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The Complex Character of the Food Preferences of Cervidae and Phytocenosis Structure [1]

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Kossak S., 1976: The complex character of the food preferences of *Cervidae* and phytocenosis structure. Acta theriol., 21, 27: 359—373 [With 4 Tables].

Using data obtained by studies of food relations of the roe deer and red deer in the Białowieża Primeval Forest analysis was made of the structure of the diet of *Cervidae* in 6 associations of this Forest. Three parameters were employed: 1) coefficient of abundance with which the given plant occurred (*D*), 2), intensity with which the deer fed on a given plant (*n* of contacts), 3) percentages formed by the different plant species in the animals' diet over the three-year study period (1969—1971). A discussion is given of food consisting of twigs and branches of trees, bushes and shrubs. The hypothesis of food blocks being present in the diet of deer is put forward. An animal feeding in an ecosystem prefers not so much particular species of plants as a whole group (block) of them, the degree to which the animals feed on one species determining the intensity of their feeding on others. Food blocks are characteristic of the different ecosystems and depend on the structure of the phytocenosis of the given ecosystem. The species and quantitative composition of food blocks in 6 ecosystems is given, dividing plants into basic, supplementary, sought-after and avoided in a given ecosystem. The links between plants in successive food blocks are traced.

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1. INTRODUCTION

The composition of deer's food is determined by two factors, one of which is the animal's food requirements, *i. e.* its diet must contain suitable amounts and proportions of different components, while the second is that its diet must be capable of being supplied by the animal's habitat. It may be said that the food requirements of deer inhabiting the forests of Europe are adapted to the natural structure of vegetation. The changes introduced by man into nature have a relatively short history. This process took place sufficiently quickly for animals not being able to keep pace with changes in the habitat to retain food needs reflecting

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the conditions which at one time prevailed in European forests. Nowadays a considerable part of forest ecosystems consist of forest stands planted by man, often forming monocultures, which determines the composition of the food available to the deer living in them. The results of studies on composition of food consumed by deer in tree stands transformed by man do not therefore reflect the real food preferences of these animals. This is confirmed by, *inter alia*, the results of studies in which it has been shown that in a series of tests to reveal preferences, carried out on deer kept in an enclosure, pine forms a hunger diet, but under conditions of freedom pine forms the basis of these animals' food (Dzięciołowski, 1970, 1971).

In order to define the natural food preferences of deer it would be essential to carry out studies in ecosystems only slightly deformed by man. The results obtained from such studies could then form a model of the natural relations between the animal and the ecosystem.

Conditions for such studies are to be found in the Białowieża Primeval Forest, which is one of the last relatively natural forest complexes left in Europe, and which occupies a very extensive area. Control by man of the numbers of ungulate animals prevents disturbance of the biological balance of the forest. Initial observations of feeding by deer in the Białowieża Forest have already revealed the phenomenon of the different percentage formed in the animals' diet by the same plant species depending on the type of ecosystem in which the animals feed, the extent of feeding not always depending on abundance of the given plant species (Borowski & Kossak, 1975).

The present study is intended to provide complex treatment of the diet of deer and to trace the connections between species of plants forming the food of these animals.

2. MATERIAL AND METHODS

Data on food relations of the roe deer and red deer in the Białowieża Primeval Forest, published in an earlier study (Borowski & Kossak, 1975), were used for the whole of the present discussion. Six types of tree stands representative of the Forest have been taken into consideration in the analysis, as follows: *Peucedano-Pinetum* (*P-P*), *Pino-Quercetum* (*P-Q*), *Calamagrostio-Quercetum* (*C-Q*), *Tilio-Carpinetum typicum* ($T\text{-}C_1$), *Tilio-Carpinetum stachyetosum* ($T\text{-}C_2$) and *Circaeo-Alnetum* (*C-A*). On account of small amount of data available on the percentage of herb plants in the diet of deer, analysis has been limited to food consisting of the twigs, branches and shoots of trees, bushes and shrubs. Material from the three study years (1968—1971) has been treated jointly, without taking seasons into account. The study was concerned with two ungulate species occurring in the study area: the red deer *Cervus elaphus* (Linnaeus, 1758), and the roe deer *Capreolus capreolus* (Linnaeus, 1758). Data on the feeding of these two species of animals have been treated jointly, on account of the impossibility of differentiating between food consumed by the roe and the red deer. Three auxiliary parameters have been employed to define the degree of food preference exhibited by deer:

(1) The abundance of the plant available to the animals and forming their food. Such abundance was expressed by means of the coefficient of abundant occurrence of the given species (D) (cf. Braun-Blanquet, 1946, 1951; Borowski & Kossak, 1972).

(2) Intensivity of the animals' feeding on the given plant species, expressed by means of units of feeding unified in respect of mass, that is, so-called contacts (n). Contacts were obtained by recording all traces of feeding by deer within experimental areas. Cropping or stripping the leaves from 1 branch of a tree, bush or shrub was regarded as a feeding unit. Samples consisting of parts of plants corresponding approximately to units of feeding by deer were next taken from near the study area. The dry mass of these samples was compared to obtain conversion units unifying the field material (Borowski & Kossak, 1972).

(3) The percentage formed by different species of plants in the whole of the twig and branch food consumed by deer in different forest associations.

3. DEGREE TO WHICH DEER USE BRANCHES AND TWIGS AS FOOD

The most important part of the whole of these discussions is to make comparisons of the degree to which deer feed on the different species of trees, bushes and shrubs in different ecosystems of the Białowieża Primeval Forest. It was assumed that the degree to which a plant is utilized is defined indirectly by the ratio of the number of contacts to the coefficient of abundant occurrence of the plant. It was therefore assumed that the plant is fully utilized as food by the animals, if intensivity of feeding by the animals, expressed in contacts, increases in accordance with the increasing coefficient of abundance of the given species of plant when ecosystems are compared in the form of a sequence. All deviations from the above are treated as apparent food inconsistences.

Table 1 contains 25 species of trees, bushes and shrubs forming 97.9% of the whole of the ligneous food of deer within the Białowieża Primeval Forest. In each case the order of ecosystems has been arranged in accordance with the increasing coefficient of abundance D and compared with the number of contacts n.

When the different species are considered it can be seen that in general in an ecosystem with high D of the plant a considerable number of contacts were recorded and *vice versa*, the same species of plant occurring in another ecosystem in small numbers only was eaten to a slight degree only. In a certain number of cases, however, deviations from the above rule were observed. On this account all species of plants were grouped into the following classes:

(a) Increase in coefficient of abundance (D) of the species in suc-

Table 1

Division into feeding groups (a-e) of 25 species of trees, bushes and shrubs based on comparison of the cofficient of abundance (*D*) of occurrence of the given species with the number of feeding units (contacts *n*) by deer in 6 ecosystems of the Białowieża Primeval Forest.

Ecosystem	*D*	*n*	%
Group a			
1. *Fraxinus excelsior*			
C—Q	+	197	0.2
T—C_1	170	1,183	1.4
C—A	290	20,355	36.4
T—C_2	345	32,126	45.4
2. *Pinus silvestris*			
C—Q	10	389	0.3
P—Q	150	7,340	14.0
P—P	745	12,656	27.6
3. *Vaccinium myrtillus*			
C—Q	200	476	0.4
P—Q	1,085	4,509	8.6
P—P	1,825	10,223	22.3
4. *Calluna vulgaris*			
P—Q	10	64	—
P—P	145	8,807	19.2
5. *Citisus nigricans*			
P—Q	10	299	0.6
P—P	45	6,696	14.6
6. *Prunus padus*			
P—Q	+	9	—
C—A	70	9,471	6.2
7. *Ribes nigrum*			
T—C_2	+	12	—
C—A	15	1,998	3.6
8. *Frangula alnus*			
T—C_1	+	6	—
P—Q	5	6	—
C—A	10	447	0.8
P—P	55	856	1.8
Group b			
9. *Viburnum lantana*			
T—C_1	5	—	—
C—Q	5	26	—
T—C_2	5	64	—
P—Q	10	270	0.5
C—A	45	1,186	2.1
10. *Ulmus laevis*			
P—Q	+	29	—
T—C_1	+	200	0.2
C—Q	5	626	0.5
C—A	20	1,755	3.1
T—C_2	20	2,926	4.1
11. *Ulmus campestris*			
P—P	+	15	—
T—C_2	+	145	0.2
C—A	+	725	1.3
Group c			
12. *Evonymus europea*			
P—Q	+	3	—
P—P	+	28	—
T—C_1	5	15	—
C—A	25	1,734	3.1
T—C_2	55	1,685	2.4
13. *Carpinus betulus*			
P—P	10	304	0.7
C—A	25	4,924	8.8
P—Q	30	7,056	13.5
C—Q	135	45,112	39.1
T—C_2	260	14,114	19.9
T—C_1	370	37,645	44.8
14. *Quercus robur*			
C—A	25	93	—
T—C_1	50	9,396	11.2
T—C_2	65	943	1.3
C—Q	115	22,701	19.7
P—Q	125	4,292	8.2
P—P	220	238	0.5
15. ***Rubus idaeus***			
P—P	15	93	—
C—Q	75	1,528	1.3
P—Q	80	951	1.8
T—C_1	160	4,425	5.3
T—C_2	195	5,719	8.1
C—A	255	3,796	6.8
16. *Betula verrucosa*			
T—C_2	10	131	0.2
C—A	30	9	—
P—P	85	1,702	3.7
T—C_1	180	1,064	1.3
C—Q	395	8,941	7.7
P—Q	400	3,065	5.6

Ecosystem	*D*	*n*	%
Group d			
17. *Salix cinerea*			
$T—C_2$	5	87	0.7
$C—A$	10	96	—
$P—Q$	20	1,789	3.4
$P—P$	25	299	0.7
$C—Q$	25	1,923	1.7
$T—C_1$	35	4,176	5.0
18. *Salix caprea*			
$C—A$	+	9	—
$T—C_2$	+	133	0.2
$P—P$	+	209	0.5
$P—Q$	30	13,999	26.7
$C—Q$	45	6,241	5.4
$T—C_1$	105	11,011	13.1
19. *Corylus avellana*			
$P—P$	10	681	1.5
$P—Q$	10	870	1.7
$T—C_1$	65	3,361	4.0
$C—Q$	75	2,830	2.5
$T—C_2$	110	5,588	7.9
$C—A$	225	6,397	11.5
20. *Tilia cordata*			
$P—P$	+	171	0.4
$C—A$	10	623	1.1
$T—C_2$	10	1,203	1.7
$P—Q$	10	2,523	4.8
$T—C_1$	105	5,777	6.9
$C—Q$	420	5,040	4.4
21. *Populus tremula*			
$C—A$	+	58	—
$T—C_2$	15	267	0.4
$P—Q$	20	684	1.3
$P—P$	35	305	0.7
$T—C_1$	45	1,111	1.3
$C—Q$	45	2,120	1.8
22. *Betula pubescens*			
$T—C_2$	+	3	—
$T—C_1$	+	73	—
$P—Q$	15	2,485	4.7
$C—Q$	20	8,947	7.7
$P—P$	30	1,737	3.8
23. *Sorbus aucuparia*			
$T—C_1$	+	29	—
$C—Q$	15	35	—
$P—Q$	15	641	1.2
$T—C_2$	25	64	—
$C—A$	25	641	1.1
$P—P$	40	429	0.8
24. *Alnus glutinosa*			
$P—Q$	5	49	—
$C—Q$	5	734	0.6
$T—C_2$	45	116	0.2
$C—A$	215	183	0.3
Group e			
25. *Picea excelsa*			
$T—C_2$	50	3,579	5.1
$C—Q$	90	6,641	5.7
$C—A$	90	6,934	12.4
$T—C_1$	110	4,205	5.0
$P—Q$	710	858	1.6
$P—P$	915	128	0.3

(a) increase in coefficient of abundance (*D*) is combined with increase in number of contacts (*n*); (b) In successive ecosystems *D* is equal but number of contacts (*n*) differs; (c) Certain ecosystems are distinguished by higher or lower *n* than could be expected from *D* sequence; (d) Phenomena *b* and *c* occur; (e) *n* is in reverse proportion to *D*; % — Percentage formed by species in the whole of browse consumed by deer in the given ecosystem.

cessive ecosystems is connected with increase in the number of contacts (*n*),

(b) Value *D* of a species unvarying in successive ecosystems, while value *n* differed in them,

(c) Species characterized in some ecosystems by a greater or smaller number of contacts than would be expected from the order of their coefficients of abundance,

(d) Species in which phenomenon *b* and *c* occurred.

(e) Species consumed to an extent in reverse proportion to their abundance of occurrence.

It is difficult to find an explanation of why certain species of plants are more readily eaten by deer in certain ecosystems than in others and even so irrespective of their abundance, for example approx. 45 thousand contacts were recorded for *Carpinus betulus* in *C-Q*, with $D = 135$, whereas in $T\text{-}C_1$, characterized by greater D (370) less cropping was observed (about 38 thousand contacts). In the case of *Corylus avellana* the reverse situation occurred: in *C-Q* with abundance of the plant equal to 75, 2,830 contacts were recorded, while in $T\text{-}C_1$, which was poorer in *Corylus avellana* ($D = 65$), the number of contacts was greater, *i. e.* 3,361 (Table 1).

In the case of *Picea excelsa* we have the phenomenon of particularly strong preference by deer plants in certain ecosystems. It was most intensively eaten in associations in which it occurred in small numbers (D from 50 to approx 100), whereas in associations in which it occurred in large numbers (D from 700 to 1000) only a small number of contacts was observed.

When the percentage formed by different species of plants in the whole of the deer's food consumed in succeccive ecosystems was traced this proved helpful in explaining differences in the number of contacts recorded for the various ecosystems (Table 1). It was found that the percentage of different species in the animals' diet varies greatly. In a certain number of cases it was, however, noticed that this percentage is more or less equal in two or more ecosystems, and that regardless of D and n.

In connection with the foregoing, analysis was made of the species and quantitative composition of the animals' diet in different ecosystems. For this purpose the plant species on which the animals fed in each ecosystem were divided into the following groups (Table 2):

(1a) Basic and supplementary species in the diet of deer in a given ecosystem. Eaten in accordance with abundance of occurrence.

(1b) Species forming a similar percentage in the animals' diet in several ecosystems. Eaten in accordance with abundance of occurrence.

(2a) Species sought-after by the animals — characterized in a given ecosystem by small D and considerable n.

(2b) Species sought-after by the animals and characterized by a similar percentage in the food consumed by deer in different ecosystems.

(3a) Avoided species, characterized in a given ecosystem by high D and low n.

(3b) Avoided species, characterized by similar percentage in the food consumed by deer in different ecosystems.

Relative data were used to allocate the species to the above groups, that is, plants of which n in the order of ecosystems (Table 1) increased with increase in D were treated in the various ecosystems as eaten in proportion to occurrence (group 1 a, b). Classification of a species to the group of plants sought-after in a given ecosystem (groups 2 a, b) does not mean that mass cropping of this species was observed, but only that in comparison with the preceding or succeeding ecosystem in the sequence the number of contacts was greater than might have been expected, judging by the value of D. Criteria used for allocating a species to plants avoided in a given ecosystem (group 3 a, b) were similar.

Definition of a »high« or »low« coefficient of abundance (D) is also treated as relative and applies to a given plant, namely the participation of a plant in the animals' diet is limited by its numbers in the area, that is, the abundance of the plant must reach a certain level, making it possible for the animals to eat large amounts of it. This level differs for different species of plants. Value n was taken as a guide when defining value D. Thus in the case of *Vaccinium myrtillus* the value 200 was considered as low D, since with a coefficient of abundance of 200 only 476 contacts were recorded, whereas with $D=1825$ there were as many as 10,223 contacts. This high level of abundance of a plant, making it possible for the animals to feed intensively on it, can be explained by the fact that deer feed on a stretch of vegetation covering the ground over a large area. The case is quite different in regard to trees, where abundance 1 — 20 was considered as low value D, and abundance over 100 as high D (abundance in the phytosociological sense relates to the number of trees occurring in an area, without taking into account the degree to which they are branched). In an extreme case when examining the number of contacts with *Betula pubescens*, D of only 15 was held to be high, since the abundance of this species was sufficient to be eaten in large numbers. Owing to the number of contacts being taken as the indicator of the abundance of different species of plants a situation might occur in which, when two species of plants had the same phytosociological value of the coefficient of abundance, one was defined as numerous, and the other as scanty, from the aspect of the potential feeding of the animals.

4. FOOD BLOCKS OF DEER

The phenomena described above formed the grounds on which a hypothesis was put forward as to the existence of food blocks in the diet of deer. Individual ecosystems differ from each other in respect of the species composition of plants and their abundance. The intensivity with which animals feed on a given species of plant depends to some extent on the species and quantitative compossition as a whole of the plants forming the food supply in the ecosystem. Consequently the animal feeding in a given habitat prefers a definite set of plant species (a block). This set includes both common species in the ecosystem and those occurring only in small numbers. The most important feature of the food block is that the intensivity of the animals' feeding on certain species determines intensivity of feeding on others. This in consequence results in the same species of plant, forming a component of different blocks, being eaten to a different degree by deer in different ecosystems. In one it may be eaten in very large amounts (even if it does not occur abundantly) while in another the animals avoid it. Also the relatively constant percentage of certain species of plants in several food blocks results in cases of either very intensive or very slight cropping of these plants by deer in different ecosystems.

Using the foregoing criteria as guiding principles the components of 6 food blocks have been given for deer (Table 2).

5. TYPES OF RELATIONS BETWEEN DIFFERENT SPECIES OF PLANTS FORMING A FOOD BLOCK

Studies were made to ascertain exactly which plant species, or groups of species influence intensivity of feeding by animals on other plants. A detailed analysis of the data obtained revealed three types of relations between plants composing a food block in the given ecosystem:

(1) Replacement of Certain Species of Plants by Others in the Animals' Diet

A particularly strongly preferred plant, if it occurs in suitable numbers, may replace another plant species preferred by deer in the diet of these animals. An example of this is the relation between *Carpinus betulus* and *Fraxinus excelsior*, and between *Pinus silvestris* and *Picea excelsa* (Table 3).

Fraxinus excelsior — Carpinus betulus

The more numerous the occurrence of *F. excelsior* the more intensively the deer feed on it (that is, the number of contacts within the sequence of ecosystems increases with increase in the value of the coefficient of abundance — Table 1). Maximum feeding by deer on this species was found in $T\text{-}C_2$, where its D is highest (345). In this ecosystem the animals were observed to feed to a decreasing extent on *Carpinus betulus* (despite its high $D = 260$). It may therefore be concluded that *C. betulus* was replaced in the deer's diet by *F. excelsior*. In *C-Q* where *F. excelsior* occurs in negligible quantities (D — trace only) the maximum number of contacts with *C. betulus* are recorded (with its moderate abundance of

$D = 135$). It may therefore be said that *C. betulus*, which is readily eaten elsewhere, is avoided by deer under conditions in which *F. excelsior* occurs abundantly.

Pinus silvestris — Picea excelsa

P. silvestris is readily eaten by deer, that is, the more abundantly it occurs the more the deer feed on it. The reverse applies to feeding on *P. excelsa*. The maximum number of contacts with species was recorded in ecosystems in which it occurs in small numbers (deciduous forest stands: T-C_1, T-C_2 and C-A). The above phenomenon can be explained by the fact that in coniferous forests (P-P and P-Q) the animals feed on the abundantly occurring *P. silvestris* and avoid *P. excelsa*, whereas in

Table 3

Replace of one preferred species by another in the deer's diet. Mass cropping (n) of plants occurring numerously (D) caused decrease in feeding by these animals on less preferred plants.

Ecosystem	D	n	D	n
	Pinus silvestris		*Carpinus betulus*	
C—Q	+	197	135	45,112
T—C_1	170	1,183	370	37,645
C—A	290	20,355	25	4,924
T—C_2	345	32,126	260	14,114
P—P	—	—	10	304
P—Q	—	—	30	7,056
	Fraxinus excelsior		*Picea excelsa*	
C—Q	10	389	90	6,641
P—Q	150	7,340	710	858
P—P	745	12,656	915	128
T—C_2	—	—	50	3,579
C—A	—	—	90	6,934
T—C_1	—	—	110	4,205

deciduous forests, where there is no *P. silvestris*, the deer supplement the composition of their food with *P. excelsa*. Evidence that this finding is correct is that in three deciduous ecosystems (Table 1) the percentage formed by *P. excelsa* in the animal's diet is similar and fluctuates between 5.0% and 5.7%.

(2) Similar Percentage Formed by Two or More Species of Plants in the Deer's Diet

The percentages formed by two or more plant species in the food block are very similar to each other irrespective of the abundance of the occurrence of these species in the area. An example of the above is supplied by the way in which the animals feed on two species of birch (Table 4).

Betula verrucosa — Betula pubescens

In *T-C*$_2$ and *C-A* both species of birch occur in small numbers only and are consequently only sporadically eaten by deer.

In *T-C*$_1$ *B. pubescens* occurred in small numbers only (and consequently formed a negligible percentage of the deer's diet) and the animals were found to feed to a moderate extent only on the abundantly growing *B. verrucosa*. In effect the percentage of *B. verrucosa* in the food block of *T-C*$_1$ was only 1.3%.

In *P-P* the maximum numbers of *B. pubescens* were observed, but the animals ate it only to a moderate degree. Despite this, its percentage in the food block *P-P* (3.8%) is very similar to that of *B. verrucosa* (3.7%).

Table 4

Similar percentage formed by two plant species in food blocks of different ecosystems.

Ecosystem	Betula verrucosa D	n	%	Betula pubescens D	n	%
C—A	30	9	—	—	—	—
T—C$_2$	10	131	0.2	+	3	—
T—C$_1$	180	1,064	1.3	+	73	—
P—Q	400	3,065	5.6	15	2,485	4.7
P—P	85	1,702	3.7	30	1,737	3.8
C—Q	395	8,941	7.7	20	8,947	7.7

D — coefficient of abundance,
n — number of contacts,
% — percentage formed by a plant in a whole food block of the given ecosystem,
— — negligible percentage,
+ — trace occurrence of a plant in the area.

In *P-Q* occurring in moderate numbers *B. pubescens* is intensively cropped, and the abundantly occurring *B. verrucosa* — moderately, resulting in their percentages in the food block of *P-Q* being similar, *i. e.* respectively 4.7% and 5.6%.

In *C-Q* both species of birches were eaten very intensively. Their percentage in the food block of *C-Q* was the same, that is, 7.7%.

It can be seen from the above that in the case of species forming a similar percentage in the deer's diet, the plant occurring in a given ecosystem in small numbers determines intensivity of feeding by these animals on the species occurring abundantly.

(3) Constant Percentage of Species in Several Food Blocks

Some species of plants are characterized by a similar percentage in the food consumed by deer in different ecosystems (Table 1). This regularity was recorded in the case of 10 plants from the group of trees, bushes and shrubs forming the animal's food. Some examples illustrating the above phenomenon are given below:

Rubus idaeus — *C-Q*, with $D = 75$, — 1,528 contacts recorded, which formed 1.3% of the whole of the food consumed by these animals in this ecosystem. In *P-Q* on the other hand, with $D = 80$, only 951 contacts were recorded. Despite this the percentage of *R. idaeus* in the food eaten by deer in *P-Q* was 1,8%, that is, very similar to that noted in *C-Q*. Similarly in $T\text{-}C_1$ and *C-A* the percentages formed by *R. idaeus* were respectively 5.3 and 6.8%, despite the considerable difference in abundance of occurrence and number of contacts recorded in each of these ecosystems.

Tilia cordata — The phenomenon described occurred particularly markedly in the case of this species. In *P-Q* with the coefficient of abundance of only 10, as many as 2,523 contacts were recorded. At the same time in *C-Q*, with $D = 420$, the number of contacts was 5,040. The percentage for *T. cordata* was very similar in the ecosystems described and was respectively 4.8% and 4.4%.

Populus tremula — the phenomenon described occurred in three ecosystems: *P-Q*, $T\text{-}C_1$ and *C-Q* in which, with different *D* value and different number of contacts, the percentage of *P. tremula* in the whole of the food eaten in each of them is similar being respectively 1.3%, 1.3% and 1.8%.

6. DISCUSSION

In determining the role of deer in forest ecosystems it is important to obtain the most accurate possible information on the qualitative and quantitative composition of the food of these animals. Studies on the food preferences of deer have been made from different aspects, *inter alia*, taking into consideration variations in food over the yearly cycle (Sablina, 1955; Yurgenson, 1968; Borowski & Kossak, 1975; Dzięciołowski, 1970a; Morow, 1976); and during the animal's life (Knorre, 1959; Morow, 1976). Many papers have been concerned with differences in the animal's food preferences depending on the type and age of the forest stand in which they live (Dzięciołowski, 1971; Sablina, 1955). Studies on the chemical composition of food and the animals' need for certain components have formed a separate problem (Hadley & Bliss, 1964; Markgren, 1969; Dzięciołowski, 1970). Despite the fact that so many aspects of the food preferences of deer have been examined, the animals' diet is usually treated as a collection of units independent of each other, that is, of different species of plants. Each of such units forms a given percentage of the animal's diet, but this percentage is not constant but is subject to fluctuations due to various factors.

The material presented in this study shows that, taking into account all the above factors forming the deer's food preferences, it must be assumed that the animals' diet forms a whole in which the different plant species are only elements directly dependent upon one another. This view of the question would appear to be confirmed by data in literature. Generally speaking the lists of plants preferred by deer, drawn up by similar methods in different countries in which the species composition of tree stands is similar, exhibit greater or lesser differences. A similar phenomenon is to be found in studies taking into account different ecosystems, for instance Dzięciołowski (1971) examined the percentage formed by basic groups of foods in deer's diet in three different forest administration districts. This author found that in poor habitats deer eat far fewer branches of trees and bushes than in rich habitats. The animals compensate for the lack of fibrous food by more intensive cropping of shrubs and shrub-like plants. He found not only distinct differences in the percentage of different groups of plants in the deer's diet, but also in the species composition of the animals' diet in the three forest complexes studied.

Peterson (1955) gave differences in the composition of the food of elk in the west and east of America. During the autumn-winter period in Montana, Wyoming and Alaska (west) willow forms the basis of the elk's diet, whereas in Ontario, Isle Royale and Michigan (east) — fir, aspen and birch.

Morow (1976) emphasises the considerbale regional differences in the composition of the elk's food. In the Augustow Forest a marked preference for pine is observed in some forest ecosystems, whereas osier, aspen and buckthorn (*Frangula*) form secondary food, but in other ecosystems these three species are more readily cropped by elk than in pine.

The hypothesis put forward in this paper as to the existence in the deer's diet of the so-called food blocks is an attempt at treating the animals' food as a whole. In these discussions it is not the actual proportions of the components of this food (*e. g.* from stomach analysis) which have been taken as a basis but the degree to which the food supply in the area is utilized. It is thus a measure of the relative consumption of plant species in relation to the »supply« of other plants on which the animals feed in the given ecosystem. The example with pine and spruce (Table 3) shows that there is no preference »as such«, but that there is only relative preference depending on the botanical structure of the ecosystem. In fact it most probably depends further on the season, species of mammal, its age and possibly even its physiological state, the character of vegetation in a given year and degree of availability of food in the winter. It is obvious that it is not possible in this study to discuss all aspects of so complicated a phenomenon.

It has been found that the material collected is insufficient to take into account the group of herb plants and the bark of trees included in the composition of deer's food. The food of two species of deer (roe deer and red deer) occurring in the study area has been discussed simultaneously. and variations in the feeding habits of these animals over the yearly cycle have been taken into consideration. It may therefore be said that we have limited ourselves to describing (over a cycle of several years) the phenomena relating to whole populations of roe deer and red deer within the area of a large and varied forest complex.

It is known that the composition of deer's food varies greatly over the course of a year (cf. B o r o w s k i & K o s s a k, 1975). The phenomenon grasped in the case of *Betula verrucosa* and *Betula pubescens* is therefore even more astonishing, that is, the percentage formed by these two birches in the food blocks of successive ecosystems is very similar to each other (Table 4). When the yearly cycle of the deer's feeding on birches is considered (B o r o w s k i & K o s s a k, 1975) it will at once be noticed that *B. verrucosa* is eaten mainly from December to March inclusive, and *B. pubescens* from June to November. What causes their participation in the animals' diet in a given ecosystem to be so greatly alike over a cycle of several years? Some explanation is afforded by the data given in a separate paper (K o s s a k, in prep.), in which it has been shown that times of maximum feeding by deer on different plant species coincide with the times at which they pass through the apogeum of active bodies content. In the case of *B. verrucosa* this time occurs during the second half of winter and very early spring. It may be that during summer *B. pubescens* contains the same active bodies as *B. verrucosa* in early spring. It is also possible that the animals' requirements for the components which birch contain is constant over the whole year and the animals obtain them seasonally first from *B. verrucosa*, then from *B. pubescens*.

In the light of the foregoing the urgent need for carrying out detailed studies for the purpose of defining the reciprocal compounds of plants in the deer's diet becomes plain. Before they are completed it is only possible to suggest that considerable caution is taken in deciding upon sets of plants given to control animals in tests on their food preferences, as such preference may depend on which species of plants, and in what amounts, enter the composition of the set and also on the season in which the tests are made.

At the same time a knowledge of the structure of deer's diet may be of considerable economic importance, namely, if it is known which plant species are particularly preferred in a given ecosystem (Table 2, group of plants sought-after and basic) it will be possible to undertake several measures to limit the damage done by game animals. If the food block of the given ecosystem is known it will be possible for instance, in stocking a shoot, to use less valuable species of plants as the so-called »counter-attraction« for the animals to valuable species from the aspect of forest management.

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KOMPLEKSOWY CHARAKTER PREFERENCJI POKARMOWYCH JELENIOWATYCH A STRUKTURA FITOCENOZ

Streszczenie

Na podstawie danych uzyskanych w badaniach stosunków pokarmowych sarny i jelenia w Puszczy Białowieskiej przeprowadzono analizę struktury diety jeleniowatych w 6 zespołach leśnych. Operowano trzema parametrami: 1) współczynnikiem obfitości występowania danego gatunku rośliny (*D*), 2) intensywnością żerowania jeleniowatych na danej roślinie wyrażoną w kontaktach (*n*), 3) procentowym udziałem poszczególnych gatunków roślin w całości żeru pędowego (drzewa, krzewy i krzewinki), zanotowanego w diecie jeleniowatych łącznie w ciągu trzech lat badań (1969—1971).

Przeprowadzono porównania stopnia wykorzystania przez jeleniowate poszczególnych gatunków roślin zakładając, że jest on pośrednio określony przez stosunek współczynnika obfitości rośliny do ilości kontaktów (Tabela 1).

Prześledzono udział procentowy poszczególnych roślin w całości żeru jeleniowatych w różnych ekosystemach (Tabela 1).

Śledząc strukturę ilościową i jakościową diety jeleniowatych w różnych ekosystemach, wysunięto hipotezę istnienia w diecie tych zwierząt bloków pokarmowych. Zwierzę żerując w danym ekosystemie preferuje nie tyle poszczególne gatunki roślin, co cały ich zestaw (blok), przy czym stopień żerowania zwierząt na jednych gatunkach, decyduje o intensywności żerowania na innych. Bloki pokarmowe są charakterystyczne dla poszczególnych ekosystemów i są zależne od struktury fitocenozy danego ekosystemu. Może się zdarzyć, że ten sam gatunek rośliny, będąc składową różnych bloków, może być różnie żerowany przez jeleniowate w poszczególnych ekosystemach.

Podano skład gatunkowy i ilościowy bloków pokarmowych 6 ekosystemów, dzieląc rośliny na podstawowe, uzupełniające, poszukiwane i omijane w danym ekosystemie (Tabela 2).

Wykazano następujące związki między gatunkami roślin w bloku: 1) zastępowanie się gatunków w diecie, gdy szczególnie preferowany gatunek rośliny spowoduje spadek żerowania zwierząt na innym preferowanym i licznym gatunku (Tabela 3), 2) podobny udział procentowy kilku roślin w bloku, niezależnie od obfitości ich występowania (Tabela 4), 3) podobny udział procentowy niektórych gatunków w kilku blokach pokarmowych (Tabela 1).

Table 2

Species structure of 6 food blocks in 6 ecosystems in the Białowieża Primeval Forest.
* total for all species below.

1 a	%	1 b	%	2 a	%	2 b	%	3 a	%	3 b	%
						Peucedano-Pinetum					
P. silvestris	27.6					*B. verrucosa*	3.7	*Q. robur*	0.5	*B. pubescens*	3.8
V. myrtillus	22.3							*P. excelsa*	0.3	*S. aucuparia*	0.8
C. vulgaris	19.2									*P. tremula*	0.7
C. nigricans	14.6										
F. alnus	1.8										
C. avellana *	3.1										
T. cordata											
C. betulus											
S. caprea											
R. idaeus											
U. campestris											
E. europea											
						Pino-Quercetum					
P. silvestris	14.0	*C. avellana*	1.7	*S. caprea*	26.7	*T. cordata*	4.8	*Q. robur*	8.2	*B. verrucosa*	5.6
C. betulus	13.5	*P. tremula*	1.3			*S. aucuparia*	1.2	*P. excelsa*	1.6	*R. idaeus*	1.8
V. myrtillus	8.6	*B. pubescens*	4.7								
S. cinerea	3.4										
C. nigricans *	1.1										
V. lantana											
U. laevis											
A. glutinosa											
C. vulgaris											
F. alnus											
E. europea											
						Calamagrostio-Quercetum					
S. caprea	5.4	*C. avellana*	2.5	*C. betulus*	39.1	*B. verrucosa*	7.7	*S. aucuparia*	—	*T. cordata*	4.4
S. cinerea	1.7	*P. tremula*	1.8	*Q. robur*	19.7	*B. pubescens*	7.7				
V. lantana *	1.4	*R. idaeus*	1.3			*P. excelsa*	5.7				
F. excelsior											
P. silvestris											
V. myrtillus											
U. laevis											
						Tilio-Carpinetum typicum					
C. betulus	44.8	*R. idaeus*	5.3	*Q. robur*	11.2			*F. excelsior*	1.4	*P. excelsa*	5.0
S. caprea	13.1			*C. avellana*	4.0					*B. verrucosa*	1.3
T. cordata	6.9									*P. tremula*	1.3
S. cinerea	5.0										
U. laevis *	0.2										
B. pubescens											
V. lantana											
S. aucuparia											
F. alnus											
E. europea											
						Tilio-Carpinetum stachyetosum					
F. excelsior	45.4	*P. excelsa*	5.1	*U. laevis*	4.1	*T. cordata*	1.7	*C. betulus*	19.9	*E. europea*	2.4
R. idaeus	8.1							*Q. robur*	1.3	*A. glutinosa*	0.2
C. avellana	7.9									*S. aucuparia*	--
P. tremula *	1.7										
S. cinerea											
B. verrucosa											
U. campestris											
B. pubescens											
V. lantana											
R. nigrum											
						Circaeo-Alnetum					
E. excelsior	36.4			*U. campestris*	1.1	*S. aucuparia*	1.1	*Q. robur*	—	*R. idaeus*	6.8
P. excelsa	12.4									*A. glutinosa*	0.3
C. avellana	11.5										
C. betulus	8.8										
P. padus	6.2										
R. nigrum	3.6										
U. laevis	3.1										
E. europea	3.1										
V. lantana	2.1										
T. cordata	1.1										
F. alnus *	0.8										
P. tremula											
S. caprea											
S. cinerea											
B. verrucosa											

(1a) Basic and supplementary species in the deer's diet in the given ecosystem. Consumed appropriately to abundance of occurrence; (1b) Species forming a similar percentage in several food blocks. Consumed appropriately to abundance of occurrence; (2a) Sought-after species; (2b) Sought-after species characterized by similar percentage in several food blocks; (3a) Avoided species; (3b) Avoided species characterized by similar percentage in several food blocks.

% — percentage formed by plant in whole food block
—— negligible percentage