Quercetum (P—Q)*. In all months of the year deer consumed the greatest amount of food in the thickets. Feeding was maintained on fairly low level in the tree stands of the remaining age classes, with some degree of intensification in June and October in the plantation, in February and December in the pole-size stand and in March and December in the timber stand. The highest monthly number of contacts was observed in December, to which food consumed in the plantations and timber stands, and to a lesser degree in the pole-sized stands, contribute (Fig. 4A).

*Calamagrostio — Quercetum (C—Q)*. From September to March the deer consumed the majority of their food in the thickets and (with exception of March) the plantations. There were three decreases in feeding in the timber stands: in February, May—June and in October. Feeding in the pole-sized stands was maintained on a fairly low and even level. The winter peak in feeding lasted from November to February inclusive, a constant order of preference for the following age classes being maintained: thicket, plantation, timber stand and pole-sized stand (Fig. 4A).

*Tilio — Carpinetum typicum (T—C<sub>1</sub>)*. In this ecosystem deer consumed by far the greatest part of their food in the plantations and thickets throughout the whole year. The number of contacts in tree stands of these age classes decreases in February and is equal to the number of contacts observed in this month in the pole-sized stand. From April to December inclusive the animals consumed only a small amount of food in the pole-sized stand and timber stand. From January to March inclusive there was a slight increase in the number of contacts in tree stands of these age classes. Maximum feeding was observed in *T—C<sub>1</sub>* in June, in which month contacts were observed chiefly in the plantations and thickets (Fig. 4A).

*Tilio — Carpinetum stachyetosum (T—C<sub>2</sub>)*. In January, June and July, out of the three age classes of tree stand examined, the deer feed to the greatest extent in the thickets. In the other months the numbers of contacts recorded in the thickets and pole-sized stands are more or less even. Over the course of the whole year feeding in the timber stand is maintained on a fairly low level. Contacts observed chiefly in the thicket, then the pole-sized stand and timber stand, account for the summer peak of feeding (Fig. 4A).

*Circaeo — Alnetum (C—A)*. As was the case with *T—C<sub>2</sub>*, no studies

were carried out in the plantation. From December to March the deer feed mainly in the thickets and pole-sized stands, but in April in the timber stand. In this ecosystem only a small combined number of contacts was observed, and consequently no significant differences were shown in intensity of feeding by deer in the different age classes of tree stand (Fig. 4A).

#### 6.2. Dicotyledonous Forbs, Grasses and Sedges

*Peucedano — Pinetum (P—P)*. The small number of contacts observed in this ecosystem made it impossible to show any distinct domination of the animals' feeding in a tree stand of a given age. It would, however, seem significant that in spring (March—May) the deer feed on herbaceous plants in plantations, in summer (June—August) in the plantations, thickets and pole-sized stands, while in autumn (September—November) they feed chiefly in thickets. Only a negligible number of contacts were found in the timber stand (Fig. 4B).

*Pino — Quercetum (P—Q)*. Except for May and June, when deer feed intensively on herbs in the thickets, feeding is approximately similar in all the other age classes of tree stand and is maintained on a low level (Fig. 4B).

*Calamagrostio — Quercetum (C—Q)*. The greatest amount of food consumed by deer in the plantation occurred in May and June, and in this latter month the intensity of the animals' feeding also increases in the pole-sized. In August feeding reaches a peak in the timber stand. In the other months the number of contacts is similar in tree stands of different age classes (Fig. 4B).

*Tilio — Carpinetum typicum (T—C<sub>1</sub>)*. In this ecosystem the deer fed most intensively on herbs in April in the timber stand. In May the number of contacts observed in this age class drops considerably, to be maintained on a similar, moderate level up to November inclusive. Deer fed throughout the whole year in the plantation, particularly intensively in June and July. From May to November—December herbaceous plants were also cropped in the thickets and the pole-sized stands (Fig. 4B).

*Tilio — Carpinetum stachyetosum (T—C<sub>2</sub>)*. Intensity of feeding in tree stands of different age was balanced in successive months. It was only exceptionally in August that considerable cropping of herbaceous plants was observed in the timber stand. Peak feeding by deer occurred in this ecosystem in June and was accounted for the food consumed in the thickets, pole-sized and timber stands (Fig. 4B).

*Circaeo — Alnetum (C—A)*. In the spring-summer months (May—July) the deer fed in the thickets and pole-sized stands. After the drop in the number of contacts in August and September, there is a renewed peak

of feeding in these age classes, lasting through October and November. Intensity of feeding in the timber stand takes the reverse course. The first slight increase in the number of contacts taken place in June, the second — very intensive — in October and November (Fig. 4B).

It must be assumed that intensive feeding by deer in a tree stand of a given age class usually includes both ligneous and herbaceous plants. This phenomenon occurs *inter alia* in  $P-P$ , where in July food consumed in the thickets dominates in both groups of plants. A similar phenomenon occurred in June in  $P-Q$ . In  $T-C_1$  in June and July the two groups of plants are intensively cropped by deer in the plantations and thickets. In  $T-C_2$  in June the order of preferences for age classes of tree stands in the same — thickets, pole-sized and timber stands.

Differences in the animals' preference for age classes of tree stand between the groups of plants discussed relate chiefly to the timber stand. In  $T-C_2$  the greatest number of contacts with herbs was observed in this age class in June and August, when there was little feeding on ligneous plants. A similar phenomenon occurred in November in  $T-C_1$  and  $C-A$ . As can be seen from Fig. 4, the deer consume considerable amounts of herbs, and grasses, but only small amounts of trees and shrubs in timber stands, in which there is usually a luxuriant herb layer but only a small amount of accessible browse.

## 7. DISCUSSION OF THE ANIMALS' FEEDING ON SELECTED SPECIES OF PLANTS

Calculation was made of the average number of contacts per study area in the different age classes of tree stands for 12 species of trees, shrubs and dwarf-shrubs (forming 87.2% of the whole of the food eaten by deer from this group of plants), and for 8 species of herbaceous plants (61.5% of food from this group). Examination was made of which species contribute chiefly to the diet of deer in different seasons, and types and age classes of tree stands, and a description has been given of feeding by deer on different species of plants in time and space.

As intensity of the animals' feeding is subject to great variation over the yearly cycle the rhythms of their phenological phases have been taken into account in discussing feeding on different species of plants.

### 7.1. Trees, Shrubs and Dwarf-shrubs

Comparison was made between the time of leafing, flowering, fruiting and seed dispersal of 12 species of trees and shrubs, growing in the Białowieża Primeval Forest (acc. to Graniczny, 1957) and the yearly distribution of feeding by deer, but no regularity was observed. In none

of the cases does the summer (June—July) peak of feeding coincide with any of the phenological appearances of the species examined, and it may therefore be concluded that this peak is due to the occurrence of young shoots and leaves of trees and shrubs. On the other hand the winter (December and January) peak of feeding is due to the lack of succulent food. Consequently the dates of phenological appearances have not been given in discussing the course taken by the animals' feeding.

*Carpinus betulus* — forms 25.7% of the whole of the browse consumed by deer. It is eaten chiefly in C—Q (39% of the whole of their food) and in T—C<sub>1</sub> (45%), being particularly intensively eaten in C—Q, despite its usually not very numerous occurrence (see section 4). It is cropped most intensively in the thickets and plantations, being consumed to a far lesser extent in pole-sized and timber tree stands. It can be seen from the annual distribution of the animals' feeding (Fig. 5) that *Carpinus betulus* is eaten mainly in winter, and to a lesser degree in autumn and spring, and least in summer. This phenomenon occurs in all ecosystems and age classes of tree stand.

*Carpinus betulus* is thus a species readily eaten by deer. It occurs very frequently in large amounts in the animals' diet in the autumn — winter and spring months, whereas in summer its importance as food decreases. It is eaten chiefly in thickets and plantations of C—Q and T—C<sub>1</sub>.

*Fraxinus excelsior* forms 12.7% of the whole of the shoots consumed by deer, and is eaten chiefly in ecosystems in which it occurs numerously (see section 4) i.e. in T—C<sub>2</sub> (45% of food eaten) and in C—A (36%). The highest average number of contacts per study area was observed in thickets T—C<sub>2</sub> and C—A. Shoots of *Fraxinus excelsior* are slightly less intensively eaten in the pole-sized stands. The smallest number of contacts was observed in the timber stands (Fig. 5).

Two peaks of feeding by deer on this species can be observed over the yearly cycle: in T—C<sub>2</sub> a winter peak (in December and January) and a slightly greater peak in summer, lasting from June to September. In C—A the summer peak is less clearly marked and lasts for a shorter time (June—July).

*Fraxinus excelsior* is thus a species readily eaten by both roe deer and red deer, and the more numerous its occurrence, the more intensively is it eaten (see section 4). It is a species characteristic of the food consumed in T—C<sub>2</sub> and C—A thickets and pole-sized stands, in winter and summer months.

*Quercus robur* forms 8.9% of the whole of food eaten in the form of shoots by deer. It is most intensively eaten in C—Q (20% of browse consumed by the animals in this ecosystem) and in T—C<sub>1</sub> (11%), parti-

cularly in plantations and thickets. Only a small number of contacts was, however, observed in pole-sized and timber stands. During the course of the year there were two periods of particularly intensive consumption of the shoots of *Quercus robur* by deer. The winter peak lasted in plantations from November to February inclusive, and in December and January in thickets. A particularly large number of contacts was observed in January in the thickets of C—Q. The summer peak of feeding on *Quercus robur* by these animals, less intensive than the winter peak, occurs in all ecosystems and age classes in June (Fig. 5).

*Quercus robur* is a species characteristic of the winter, and to a lesser degree of the summer, browse of deer. It is readily eaten in C—Q and T—C<sub>1</sub> plantations and thickets.

*Salix caprea* forms 7.4% of the whole of the browse. It is consumed to a similar, moderate degree in P—Q, C—Q and T—C<sub>1</sub>. In P—Q the majority of the contacts were observed in the thickets, whereas in the two other ecosystems amounts were similar in thickets and plantations. On account of the moderate combined number of contacts recorded, the summer and winter intensifications of consumption of *Salix caprea* are faintly marked (Fig. 5).

*Salix caprea* is thus a species eaten to a moderate degree in plantations and thickets of P—Q, C—Q and T—C<sub>2</sub> over the course of the whole year. Some degree of intensification is observed in June, December and January.

*Picea excelsa* — forms 5.3% of the whole of browse eaten by deer. Although it occurs very numerously in coniferous forest ecosystems, only small quantities of it are eaten by deer (see section 4.3.). A moderate number of contacts were observed in thickets and pole-sized stands of deciduous forests. Consumption of *Picea excelsa* in timber stands was observed only in C—Q and T—C<sub>1</sub>. Over the yearly cycle it occurs in the animals' diet from December to March—April. The largest number of contacts with *Picea excelsa* were observed in the thickets of C—Q in January (Fig. 5).

*Pinus silvestris* forms 4.8% of the whole of browse taken by deer. It is consumed almost solely in coniferous forest habitats, where it occurs in large numbers (see section 4). The largest number of contacts was observed in the thickets and plantation of P—P and in the thickets of P—Q. *Pinus silvestris* is characteristic of the winter diet of deer. The majority of contacts were observed in December and January (Fig. 5). *Corylus avellana* forms 4.7% of the browse. It is consumed to a more or less balanced degree in all ecosystems and age classes of tree stands in which it occurs, over the whole of the year (Fig. 5).

*Rubus idaeus* forms 3.9% of the shoot food eaten by deer, and is eaten moderately in all ecosystems. The largest number of contacts were observed in the plantation and thickets of T-C<sub>1</sub>, the thickets and pole-sized stand of T-C<sub>2</sub> and in the pole-sized stand of C-A. *Rubus*

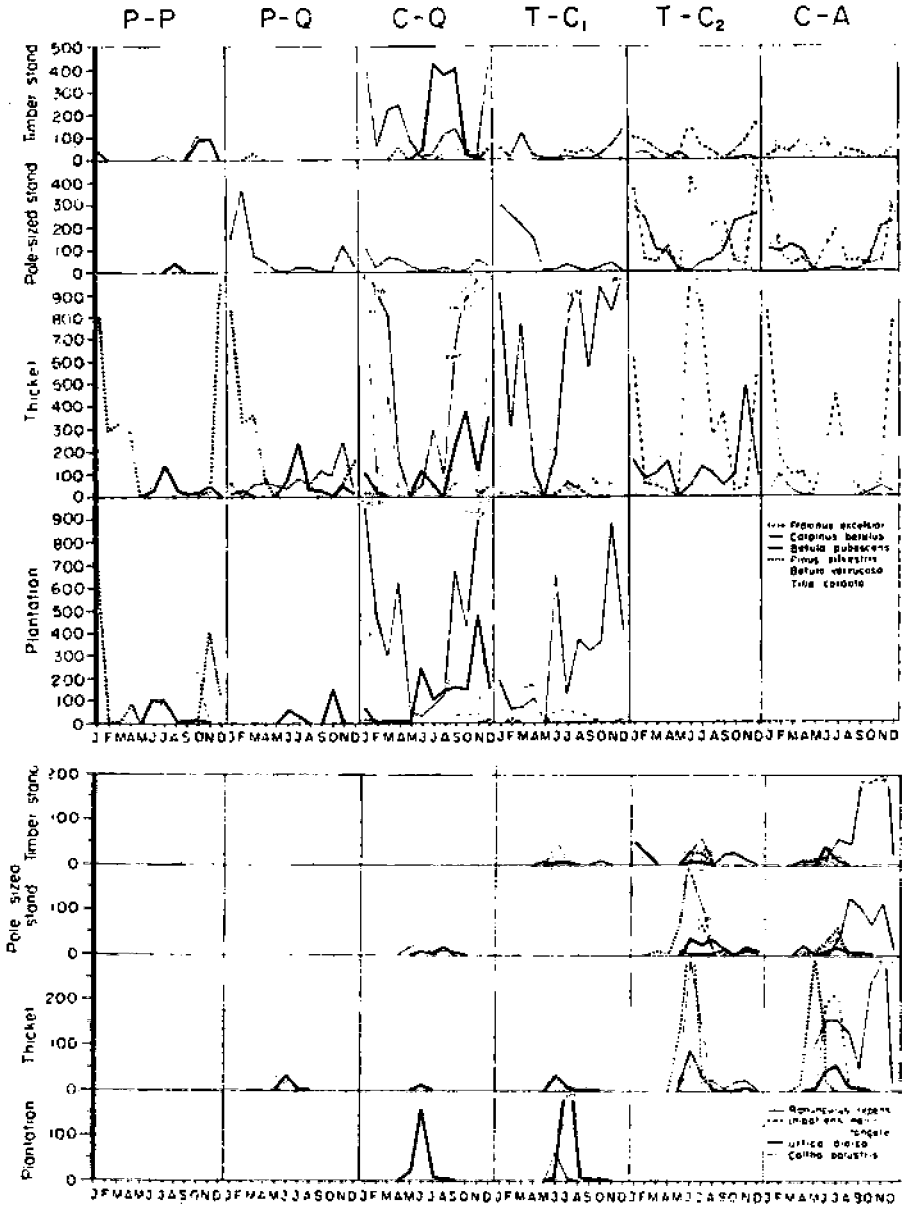


Fig. 5. Feeding by deer on selected species of trees, shrubs, dwarf-shrubs and dicotyledonous plants in 6 types and 4 age classes of tree stands, as expressed in number of contacts.



*idaeus* is eaten over the whole of the year, particularly from June to October — November (Fig. 5).

*Tilia cordata*, like the preceding species, is eaten to a moderate degree (3.6 of the whole of browse) in all ecosystems. The largest number of contacts were observed in plantations and thickets of C—Q

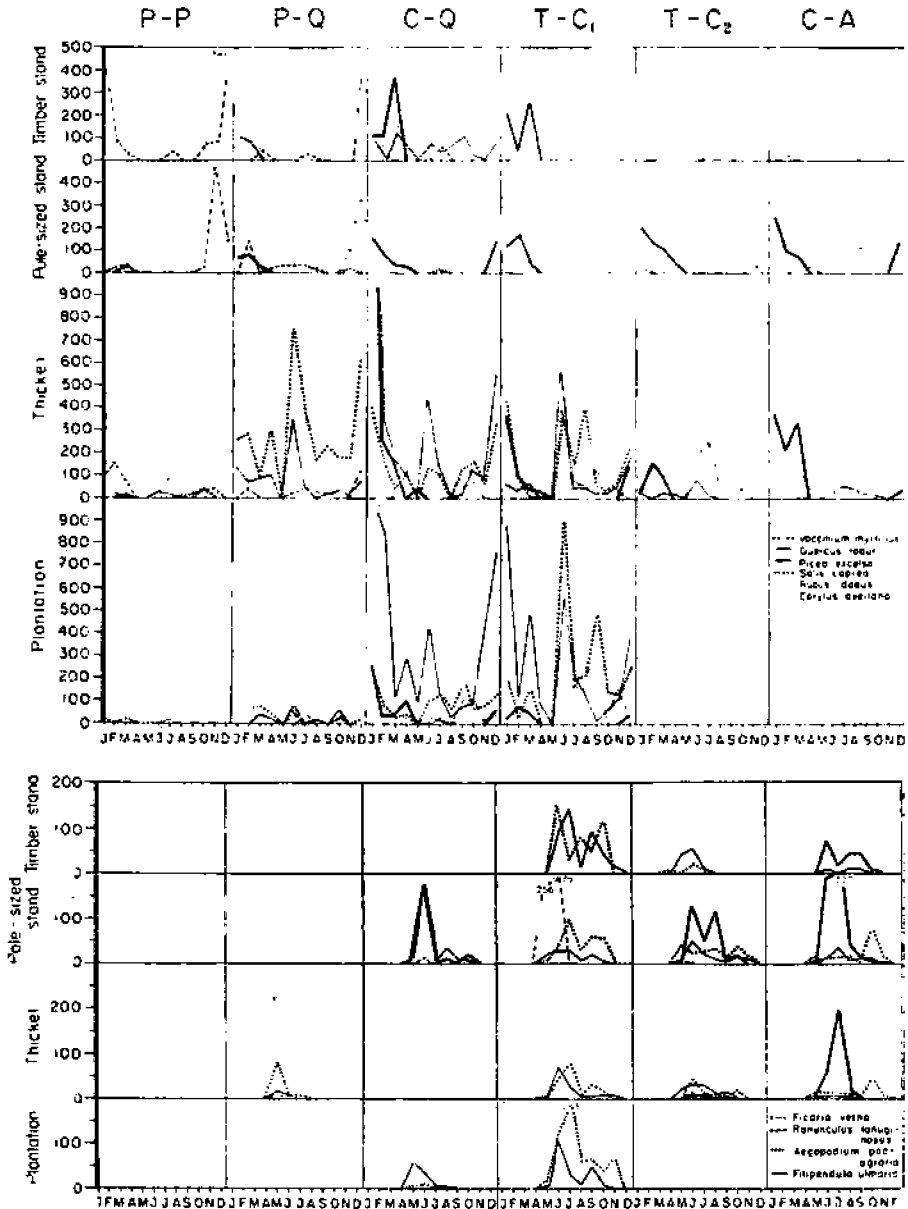


Fig. 5. continued.

and T—C<sub>1</sub>. Over the yearly cycle greater consumption of *Tilia cordata* occurs in the summer months (June—September) and in winter (January) (Fig. 5).

*Vaccinium myrtillus* forms 3.6% of shoot food eaten by deer. It is eaten in habitats in which it occurs numerously (coniferous forests) (see section 4.2.), chiefly in timber stands. It is a typical food of deer in the winter period. Intensive feeding by deer on *Vaccinium myrtillus* begins in November, with a maximum in December. Its importance in the animals' diet decreases from January onwards, presumably due to the persistence of snow cover deeper than at the beginning of winter. The largest number of contacts was observed in December in the old P—P tree stand (Fig. 5).

*Betula verrucosa* forms 3.5% of the whole of browse taken by deer. It is eaten by the animals chiefly in C—Q, and to a lesser degree in P—P and P—Q, mostly in thickets and plantations. The yearly distribution of the animals' feeding on *Betula verrucosa* differs in different ecosystems. In P—P feeding was not found to be very intensive, being maintained on an even level from July to October. In the timber stand P—Q *Betula verrucosa* was eaten during April, but in considerable quantities. In C—Q in all age classes of tree stand feeding was observed to intensify in December and January (Fig. 5).

*Betula pubescens* forms 3.1% of the browse eaten by deer. Like the previous species, it occurs in the animals' diet in both coniferous habitats (P—P and P—Q) and in C—Q. It is eaten in all age classes of tree stands, except pole-sized stands, in which only sporadic contacts were observed. Consumption of *Betula pubescens* over the yearly cycle differs from the way deer feed on *Betula verrucosa*, since it occurs during the period from June to December (Fig. 5).

## 7.2. Dicotyledonous Forbs

The distribution in time and space of feeding by deer on selected species of herbs has been discussed. At the same time, on the basis of data concerning the seasonal dynamics of the herb layer of forest associations in the Białowieża Primeval Forest (Falińska, 1973), the influence of the life cycles of plants has been traced on the yearly distribution of feeding by deer. In these comparisons 8 species of dicotyledonous forbs occurring numerously in the Białowieża Forest, and simultaneously forming 66.6% of the succulent food of deer, have been taken into consideration. All data relating to the phenological characters of the species discussed in this action have been given after Falińska (1973).

*Ranunculus repens* forms 16.2% of the whole of the herbaceous food of deer. It was observed to be eaten in very large amounts in C—A. In the other ecosystems it is not eaten to any great extent. In the three age classes of the C—A tree stand examined, the largest number of contacts calculated per 1 study area was observed in the timber stand, then in turn in the thickets and pole-sized stands (Fig. 5). Over the yearly cycle the greatest differences in number of contacts in successive months were also observed in the C—A timber stand. In this ecosystem the first contacts with *Ranunculus repens* took place in April, and in subsequent months intensity of the animals' feeding on this species increased to reach a maximum in October and November, after which it decreased and only a small number of contacts was observed in December. In the young C—A tree stand the first scanty traces of the animals having fed on *Ranunculus repens* were found in April. In May the number of contacts increased and were maintained on a similar level until August inclusive. In September feeding by deer on this species decreased transitorily, then in the next two months reached the yearly maximum (in a way similar to that in the old tree stand). In the pole-sized stand feeding was more even in character and was maintained on a similar level from August to November inclusive.

*Ranunculus repens* is a species which begins its flowering phase during the first part of June, fruits from the end of June to the beginning of August, and seeds from August to October.

When comparing the yearly distribution of the animals' feeding on *Ranunculus repens* with its yearly cycle it can be seen that this species is eaten in all stages of its life cycle, in the greatest amounts during the seed-scattering period and immediately after the end of the phase.

*Caltha palustris* forms 12.8% of the succulent food of deer. It is eaten particularly intensively in T—C<sub>2</sub> and C—A. In T—C<sub>2</sub> the greatest number of contacts were noted in the thickets and pole-sized tree stands, but only a small number in the timber stand. In C—A the thickets dominated in respect of the number of contacts. Only a small degree of feeding on *Caltha palustris* was observed in the timber and pole-sized stands (Fig. 5). This species occurs in the animals' diet over the yearly cycle from sporadic contacts in March and April as to the considerable percentage of the animals' diet it forms in May, June and July. The yearly distribution of the amount of *Caltha palustris* eaten by deer is due to its development cycle. Under field conditions *Caltha palustris* appears sporadically in March and April in the form of scanty leaves. It reaches maximum development in May and June, and begins the resting phase as early as July. This explains the comparatively short

period of the occurrence of *Caltha palustris* in the diet of deer, coinciding the time of mass occurrence of this plant.

*Filipendula ulmaria* forms 8.4% of the succulent food of deer, and was observed to be consumed in small amounts in C—Q and in T—C<sub>2</sub>. It is frequently eaten in C—A, and the largest number of contacts was found in the pole-sized stands of the above ecosystems. *Filipendula* occurs in the animals' diet from May to October, being eaten in considerable quantities from June to August inclusive (Fig. 5).

*Filipendula* is a species characteristic of high summer. It begins flowering during the first or second ten-day period of July. Since the number of contacts decreases in August the statement is justified that *Filipendula ulmaria* is eaten by deer in the greatest amounts during its flowering period.

*Aegopodium podagraria* forms 8.1% of the succulent food of deer. Contacts with this species were observed in all ecosystems in which this plant occurs. It was eaten in the largest amounts in T—C<sub>1</sub>, in which ecosystem the animals readily fed on *Aegopodium podagraria* in all age classes of the tree stand. The largest number of contacts was observed in the plantation, then in the thickets, with slightly fewer in the pole-sized and timber stands. This plant occurs in the animals' diet from May to November inclusive. The majority of the contacts were observed from June to October, the maximum occurring in June and July (Fig. 5).

*Aegopodium podagraria* is characterized by a long growing period from spring to late autumn. Its maximum development occurs in late spring or summer. It flowers at the end of June and beginning of July. It is consumed with maximum intensity by deer during its flowering period.

*Impatiens noli-tangere* is characterized by a short development cycle. It is most often eaten in T—C<sub>2</sub> and C—A, particularly intensively in thickets. The animals feed on *Impatiens noli-tangere* chiefly in June and July, only a negligible number of contacts being observed in other months (Fig. 5).

*Impatiens noli-tangere* is characterized by a short development cycle. Its most intensive growth occurs in early summer, it flowers during the first or second ten-day period of July and fruits at the end of July. The foregoing shows that *Impatiens noli-tangere* is most readily eaten by deer during its flowering and fruiting periods.

*Ranunculus lanuginosus* forms 5.7% of the succulent food of deer, and is eaten to a moderate degree in all the ecosystems in which it occurs. The largest number of contacts was observed in T—C<sub>1</sub>. This species is cropped by deer in all age classes of tree stands, but chiefly in the

pole-sized stand of  $C-Q$ , and the timber stand of  $T-C_1$  and  $T-C_2$ . Two peaks can be distinguished over the annual cycle of the animals feeding on this species: in June—July and September (Fig. 5).

*Ranunculus lanuginosus* has a long growing period — from spring to late autumn. It flowers during the first ten days of May, fruits in June—July, and seeds in September. When the life cycle of *Ranunculus lanuginosus* is compared with the annual cycle of its consumption by deer, it can be seen that it is most readily cropped by the animals during the stages of its fruiting and seeding. Only a small number of contacts was observed during the flowering period of this species.

*Urtica dioica* forms 5.1% of the succulent food of deer, and is eaten in all the ecosystems in which it occurs, but to the greatest extent in plantations. In  $C-Q$  the largest number of contacts was observed in June, in  $T-C_1$  in July, and in  $T-C_2$  and  $C-A$  in June and July. Feeding on *Urtica dioica* was observed in January and February in the old  $T-C_2$  tree stand (Fig. 5).

*Urtica dioica* reaches maximum development during summer, flowers in July, and fruits in August—September. The maximum consumption of this species by deer therefore occurs during its flowering period.

*Ficaria verna* forms 3.2% of the whole of the succulent food of deer. It is an interesting species on account of the fact that it is eaten almost solely in the old  $T-C_1$  tree stand in April, and to some extent in May. The place in which the deer feed on *Ficaria verna* was determined by the abundance of the occurrence of this species. In  $T-C_1$  the coefficient of abundance is 300. In the other ecosystems and age classes of tree stand this species occurs in small number (see section 4.2.2) (Fig. 5).

*Ficaria verna* is characterized by a short annual growing period. Its most intensive development occurs in spring and it flowers during the first ten days of May. It also fruits in May and partly in June. It completes its growing period at the end of July. This justifies the statement that *Ficaria verna* is cropped by deer during the period of its flowering and fruiting.

It can be seen from the examples given above that there is a distinct connection between the life stages of plants and the intensity with which deer feed on them. It would seem significant that it is plants passing through a generative stage (flowering and fruiting) which are particularly intensively cropped. This question has been dealt with in greater detail in the study by Kossak (1976).

#### 8. WINTER FOOD OF THE ROE DEER AND RED DEER

The authors consider that one of the most important factors governing the role of deer in forest ecosystems is their winter food, and con-

sequently a more detailed analysis has been made of feeding by roe deer and red deer in the Białowieża Primeval Forest during the winter months. During this period, the tracks left by the animals in the snow made it possible to attempt to distinguish between food consumed by roe deer and red deer from the whole of the material on winter feeding by deer in the following way: all traces of feeding near tracks left by a red deer were attributed to this species, and the same procedure was adopted for roe deer. The winter period was considered as lasting 5 months (from December to April inclusive), since there was usually snow cover in the Forest during this time. Only a very few dicotyledonous forbs occur in the animals' diet in winter (see section 5.3.) and these would not appear to be of any great importance. As a result we have limited ourselves in this section to discussing the group formed by trees, shrubs and dwarf-shrubs.

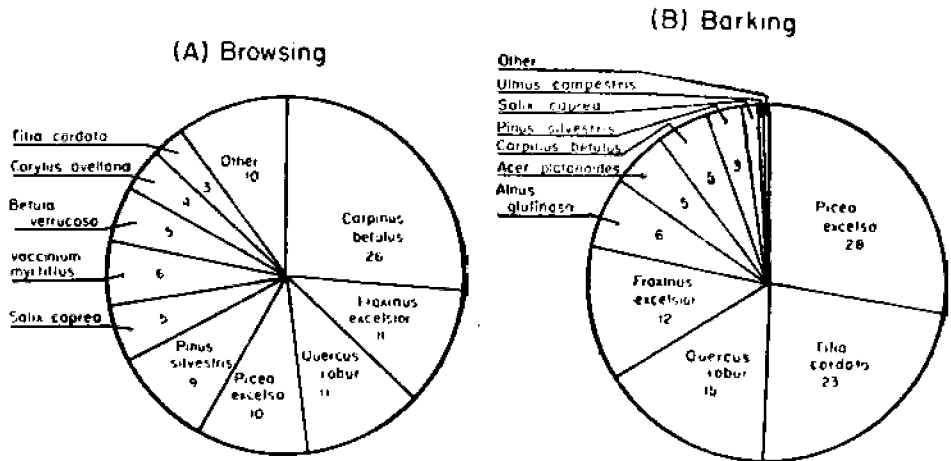


Fig. 6. Comparison of the percentages formed by different species of trees, shrubs and dwarf-shrubs consumed by deer either by browsing (A) or barking (B). The total amount of barking or browsing was taken as 100%.

Deer obtain a certain amount of food by means of bark stripping, this applying mainly to red deer. As bark stripping was not observed during the summer (which does not necessarily mean that it does not take place at all), a discussion is given in this section of this means of obtaining food by deer.

In winter 33 species of trees, shrubs and dwarf-shrubs, consumed by browsing or barking, were found in the diet of roe deer and red deer. In winter the species most frequently consumed are *Carpinus betulus* (26% of browse), *Fraxinus excelsior* (11%), *Quercus robur* (11%), *Picea*

*excelsa* (10%) and *Pinus silvestris* (9%) (Fig. 6A). The percentage formed by species from which the animals strip bark is as follows: *Picea excelsa* (28%), *Tilia cordata* (23%), *Quercus robur* (15%) and *Fraxinus excelsior* (12%) (Fig. 6B).

### 8.1. Browsing

The combined number of contacts attributed to feeding by roe deer in winter months was 130,640, the corresponding figure for red deer being 53,186. The decided predominance of feeding by roe deer was due partly to the fact that they more frequently wandered over the study areas and also that bark stripped from trees formed a considerable part of the winter food of red deer (in the light of our studies this was about 47%).

Table 4

Percentages formed by the 10 species of trees, shrubs and dwarf-shrubs most often included in the winter diet of the roe deer and red deer.

Roe deer			Red deer		
No.	Species	%	No.	Species	%
1.	<i>Carpinus betulus</i>	26.5	1.	<i>Carpinus betulus</i>	22.5
2.	<i>Fraxinus excelsior</i>	16.3	2.	<i>Pinus silvestris</i>	20.5
3.	<i>Picea excelsa</i>	11.8	3.	<i>Quercus robur</i>	13.5
4.	<i>Quercus robur</i>	10.8	4.	<i>Salix caprea</i>	8.5
5.	<i>Vaccinium myrtillus</i>	7.3	5.	<i>Picea excelsa</i>	8.5
6.	<i>Corylus avellana</i>	4.8	6.	<i>Betula verrucosa</i>	7.5
7.	<i>Salix caprea</i>	4.5	7.	<i>Tilia cordata</i>	6.0
8.	<i>Betula verrucosa</i>	4.2	8.	<i>Fraxinus excelsior</i>	3.2
9.	<i>Pinus silvestris</i>	4.2	9.	<i>Salix cinerea</i>	3.0
10.	<i>Tilia cordata</i>	2.4	10.	<i>Corylus avellana</i>	1.8
	Other	7.2		Other	5.0
Total		100.0	Total		100.0

In order to grasp differences in the composition of the winter diet of roe deer and red deer calculation was made (separately for the two species of animals) of the percentage formed in intensity of browsing (Table 4). In the case of the roe deer these plant species form 92.8%, and in the case of red deer 93.7%, of their winter food. It was found that the species composition of the diet of the two species of animals is similar, except that in the case of the roe deer there is no *Salix cinerea* in the first 10 species preferred and in the case of the red deer this applies to *Vaccinium myrtillus*. Differences in the percentage formed by different species in the diet of the animals examined apply chiefly to the following plants: *Fraxinus excelsior* forms 16.3% in the

case of the roe deer, and 3.2% in the case of the red deer, while *Pinus silvestris* forms respectively 4.2% and 20.5%. The other species of browse form similar percentages in the diet of the two species.

### 8.2. Barking

Deer strip bark from a total of 14 species of trees and shrubs. The combined number of contacts recorded for this kind of feeding is 50,027 (Table 5), of which 47,089 was attributed to the red deer, and 2,938 to the roe deer. Bark-stripping varies in intensity in time: it is least intensive in October and November, and in April. Contacts recorded in these months form 5% of the whole of the material. In December and Ja-

Table 5

Percentages formed in the diet of deer by bark of different species of trees and shrubs in consecutive months from October to April inclusive.

Species	Contacts	Oct.	Nov.	Dec.	Jan.	Febr.	March	April
<i>Picea excelsa</i>	13,826	—	—	1.5	16.7	74.9	34.4	—
<i>Tilia cordata</i>	11,365	—	—	17.9	33.2	4.6	25.8	45.2
<i>Quercus robur</i>	7,592	—	—	10.8	5.8	15.0	21.6	—
<i>Fraxinus excelsior</i>	6,052	100.0	—	38.8	8.4	—	2.4	—
<i>Alnus glutinosa</i>	3,200	—	41.4	16.4	15.2	0.9	—	—
<i>Acer platanoides</i>	2,512	—	—	—	—	—	10.4	—
<i>Carpinus betulus</i>	2,467	—	58.6	11.9	5.4	1.5	1.6	—
<i>Pinus silvestris</i>	1,477	—	—	—	11.0	3.1	—	54.8
<i>Salix caprea</i>	769	—	—	—	—	—	3.2	—
<i>Ulmus campestris</i>	335	—	—	—	4.1	—	—	—
<i>Sorbus aucuparia</i>	204	—	—	0.6	—	—	0.6	—
<i>Corylus avellana</i>	194	—	—	1.9	—	—	—	—
<i>Populus tremula</i>	21	—	—	0.2	—	—	—	—
<i>Malus silvestris</i>	13	—	—	—	0.2	—	—	—
Total	50,027	100.0	100.0	100.0	100.0	100.0	100.0	100.0

nuary bark-stripping intensifies and forms 15—20%, but decreases slightly in February (approx. 10% of the whole number of contacts). In March intensity of bark-stripping increases abruptly, about 50% of all contacts being recorded in this month (Fig. 7).

On the basis of Table 5 we traced which species of ligneous plants are subjected to bark-stripping during successive months. In October bark was stripped from only one species — *Fraxinus excelsior* — in November from *Carpinus betulus* and *Alnus glutinosa*. In December the deer stripped bark from 9 species, among which bark from *Fraxinus excelsior* predominated (38.8%), and also *Tilia cordata* (17.9%) and *Alnus glutinosa* (16.4%). In January bark was stripped from 9 species



also, amongst which the following predominated: *Tilia cordata* (33.2%), *Picea excelsa* (16.7%) and *Alnus glutinosa* (15.2%). In February the number of species from which bark was stripped decreased to 6, with *Picea excelsa* (74.9%) clearly predominant, and *Quercus robur* (15.0%) coming second. Intensive barking in March affected 8 species, and during this time the following species predominated: *Picea excelsa* (34.4%), *Tilia cordata* (25.8%) and *Quercus robur* (21.6%). Only *Pinus silvestris* (54.8%) and *Tilia cordata* (45.2%) were stripped in April (Table 5).

#### 9. WINTER PENETRATION OF ECOSYSTEMS BY ROE DEER AND RED DEER

The tracks left by deer in the snow during the winter period (December—April) permitted of determining which species of animal had

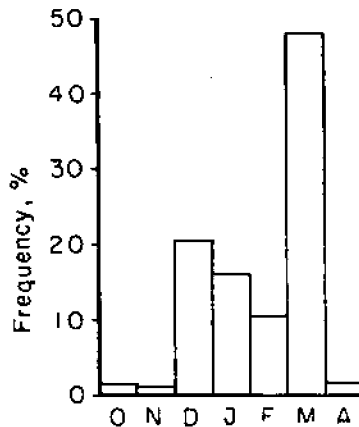


Fig. 7. Distribution in percentages of barking by deer from trees and shrubs in consecutive months from October to April inclusive.

been feeding. On the basis of the frequency of visits by the animals to different ecosystems and their intensity of feeding, we traced differences in preferences for ecosystems between roe deer and red deer. The order of ecosystems was arranged in accordance with the decreasing percentage of visits to them by roe deer, feeding meaning also contacts of the animals through both browsing and barking (Fig. 8).

The roe deer moves over the area of its habitat in a very even manner, and animals were recorded as having most often passed through study areas situated in C—A (19.9%), and least frequently in P—Q (15.2%), and thus differences in the distribution of percentages of visits by roe deer to the ecosystems are at most 4.7% (Fig. 8).

In respect of the amount of food consumed the preferences shown by the roe deer for different ecosystems are very distinct. Peak feeding (32.6%) was observed in C—Q and C—A (20.8%). Intensity of feeding was similar in T—C<sub>2</sub> and T—C<sub>1</sub>, being respectively 12.9% and 15.7% of the whole of the winter food of the roe deer. The smallest number of contacts was observed in coniferous forests: in P—Q 10.3% and in P—P 7.7% (Table 6, Fig. 8A).

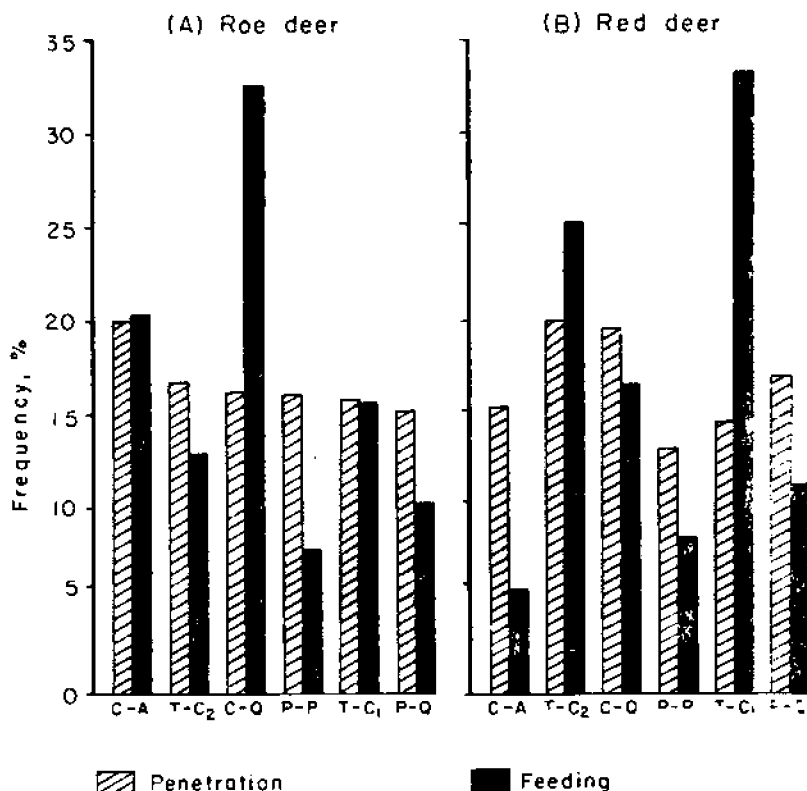


Fig. 8. Distribution in percentages of the whole (barking and browsing) of winter feeding by the roe deer (A) and the red deer (B) and of their penetration of the study ecosystems. Symbols of the ecosystems are given in Table 1.

The red deer also penetrates its habitat to a more or less even degree in winter. Extreme differences in the distribution of percentages of visits by red deer to different ecosystems are 6.7%. In that most often visited, T—C<sub>2</sub>, 20.0% of all visits by red deer were recorded in the study areas, and in the least frequently visited P—P — 13.3%.

Decided preference for a given ecosystem occurs when intensity of feeding by these animals is considered in the various biotopes. The

maximum number of contacts (33.1%) was found in  $T-C_1$ , then 25.1% in  $T-C_2$ , with a similar moderate number of contacts in  $C-Q$  (16.7%) and  $P-Q$  (11.3%), and minimum in  $P-P$  (8.3%) and in  $C-A$  (5.5%) (Fig. 8B, Table 6).

Both roe deer and red deer penetrate ecosystems in an even and similar way. It may be said that these two species spend slightly more time in deciduous than in coniferous forests, and that the roe deer penetrates  $C-A$  slightly more intensively than does the red deer. In general, however, it must be concluded that deer move about the whole area in which they live to an even extent. This is understandable in view of the very mosaic-like character of the occurrence of given forest associations in the Białowieża Primeval Forest.

Table 6

Differences in the distribution in percentages of feeding by roe deer and red deer in 6 different ecosystems during the winter season.

Ecosystem	Roe deer	Red deer
$P-P$	7.7	8.3
$P-Q$	10.3	11.3
$C-Q$	32.6	16.7
$T-C_1$	15.7	33.1
$T-C_2$	12.9	25.1
$C-A$	20.8	5.5
Total	100.0	100.0

The intensity of feeding of roe deer and red deer, on the other hand, differs greatly in different ecosystems, such intensity showing the degree of the animals' food preferences in the ecosystems. It can be seen from Fig. 8 that the roe deer prefers  $C-Q$  (it consumes  $\frac{1}{3}$  of the whole of its winter food in  $C-Q$ ) but feeds to the least degree in  $P-Q$  (10.3%) and in  $P-P$  (7.7%). The distribution of winter feeding by the red deer is, however, completely different, as this species consumed  $\frac{1}{3}$  of its winter food in  $T-C_1$  with  $T-C_2$  as the second preferred ecosystem (25.1% of food). The red deer was observed to feed least in  $P-P$  (8.3%) and in  $C-A$  (5.5%). It is clear from the above comparison that in no case were roe deer and red deer simultaneously observed to eat intensively in any of the ecosystems examined, and it may therefore be concluded that the differences in food preferences in the ecosystems reduce food competition between these species of animals.

### 10. EFFECT OF DEPTH OF SNOW COVER ON THE ACTIVITY OF ROE DEER AND RED DEER

The three consecutive winter seasons during which the studies were carried out differed considerably from each other in respect of the depth and persistence of the snow cover, and consequently studies were made to determine whether, and to what degree, the snow cover affects the activity of deer. For this purpose calculation was made of the number of tracks left by these two species of animal in the study areas in successive winter seasons. A total of 2,640 traces of the presence of deer were found, 1,572 of which were attributed to the roe deer, and 1,058 to red deer.

The winter season of 1968/69 was characterized by only slight snowfall, reaching a maximum of 40 cm (February). The distribution of percen-

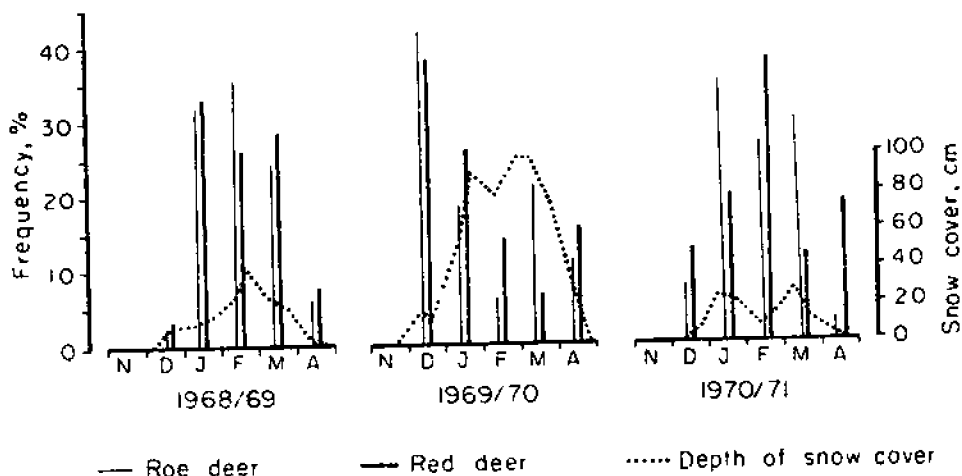


Fig. 9. Effect of the depth of the snow cover on the activity of deer, expressed in the animals' frequentation of the study areas.

tages of tracks from January to March inclusive was even (Fig. 9), and it may therefore be said that the snow cover does not limit the animals' activity. As the first observations of feeding by deer were begun in the second half of December 1968, the number of tracks found is small. In April 1969 the snow cover had disappeared by the first half of the month, which made it difficult to record tracks left by these animals.

The winter season of 1969/70 was characterized by a long-lasting snow cover up to 85 cm in depth in January, and 100 cm in February and March, and was sufficiently deep to reduce the activity of the deer to a considerable degree. The roe deer's movements decreased particu-

larly markedly in February, 6% of all winter tracks of the animals being found at this time. In March the roe deer's activity increased, despite the fact that there was still a deep snow cover. This increase in the animal's activity was presumably due to weather conditions, namely the last heavier snow fall took place in mid-February, while in March there were very strong winds which brought about considerable hardening of the snow cover, chiefly on the open spaces of tree plantations. The surface of the snow was sufficiently hard to support the weight of roe deer, and this made an increase in their activity possible. During this period, however, the activity of the red deer decreased noticeably (to approx. 5% of all winter tracks of this animal), since the hard surface layer of snow could not support the considerable weight of these animals. The activity of both species of animals increased in April.

During the winter season of 1970/71 there was only a light snow cover, with maximum depth of 30 cm, and even so it only lasted for a few days at a time. A relatively small number of tracks were observed in December and April on account of the difficulty in descrying them. In January and February the deer penetrated the areas to a more or less even extent. When the two species of animals are considered separately it can be seen, that the largest number of roe deer tracks were observed in January and red deer tracks in February.

The foregoing shows that a light snow cover does not hinder the animals' activity, but with a deep snow cover (such as occurred in the winter 1969/70) the deer are greatly limited in their movements (Fig. 9).

## 11. DISCUSSION

The composition of the food of deer has been examined by different authors, using a large number of methods, among which those most frequently employed are: (1) Field studies — consisting in observations of free-living animals (Sablina, 1955; Wilkins, 1957; Lovaas, 1958), of their feeding places (Sablina, 1955; Ahlen, 1965), by means of tracks left in the snow and observations of tamed animals (McMahan, 1964; Dzieciołowski, 1967) and by means of tests in an enclosure (Alkon, 1961; Dzieciołowski, 1970b). (2) Laboratory studies — consisting in analysis of the contents of the rumen (Wilkins, 1957; Lovaas, 1958; Siuda *et al.*, 1969; Dzieciołowski, 1970), or analysis of excreta (Klein, 1962).

In the present study use has been made of the field method, by examining traces of the presence and feeding of deer on selected study areas. Setting up permanent study areas permitted, *inter alia*, of collect-

ing data on different habitats of a forest character, taking into account the age of tree stands and also variation in intensity of the animals' feeding over the yearly cycle. An additional advantage obtained by using the above method was the possibility of making phytosociological surveys which in effect permitted of obtaining data of the abundance of the different species of plants in the area. At the same time, on account of the fact that three species of ungulates (European bison, red deer and roe deer) live in the same area, it was possible to attempt to grasp differences in food preferences and penetration of the different ecosystems by the animals. Meteorological observations and measurements of the depth of the snow cover were made simultaneously, and data were then used to determine the effect of these factors on the food relations of ungulates. In general, the above method made it possible to carry out very comprehensive studies on the food relations of deer and the European bison in relation to the habitat in which these animals live.

There are, however, certain deficiencies in the above method, among the most important of which is the impossibility of discovering the whole of the food consumed by the feeding animal in the study areas. This applies chiefly to plants of the herb layer, observations of which were made twice a month, and traces of ungulates' feeding on herb layer plants could disappear in a natural way during the time between successive recordings in the areas. At the same time part of the traces of feeding on small plants growing compactly might escape the observer's notice. In winter a certain number of contacts were missed in cases in which snow fall during the time between the animals' feeding and the observations made. This last phenomenon took place particularly often at the end of autumn — beginning of winter, and end of winter — beginning of spring. The above reservations are borne out by data in literature; Wallmo *et al.* (1973) tested a number of the methods used to define the food preferences of deer, *inter alia*, also the method of counting traces of the animals' feeding on specially marked plots. Tame individuals of *Odocoileus hemionus* were used as a means of testing this method. The observer noted from close up each portion consumed by the animals and identified the plant species eaten. The next day another observed recorded the traces left by *Odocoileus hemionus* feeding in plots measuring 10×10 m. Each individual plant was carefully inspected and the number of missing shoots recorded. When the two methods were compared it was found that the animal's consumption of shrubs and dicotyledonous forbs had been under-estimated, and of grasses over-estimated.

Objections as to failure to grasp the whole of the food eaten by deer

are also confirmed by the results of the study made by Sieviercov & Sablina (1953) and Sablina (1955). They examined the composition of the diet of deer by means of two methods (1) by observations of feeding animals and (2) recording traces of feeding in selected areas. The percentage formed by dicotyledonous forbs in the food of roe deer and deer over the yearly cycle as given by the Soviet authors is far higher during the period from June to September than that obtained from our studies (Fig. 10).

The error in defining the participation of herbaceous plants in the diet of deer is also confirmed by the series of tests made (Kossak *in litt.*) on a tame roe deer. It was found that in early spring the basis of this animal's food was formed by small dicotyledonous forbs, chiefly *Oxalis acetosella*. In the floristic lists included in this paper this species comes very far down the list, forming only 0.1% of the succulent food eaten by deer.

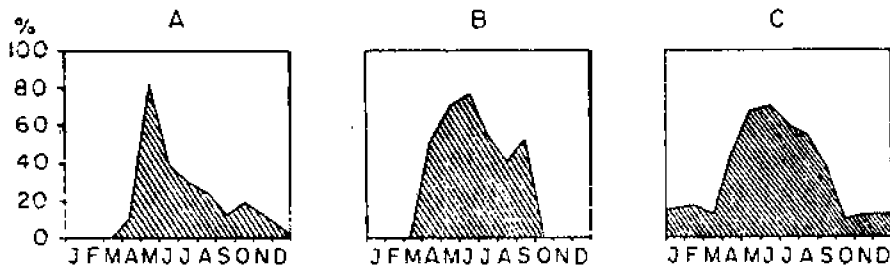


Fig. 10. Percentages formed by trees, shrubs and dwarf-shrubs, and by dicotyledonous forbs, grasses, sedges and rushes (hatched) in the food of deer over the yearly cycle.

A. deer (our own studies), B. roe deer (modified after Sablina, 1955), C. red deer (modified after Sablina, 1955).

On account of the above objections the ratio of ligneous food (83.4%) to succulent food (16.6%) calculated on the basis of Table 3 in the diet of deer over the yearly cycle in the Białowieża Primeval Forest is undoubtedly considerably under-estimated, to the disadvantage of succulent food.

Another considerable deficiency in the method used is the liability to error in defining the species of feeding animal, particularly during the season without a snow cover. In summer the majority of deer left no tracks on the ground, which made it necessary to treat material obtained during the snowfree period jointly, as relating to deer. In material relating to the winter period also, when distinguishing between food eaten

by the roe deer and red deer, a considerable amount of data had to be obtained as it proved impossible to determine which species of animal had fed on it.

Yet another disadvantage of this method is the actual distribution in the Forest of the study areas, that is, choice of the sites of the future study areas was decided chiefly by the types of biotope and age of the tree stands, while less attention was paid to the factors affecting the behaviour of deer. Some of the areas were situated in the summer ranges of the European bison, some were from time to time entered by humans or were situated near roads and forest rides. The above may have affected the biotope preferences of the deer. Since, however, data obtained in winter were used for work on the wanderings of deer over the area, during which time the European bison congregate near the places in which fodder is put out for them, while the movements of humans over the area markedly decrease, it may be considered that the results obtained in the present study give an approximate idea of the real preferences for ecosystems of the roe deer and red deer.

The data obtained in our studies show that in winter deer visit coniferous forest habitats less often than they do stands of the *Tilio-Carpinetum*, their feeding in coniferous forests forming about 20% of the whole of their winter food (from the 6 ecosystems examined). Dzieciowski (1969, 1971) found the reverse phenomenon to occur when he used the method of direct observation of feeding animals and obtaining information from their trace, that is, he found that the red deer showed marked preference for the *Peucedano-Pinetum* association (19% of the area examined), while *Stelario-Carpinetum* was the least visited association. Two associations, namely *Fago-Quercetum* and *Pino-Quercetum*, forming about 60% of the area examined, were not visited by red deer, even to the degree corresponding to the percentage of the area they form. The author concludes that they are not habitats attractive to deer. Our data showed that the smallest number of plant species were included in the diet of deer in coniferous forests (39), and the greatest number in stands of the *Tilio-Carpinetum* (95). Dzieciowski (1970b) presented similar relations between choice of food by deer and the type of habitat. According to the data given by this author, the smallest number of plant species was eaten in coniferous forests (33), and the largest in tree stands of the *Tilio-Carpinetum* (48). The above divergences in biotope preferences can be partly explained by the intensive feeding of deer on *Pinus silvestris*, which is a species occurring numerously in the coniferous tree stands of the Białowieża Forest. Over the yearly cycle, however, it forms only 4.8% of the whole of browse. In winter it forms 20.5% of browse of deer and about 2% of total bark stripped. The



results of tests made in enclosure (Dzięciołowski, 1970c) showed that *Pinus silvestris* is not readily eaten by deer and forms a »hunger« food. It may therefore be concluded that the red deer feeds only to a small extent in coniferous tree stands, since the rich deciduous tree stands provide it with a sufficient supply of food. This is also shown by the fact the remaining 80% of the winter food of this animals consists to a great extent of the shoots of ligneous plants which do not occur in coniferous forest stands.

Our studies have shown that the red deer consumes the least amount of food in winter in *Circaeo-Alnetum* (approx. 6%) which agrees with Dzięciołowski's data (1969).

In all age classes of tree stand and ecosystems the distribution of feeding over the yearly cycle is characterized by a certain decrease in spring and autumn. The spring decrease is accounted for in the first place by the reduction in activity of part of the population, due to the period of giving birth to and rearing young, and in the second place by the animals' spring migrations in search for food to the meadow and sedge associations (cf. also Dzięciołowski, 1969) in April and May. The above explanation is confirmed by the data given by Schloet *et al.* (1961) on the migration of red deer to spring pastures, which takes place in May. The autumn decrease in feeding (September—October) may be connected with the start of the rutting period. As shown by Fiser *et al.* (1958), stags taking part in reproduction consume far smaller amounts of food, in which bark and dry needles of *Picea excelsa* predominate, and also dry and green grass. Other species of plants form only a negligible percentage of the stags' food at this time.

The percentages formed by different plant species in the diet of deer over the yearly cycle, given in our paper, are very similar to data given by other authors (Baskin, 1965; Siuda *et al.* 1969; Dzięciołowski, 1970 a, b).

It can be seen from the present study that in winter shoots of *Pinus silvestris*, *Carpinus betulus* and *Quercus robur* predominated in the red deers' food (approx. 56% of the whole of the browse consumed during this period), although Malinovskaja (1972) considers *Populus tremula* as the dominating species. The author in question, however, carried out her studies on tame young red deer in an enclosure. The animals were supplied with large quantities of hay during the course of her studies (up to 47% of the dry mass of fodder per month), which resulted in the results obtained by this author being somewhat unconvincing.

In elaborating material from the three study years we did not observe

a single case of bark stripping by deer in summer. The first traces of feeding in this form were observed in October, and the last in April. Sablina (1955) states that in the Białowieża Forest red deer strip bark from two species of tree in summer: *Picea excelsa* in July and *Pinus silvestris* in September.

The periods of winter bark stripping by red deer from the various species of trees given by Sablina (1955) coincide with our data. In the part of her study dealing with roe deer the author gives *Salix caprea*, *Populus tremula*, *Pinus silvestris* and *Fraxinus excelsior* as species from which bark is stripped, whereas observations made during our studies showed that the roe deer only sporadically stripped bark from the species of trees: *Acer platanoides* and *Alnus glutinosa*.

An interesting problem arose when demonstrating differences between roe deer and red deer in respect of their penetration of, and food preferences in different types of forest associations. These two species penetrated their habitat to a more or less even extent, which may indicate that they mutually tolerate each other in the same area, but the distribution of feeding in different ecosystems differed decidedly for roe deer and red deer. Not a single case was observed of a given ecosystem being markedly preferred by the two species of animals. It may be assumed that this phenomenon is connected with mechanisms ensuring rational use of the food supply by species of animals with similar biology living for a considerable time in one area. It would therefore appear essential to carry out special studies for the purpose of defining the extent to which the ecological niches of ungulate animals overlap each other in habitats with abundant food resources. Such studies could serve as guiding principles in solving problems connected with hunting and forestry management. One of the important problems of such management is in fact the question of simultaneous occupation of a common area by different species of deer and their effect on the quality of tree stands.

A further problem of possible importance to forestry management is presented by the phenomenon described in the study by Kossak (1976), i.e. the occurrence of so-called food clusters in the diet of deer. The majority of authors have so far limited themselves to giving the order of preference for plant species in the animals' diet on the basis of the percentage formed by such species in the food consumed by deer. Comparison of the abundance of occurrence of plants in the area with the degree to which they are eaten by deer shows that this degree differs in different biotopes and depends on the degree to which other species growing in the given biotope are consumed (cf. Kossak, 1976).

The possibility referred to, that food clusters may exist in the diet of deer, may be of assistance in studies concerned with limitation of damage done by game animals. If the composition of food clusters is known, it is then possible to direct hunting management in such a way (by settling appropriate species of ungulates in different biotopes, planting the proper species of trees and shrubs in special plots for the animals to feed on, care of the quality of the herb layer etc.), as to ensure that the given ecosystem provides the animals with a wide range of food including all important plants in the cluster. In effect, by distributing the animals' feeding over a large number of plant species, frequently of less importance from the aspect of forest management, this may limit the damage done to valuable plant species.

The phenomenon of preference by deer for herb layer plants at given development stages is connected with the problem referred to above. It has been found that deer markedly prefer plants passing through the generative stages (Kossak, in prep.). This phenomenon is particularly important in the early spring and spring period, when the animals transfer from their winter diet, with the narrow range of components, to a diet composed to a great extent of early flowering and fruiting dicotyledonous forbs. If the herb layer is luxuriant and varied in the given biotope, this may considerably reduce the extent to which deer feed on ligneous plants. It is clear from the foregoing that due attention to the forest herb layer, as a factor limiting damage done by game animals, is essential.

The present study should be followed up by a series of studies aimed at calculating the optimum number of deer which can live in the Białowieża Primeval Forest. Estimation of the food resources of the Forest and the food requirements of deer should contribute to such studies.

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#### REFERENCES

1. Ahlen I., 1965: Studies on the red deer, *Cervus elaphus* L. in Scandinavia. III. Ecological investigations. *Viltrevy* 3: 177—376.
2. Alkon P. V., 1961: Nutritional and acceptability values of hardwood slash as winter deerbrowse. *J. Wildlife Manage.*, 25: 77—81.
3. Baskin L. M., 1965: O pitaniu blagorodnyh olenej. *Zool. Ž.*, 44, 3: 465—469.
4. Borowski S. & Kossak S., 1972: The natural food preferences of the European bison in seasons free of snow cover. *Acta theriol.*, 17, 13: 151—169.

5. Dzieńciołowski R., 1967a: Winter food of the red deer (*Cervus elaphus* L.) as determined by tracking techniques. *Ekol. pol.* A, 15, 11: 285—305.
6. Dzieńciołowski R., 1967b: Food of the red deer in a annual cycle. *Acta theriol.*, 12, 36: 503—520.
7. Dzieńciołowski R., 1969: Repatrition of habitat niches within the area of red deer (*Cervus elaphus* L.) population. *Ekol. pol.* A, 17, 22: 381—389.
8. Dzieńciołowski R., 1970a: Foods of the red deer as determined by rumen content analyses. *Acta theriol.*, 15, 6: 89—110.
9. Dzieńciołowski R., 1970b: Variation in red deer (*Cervus elaphus* L.) food selection in relation to enviroment. *Ekol. pol.* 18, 32: 635—645.
10. Dzieńciołowski R., 1970c: Food selectivity in the red deer towards twigs of trees, shrubs and dwarf-shrubs. *Acta theriol.*, 15, 23: 361—365.
11. Dzieńciołowski R., 1971: Sytuacja troficzna populacji jeleni w zależności od warunków środowiskowych. *Prace Inst. Bad. Leśn.* 403; 1—42.
12. Falińska K., 1973: Dynamika sezonowa runa zbiorowisk leśnych Białowieskiego Parku Narodowego. *Phytocenosis*, 2, 1: 1—118.
13. Faliński J. B. (ed.), 1968: *Park Narodowy w Puszczy Białowieskiej*. Państw. Wyd. Roln. i Leśne: 1—503. Warszawa.
14. Fiser Z., Hanus V. & Lochman J., 1958: Prirozena potrava jelenu v do-be rije. *Sbrornik Ceskosl. Akad. Zamed. Ved Lesn.* 4, 4: 229—256.
15. Graniczny S., 1957: Obeszwacje nad rozwojem wegetacji roślinnej w Białowieskiem Parku Narodowym. *Sylwan* 101, 4: 36—44.
16. Klein D. R., 1962: Rumen contents analysis as an index to range quality. *Trans. 26th North. Amer. Wildlife and nat. Res. Conf. Washington.*
17. Kossak S., 1976: Struktura diety jeleniowatych w Puszczy Białowieskiej (in preparation).
18. Lovaas A. L., 1958: Mule deer food habits and range use, Little Belt Mountains, Montana. *J. Wildl. Manage.*, 23: 275—283.
19. Malinovskaja G. M., 1972: Kormovoj racjon molodyh olenej Beloveżskoj Pušči. *Beloveżskaja Pušča* 6: 131—138.
20. Matuszkiewicz W., 1967: Przegląd systematyczny zbiorowisk roślinnych Polski. [In: Scamoni A. »Wstęp do fitosocjologii praktycznej«]. Państw. Wyd. Roln. i Leśne: 175—234. Warszawa.
21. Mc Mahan C. A., 1964: Comparative food habitats of deer and three classes of livestock. *J. Wildlife Manage.* 28: 798—808.
22. Pawłowski B., 1959: Skład i budowa zbiorowisk roślinnych oraz metodyka ich badań. [In: »Szata roślinna Polski« ed. W. Szafer]. Państw. Wyd. Nauk.: 229—263. Warszawa.
23. Sablina T. B., 1955: Kopytnye Beloveżskoj Pušči. *Akad. Nauk SSSR. Trudy Inst. morf. životnyh im. A. Severcova*: 20—114. Moskva.
24. Schloeth R. & Burckhardt D., 1961: Die Wanderungen des Rotwildes *Cervus elaphus* L. im Gebiet des Schweizerischen Nationalparkes. *Rev. Suisse Zool.*, 68: 145—156.
25. Severcov A. S. & Sablina T. B., 1953: Olen, kosula i kaban v zapovednika »Beloveżskaja Pušča«. *Trudy Inst. morf. životnyh* 9: 140—205.
26. Siuda A., Żurowski W. & Siuda H., 1969: The food of the roe deer: *Acta theriol.*, 14, 18: 247—262.
27. Wallmo O. C., Gill R. B., Carpenter L. H. & Reichert D. W., 1973: Accuracy of field estimates of deer food habits. *J. Wildl. Manage.*, 37, 4: 556—562.

28. Wilkins B. T., 1957: Range use, food habits and agricultural relationships of the mule deer, Bridger Mountains, Montana. *J. Wildl. Manage.*, 21: 159—169.

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## STOSUNKI POKARMOWE JELENIOWATYCH W PUSZCZY BIAŁOWIESKIEJ

### Streszczenie

Badania nad składem pokarmu sarny i jelenia prowadzono na terenie polskiej części Puszczy Białowieskiej w latach 1968—1971, metodą notowania wszelkich śladów bytności i żerowania zwierząt na 60 powierzchniach doświadczalnych. Powierzchnie rozmieszczone w 6 zespołach leśnych charakterystycznych dla Puszczy Białowieskiej (Ryc. 1, Tabela 1) i w 4 klasach wieku drzewostanów. Na podstawie zdjęć fitosocjologicznych obliczono współczynniki obfitości występowania poszczególnych gatunków roślin. Żerowanie zwierząt na roślinach notowano w formie kontaktów, uznając za jednostkę żeru zgryzienie 1 pędu drzewa lub krzewu, zgryzienie 1 okazu (całego lub fragmentu) rośliny zielnej, lub zgryzienie 1 kępy trawy czy turzycy. Ilość ospałowanej kory mierzono w  $\text{cm}^3$ . Ze względu na znaczne różnice w masie tak zapisanych jednostek żerowania, sporządzono przeliczniki unifikujące materiał. Przeliczniki oparto o suche masy prób pobranych w pobliżu powierzchni doświadczalnych. Dokładną metodę unifikacji danych podano w pracy Borowski & Kossak (1972).

Całość danych uzyskanych na powierzchniach doświadczalnych zebrano w listę florystyczną zawierającą spis drzew, krzewów i krzewinek oraz roślin zielnych, traw i turzyc występujących w pokarmie jeleniowatych (Tabela 3). Ogółem w diecie zwierząt stwierdzono występowanie 36 gatunków roślin drzewiastych i 137 zielnych z trawami. W grupie drzew dominuje *Carpinus betulus*, *Fraxinus excelsior*, *Quercus robur*, *Salix caprea*, w grupie roślin zielnych zaś: *Ranunculus repens*, *Caltha palustris*, *Filipendula ulmaria*, *Aegopodium podagraria* i *Impatiens noli-tangere*.

Porównano udział poszczególnych gatunków w pokarmie jeleniowatych pobranych w różnych ekosystemach z ich współczynnikiem obfitości występowania (Tabela 3). Im wyższy jest współczynnik obfitości rośliny preferowanej przez zwierzęta, tym częściej występuje ona w diecie zwierząt.

Prześlędzono cykl roczny żerowania jeleniowatych w 6 ekosystemach (Ryc. 2). Przy rozpatrywaniu składu gatunkowego diety w kolejnych miesiącach, nie zanotowano przypadku wystąpienia w niej wszystkich gatunków zamieszczonych w liście florystycznej. Największą ilość gatunków roślin drzewiastych w diecie zwierząt zanotowano w czerwcu w T—C<sub>2</sub> (24 gat.) i w Q—A w lipcu i w lutym (21 gat.) (Ryc. 2A).

We wszystkich badanych ekosystemach występuje letnie i zimowe nasilenie żerowania jeleniowatych na roślinach drzewiastych. Letni szczyt żerowania łączy się

ze wzbogaceniem diety w gatunki. Zimą zwierzęta żerują intensywnie, lecz na niewielkiej ilości gatunków. Wyjątkiem jest zespół C—A, w którym w lutym zapisano tę samą ilość żerowanych gatunków co w lipcu (21) (Ryc. 2A). W grupie roślin zielnych i traw szczyt żerowania zwierząt przypada na miesiące wczesnoletnie (Ryc. 2B). W tym czasie notuje się również najwięcej gatunków w diecie jeleniowatych.

Prześlędzono roczny rozkład żerowania jeleniowatych w 4 klasach wieku drzewostanu (Ryc. 4). W obu grupach roślin dominuje żer pobrany w młodnikach i na uprawach. W grupie roślin zielnych ma miejsce nasilenie żerowania w starodrzewiach w okresie wiosny i jesieni.

Opisano (Ryc. 5) roczny cykl żerowania zwierząt na wybranych 12 gatunkach roślin drzewiastych (stanowiących 87% żeru drzewiastego) i 8 gatunkach roślin zielnych (81% żeru zielnego) uwzględniając typ lasu, klasę wieku drzewostanu i porównano z cyklami fenologicznymi tych roślin. W grupie drzew, krzewów i krzewinek nie zauważono związku intensywności żerowania jeleniowatych z porami fenologicznymi roślin, natomiast w grupie roślin zielnych zwiększa się intensywność żerowania zwierząt na roślinach przechodzących stadia generatywne (Kossak, 1975).

Z całości materiału wydzielono żer zimowy sarny i jelenia, uwzględniając żer pobrany przez zgryzanie pędów i spałowanie kory. Skład gatunkowy diety obu gatunków zwierząt jest zbliżony (Tab. 4), z tym że jeleni pobiera znaczne ilości kory, która w pokarmie sarny nie odgrywa istotnej roli. Kora w zimowym pokarmie jelenia stanowi ok. 47%.

Prześlędzono związki między ruchliwością jeleniowatych a intensywnością żerowania w okresie zimy (Ryc. 8). Stwierdzono niewielkie różnice w penetrowaniu przez zwierzęta poszczególnych ekosystemów, natomiast pod względem ilości pobranego żeru sarna preferuje siedliska C—Q i C—A, jeleni natomiast T—C<sub>1</sub> i T—C<sub>2</sub>. Powyższe wpływa na równomierne wykorzystywanie przez jeleniowate bazy pokarmowej.

Prześlędzono wpływ wysokości pokrywy śnieżnej na ruchliwość zwierząt w trzech kolejnych sezonach zimowych (Ryc. 9). Przy pokrywie śniegu wynoszącej ok. 30 cm nie zauważono zmniejszenia się ruchliwości jeleniowatych. Pokrywa śniegu powyżej 50 cm ograniczyła penetrację sarny, powyżej 80 cm — jelenia.