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Structure and Spatial Organization of Deer Populations [1]

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Visual observations of five deer species (moose, red, sika, fallow, and roe deer) have been taken since 1966 in four forest districts in lowland Poland. Forest districts studied varied in diversity and fertility of forest sites and plant associations. Altogether, there were gathered almost 8.5 thous. of observations, most of which (6.4 thous.) concerned the red deer. Information was obtained on population structure (sex ratio, age classes, association), diurnal rhythm of activity, and frequentation of animals in different habitats. All populations studied indicated the prevalence of females. High recruitment showed moose and fallow deer, followed by red and roe deer populations. Longliving species (moose and red deer) indicated a higher proportion of old individuals, when compared to those with a shorter longevity. Analysis of sizes of animal groups indicated that (1) moose and roe deer belong to species living solitary life or in small family groups, (2) sika and fallow deer form small bands of 2—6 animals, while (3) red deer is a gregarious species with a frequent occurrence of herds of 10 animals. The size and composition of red deer aggregations revealed an obvious seasonal and spatial variation. All the species compared revealed rather uniform activity during daylight hours. Red deer indicated a definite preference towards the fresh mixed coniferous forest and grassy areas. Moose and red deer inhabiting the same forest district showed identical preferences for definite forest site types.

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1. INTRODUCTION

Behavioural studies at the level of population have quite a direct bearing upon game management (Leuthold, 1970). Red deer surveys attempting to gather information on distribution, abundance and calving rates by direct counts in sample areas of Scotland's deer ground have a long history (Red Deer Research in Scotland, 1967; Mitchel & Lowe, 1967; Mitchell, 1968; Lowe, 1969; The Red Deer Commission, 1970, 1971; Mitchell, McCowan & Parish, 1971). Similar work was attempted in high mountains of Switzerland (Schloeth, 1961, 1962, 1968, Hoffmann & Nievergelt, 1972), Norway (Thomson, 1971), Poland (Brą-

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giel, 1973) and in lowland USSR (Šostak, 1973). In North America Wilkins (1957), while studying range use, food habits, and agricultural relationships of the mule deer in Montana, collected ca 3,500 observations. Mule deer food habits and range use were also studied by Lovaas (1958) in Montana with the use of direct observations of animals along the Judith River.

So-called strip census was used to estimate the relative abundance of deer in forest types of the central Adirondack region (Krull, 1964). Activity, ranging, social behaviour, aquatic feeding behaviour, and response to human disturbance were also studied by observation of deer along roadsides and lakeshores (Behrend, 1967). Differential distribution of elk by sex and age on the winter range in Montana was studied by Peek & Lovaas (1968) with the use of the same technique. Roadside counts as a technique for deer census were discussed by Lueth (1970). Data on sex ratio and group composition of white-tailed deer were collected while driving predetermined routes in Texas by Michael (1965, 1970). Ground observations of unmarked elk were taken by Moran (1973) to obtain herd classification, information on seasonal movements, together with size and composition of bands, and seasonal use of cover types. Aerial search from small aircraft or helicopter was used in studies on the distribution and annual aggregation patterns in three pupulations of moose occupying different habitats in Montana, Alaska, and Minnesota (Peek, LeResche & Stevens, 1974).

The present paper presents a development of a preliminary attempt of the determination of repartition of habitat niches within an area of red deer population undertaken by the author several years ago (Dzięciołowski, 1969).

2. MATERIALS AND METHOD; STUDY AREAS

Visual observations of deer have been taken during occasional visits to forest. Each observation was recorded on a special card and included following information: forest district, forest range, compartment, date, hour, number of animals, their sex and age, kind of activity, by-hand sketch of situation, and the name of observer.

Such observations have been taken in four forest districts scattered over lowland Poland, namely Iława (53°32′ to 53°36′ N and 19°29′ to 19°31′ E), Płaska (53°40′ to 54°10′ N and 22°40′ to 23°32′ E), Józefów (50°25′ to 50°32′ N and 22°56′ to 23°10′ E), and Kobiór (49°08′ to 50°03′ N and 18°33′ to 19°08′ E). They were initiated in 1966. Observations included: red deer at Iława, Płaska, Józefów, and Kobiór, moose — at Płaska, and fallow deer, sika deer, and roe deer — at Kobiór.

The number of animals recorded in individual forest districts is given in Table 1. The characteristics and the distribution of forest site types in forest

districts studied is given in Table 9. The data contained in table show that Iława has the greatest diversity of forest sites and considerable acreage under rich forest site (mixed deciduous forest). Płaska also shows considerable diversity of sites with a remarkable share of alderwood. Kobiór is third in respect to diversity, the moist mixed coniferous forest prevailing there. The lowest diversity was at Józefów with fresh coniferous forest prevailing in acreage.

For parts of the three forest districts studied, namely Józefów, Kobiór, and Iława, identification and mapping of forest associations was done during years 1964—1969. The distribution of forest associations is given in Table 12. The plant sociological classification roughly corresponds with forest site type classification. Iława remained to be the first in respect to diversity of vegetation types. On the other hand Józefów takes the second place in respect to the number of forest associations present, before the Kobiór forest district, where only 6 forest associations were identified.

Table 1

Numbers of animals recorded in the four districts studied.

Forest district	Moose	Red deer	Sika deer	Fallow deer	Roe deer	Total
Józefów	—	1220	—	—	—	1220
Kobiór	—	985	233	546	653	2417
Iława	—	3373	—	—	—	3373
Płaska	632	825	—	—	—	1457
Total	632	6403	233	546	653	8467

In the Iława forest district two forest associations prevail, viz. *Fago-Quercetum* and *Pino-Quercetum*. Both characterize themselves by fertile soils, diversified vegetation with predominance of oak, beech, and pine. At Kobiór *Calamagrosti villosae-Pinetum* is the dominant forest association. It is a moist mixed coniferous forest with pine stands, spruces in understory and reedgrass prevailing in herb layer. The Józefów forest district has the dominant forest association *Dicrano--Pinetum* equivalent to the fresh coniferous forest in site classification.

Kobiór has the greatest acreage under meadows, while Płaska, Iława, and Józefów have smaller grassy areas (55—83 ha). The acreage of other open areas (fields, nurseries) is fairly high (280—400 ha) in all the forest districts, except of Płaska, which has only 86 ha of them.

Information obtained in the course of present research was coded onto cards in Fortran, transferred on magnetic tape, and processed on a digital computer ODRA 1305 in the Computation Center, Polish Academy of Sciences in Warsaw.

The method of irregular observations recorded according to predetermined procedure, used in this study, was applied previously by: Andersen, 1953; Wilkins, 1957; Dzięciołowski, 1969; Martinka, 1969; Thomson, 1971; Brągiel, 1973; Moran, 1973; and Šostak, 1973. Another procedure, involving counts along prescribed routes, was used in several studies (Lovaas, 1958; Krull, 1964; Peek & Lovaas, 1968; Michael, 1970; Osmolovskaya, 1970).

Recently, studies on the spatial organization of animal populations utilize individual marking of animals to an increasing extent (Kimball & Wolfe, 1974).

3. RESULTS

3.1. Population Structure (Sex Ratio, Age Classes, Association)

Table 2 presents the sex and age structure of populations of the five cervid species studied. It is characteristic that all populations indicate the prevalence of females (from 53% for the red deer to 75% in the fallow deer). Some bias towards females, may be expected due to the wrong classification of young males as females, especially after shedding antlers by the former, but it could not explain the difference wholly.

Table 2

Sex ratio and age structure in animal populations studied.

Animal	Sex ratio ♂ : ♀	Age groups in %%			
		Calves	Juveniles	Adult	Old
Moose	44 : 56	28	42	25	5
Red deer	47 : 53	24	34	30	12
Sika deer	38 : 62	56	21	21	2
Fallow deer	25 : 75	27	29	41	3
Roe deer	36 : 64	24	30	44	2

The best balance is indicated by red deer and moose populations, remarkable prevalence of females — by sika and roe deer populations, while the sex ratio is completely upset in the case of the fallow deer.

Data on the age structure contained in the table, apart from sika deer, reveal rather an uniform course. High recruitment show moose and fallow deer, followed by red and roe deer. Longliving species (moose and red deer) indicate a higher proportion of old individuals, when compared to those with a shorter longevity.

Table 3

Sex ratio and age structure in the four red deer populations studied

Population	Sex ratio ♂ : ♀	Age groups in %%				
		Calves	Juvenile	Adult	Old	Total
Józefów	62 : 38	38	24	26	12	100
Kobiór	41 : 59	26	38	29	7	100
Iława	40 : 60	22	35	31	12	100
Płaska	60 : 40	18	29	39	15	100
Total	44 : 56	24	34	30	12	100

The structure of red deer population given in Table 2 presents totals for the four populations studied. The comparison of them given in Table 3 is interesting. It appears that the four populations studied may be divided into two groups in respect to the sex ratio. Populations with the prevalence of males (Józefów and Płaska) inhabit eastern part of

the country with a continental climate and presence of big predators (wolves in Płaska additionally, lynxes). Two western populations (Kobiór and Iława) inhabit areas with a mild climate of Atlantic type and without big predators.

This would be an excellent explanation, when the age structure would confirm this hypothesis. This is not the case, however. Judging from the percent of calves in population, Józefów is the most productive population, followed by Kobiór. On the other hand, Płaska indicated the highest proportion of old animals in population.

Size of animal groups to be met in the five populations studied is given in Table 4. Results are entirely concordant with what is known

Table 4

Structure of aggregations of the deer studied.

Number of individuals in an aggregation	Frequencies of aggregations encountered				
	Moose	Red deer	Sika deer	Fallow deer	Roe deer
1	166	703	15	112	279
2	113	638	15	90	117
3	45	365	10	28	30
4	10	163	4	13	3
5	6	146	2	7	4
6	2	74	3	4	1
7	2	75	2	2	0
8	0	31	3	3	0
9	1	17	2	1	0
10		14	2	0	0
11		8	2	0	0
12		7	1	1	1
13		4			
14		3			
15		4			
16		1			
17		1			
18		1			
19		1			
20		1			
21		1			

about the biology and ecology of the animal species discussed. Moose and roe deer belong to species living solitary life or in small family groups. The bulk of observations falls to single animals and groups up to 3 individuals. Sika and fallow deer form small herds of 2—6 animals, their largest aggregations being of 12 individuals. Red deer is a gregarious species with frequent occurrence of herds of 10 animals, the largest one recorded in these studies exceeding 21 individuals.

Due to the abundance of data concerning the size and composition of red deer herds, this material was developed at some detail. Table 5

illustrates the seasonal variation in the size of red deer aggregations in all the four forest tracts studied. It compares actual and expected frequencies of observations of individuals and groups of deer with definite numbers. These values differ in the statistically significant way. The value $\chi^2 = 278.0558$ with 66 degrees of freedom.

The data contained in table indicate that, beginning with December, the number of lone animals of both sexes is lower than expected. Such status prevails in the case of males until June, while in the case of females — until April. This may be explained by the separation of hinds from herds before parturition (May — June). In the case of males only during September and October the number of single animals

Table 5

Seasonal variation in the size of red deer aggregations.

Month	Single ♂♂		Single ♀♀		2—4		5—7		8—10		11—15		15+	
	a	e	a	e	a	e	a	e	a	e	a	e	a	e
Jan.	31	43	5	16	99	103	43	26	13	5	3	2	1	0
Feb.	26	43	2	16	107	104	45	26	9	5	7	2	1	0
March	20	27	7	10	71	65	17	16	5	3	4	1	0	0
April	23	27	10	10	70	65	18	16	2	3	0	1	1	0
May	41	45	49	17	91	109	25	27	1	6	0	2	1	1
June	43	42	34	16	100	101	13	25	2	5	0	2	0	0
July	28	31	11	12	81	74	20	18	1	4	0	2	0	0
Aug.	40	36	8	14	89	86	18	21	4	4	5	2	0	0
Sept.	144	98	40	38	218	236	38	59	4	12	3	5	1	1
Oct.	50	40	12	15	99	98	19	24	3	5	1	2	0	0
Nov.	43	43	12	17	105	105	30	26	8	5	1	2	0	1
Dec.	23	38	7	14	105	90	21	22	11	5	4	2	1	0

a — actual numbers, e — expected numbers

observed is obviously higher than expected, what is connected with the period of an increased activity and search after females in oestrus.

The number of observed small groups of red deer (2—4 individuals) does not deviate from values expected during subsequent months of year.

Medium-sized aggregations (5—7 individuals) are to be met more frequently than one can expect during winter (January — February) and to a lesser extent during spring (March — April), and are rather rare during summer (June) and autumn (September — October).

Great red deer bands (8—10 animals) reveal an obvious seasonal variation. Their frequency is higher than expected values from November to March. From April to October their number is lower than expected.

Very great aggregations of red deer (11 and more individuals) are generally rare. They are more numerous than the values expected during the period since December to March inclusive. During the

remaining period (except of August) they are less numerous than expected. Similarly, therefore, as in the previous case, these are typically winter aggregations.

Table 6 presents the same numerical material for individual red deer population. The value $\chi^2 = 420.0172$ with 198 degrees of freedom evidences the statistically significant differentiation of data contained in the table.

The Kobiór population of red deer indicates the lowest herd instinct from among the four populations compared. The frequency of observations of lone animals of both sexes is considerably higher here than the expected values. On the other hand all kinds of red deer aggregations indicate the frequency lower than expected.

Table 6

Variation in the size of red deer aggregations in individual forest districts.

Aggregation	Kobiór		Płaska		Józefów		Iława		Total	
	a	e	a	e	a	e	a	e	a	e
Single ♂♂	126	104	60	47	78	94	248	268	512	512
Single ♀♀	107	40	1	18	33	36	56	103	197	197
2—4	207	250	83	113	229	226	716	645	1235	1235
5—7	27	62	44	28	61	56	175	160	307	307
8—10	7	13	16	6	20	12	20	33	63	63
11—15	2	6	10	3	6	5	10	15	28	28
15+	0	1	1	1	3	1	2	3	6	6

a — actual values, e — expected values

The red deer population in Płaska indicates the predominance of big bands (from 5 to 15 individuals each) in relation to the expected values. Great number of lone stags and almost complete absence of single females attract one's attention.

Similarly, the red deer population in Józefów indicates an obvious predominance of aggregations of any size in relation to the expected values with the frequency of both sex lone animals lower than the expected one.

The red deer population in Iława indicates still another pattern of aggregation structure. Here both single animals of both sexes and big bands (exceeding 8 individuals) are rare. On the other hand small groups (2—7 individuals) are more numerous than could be expected.

The seasonal variation in the composition of red deer aggregations was analyzed in a similar way. The data, compiled in Table 7, also indicated a statistically significant differentiation. The χ^2 value amounted to 468,3742 with 66 degrees of freedom.

Groups consisting of adult males start to be formed more numerously

Table 7

Seasonal variation in the composition of red deer aggregations.

Month	adult ♂♂		adult ♀♀		♀+♂		♀+juv.		♀+juv.+♂		♂+♀		Other		Total	
	a	e	a	e	a	e	a	e	a	e	a	e	a	e	a	e
Jan.	40	30	14	11	29	34	11	12	38	35	6	11	16	20	154	154
Feb.	49	33	11	12	26	37	6	13	60	38	4	12	12	22	168	168
March	27	19	8	7	18	22	7	8	25	22	8	7	4	13	97	97
April	16	18	9	6	11	20	23	7	19	21	8	7	5	12	91	91
May	29	23	19	8	10	26	29	9	16	27	7	9	9	16	119	119
June	20	23	5	8	44	26	16	9	22	27	7	9	3	15	117	117
July	17	20	5	7	36	23	4	8	30	23	6	8	4	13	102	102
August	16	22	6	8	27	25	5	9	40	26	1	8	19	15	114	114
Sept.	26	51	7	19	56	58	6	20	29	60	48	19	91	35	263	263
Oct.	13	24	4	9	39	27	7	9	24	28	17	9	17	16	121	121
Nov.	31	28	14	10	36	31	4	11	35	32	4	10	17	19	141	141
Dec.	34	28	14	10	29	31	8	11	35	33	4	10	18	19	142	142

a — actual values, e — expected values.

than expected beginning with November, maintain themselves during December, January, February until March. During the period from April to October the situation is variable, but generally groups of adult males are less numerous than may be expected.

In the case of adult hinds the prevalence of actual observations over expected ones also started in November, but extended only until January. Period of balance of both values occurred during February and March. Prevalence of the number of these observations was marked again during April and May, what may be connected with the period of parturition. From June to October the number of groups consisting of adult hinds was smaller than the expected one.

Groups, with the composition »dam — calf«, are most frequent following to parturition, and thus during June and July. Later, there comes the period of a complete rearrangement of the composition of red deer aggregations. It is connected with rut (August — September). During this period of time groups »dam — calf« occur accordingly to the expected values. During October and November these groups become again more frequent than one could expect. Afterwards, from December to May, the frequency of these groups was irreversibly lower than the expected values.

Groups with the composition »hind + yearling« were more frequent than expected during the period of time from April to June. They were rare during the remaining months.

Groups consisting of »hind + yearling + calf« were more frequent than expected beginning with November until March. During remaining months (except of July and August) they were less frequent than could be expected.

Groups consisting of male and female are not typical for red deer. They are to be met more frequently exclusively during rut (September — October).

Finally, groups with the composition other than above mentioned, occur more frequently than expected exclusively during three months, namely from August to October. This is connected with rut, because groups classed to the category »other«, consisted mainly of stags, hinds, and youth.

Table 8 illustrates the variation in the composition of red deer groups in the four forest tracts compared. The data compiled in this table revealed a statistically significant variation evidenced by the χ^2 value amounting to 302,2889 with 198 degrees of freedom.

When groups of males are considered, they were recorded more frequently at Józefów and Płaska than in the two remaining forest districts. The same was true for groups consisting of adult females.

Groups consisting of hind with calf were more numerous than expected at Kobiór and Iława, less numerous at Józefów and by far less numerous — at Płaska. One can note, thus, here a trend of exchange in relation to the two first groups. Rather similar trend was indicated by groups consisting of »hind + yearling« (it was only at Kobiór where there occurs an alteration when compared to the previous category).

Groups, consisting of hind, yearling, and calf, are more numerous, when compared to the expected values at Płaska and Iława, while less numerous — at Józefów.

Table 8

Variation in red deer aggregations in various forest districts.

Composition of group	Kobiór		Płaska		Józefów		Iława		Total	
	a	e	a	e	a	e	a	e	a	e
Adult ♂♂	27	46	33	29	88	62	170	181	318	318
Adult ♀♀	13	17	19	11	37	22	47	66	116	116
♀+♂	71	53	4	33	68	70	218	205	361	361
♀+juv.	17	18	8	12	11	24	90	72	126	126
♀+juv.+♂	54	54	43	34	51	72	225	212	373	373
♂+♀	25	18	21	11	20	23	54	68	120	120
Other	31	31	22	20	41	42	121	122	215	215
Total	238	238	150	150	316	316	925	925	1629	1629

a — actual values, e — expected values.

Generally, the three categories of groups consisting of hinds with progeny, are more numerous than expected at Kobiór and Iława, while less numerous at Płaska and Józefów. This may indicate a lower recruitment in populations of the two latter forests.

Groups consisting of male and female (to be met during rut) were more numerous than expected at Kobiór and Płaska, while less numerous at Józefów and Iława.

Finally, groups with the composition other than mentioned, were more frequent at Płaska and Józefów and less frequent than expected — at Iława.

3.2. Diurnal Rhythm of Activity

The diurnal rhythm of activity of the five cervid species is illustrated by Fig. 1. It appears that the species compared reveal rather uniform activity during daylight hours. Low per cent of animals seen during night hours results probably rather from poor visibility conditions. Moose indicates a peak in early morning hours with an even distribution of activity throughout the rest of daylight. Red deer indicates two peaks (early morning and evening hours) with a marked decrease in

activity during late morning (8:01 — 12:00 *a.m.*). Sika deer reveals highest activity during afternoon and evening hours. Fallow deer has an even distribution of activity throughout daylight hours with one peak at dusk (4:01 — 8:00 *p.m.*). The same is true for the roe deer.

The χ^2 test calculated for data contained in Fig. 1 disclosed significant differences between the actual and theoretical frequencies of the activity recorded for all the five cervid species.

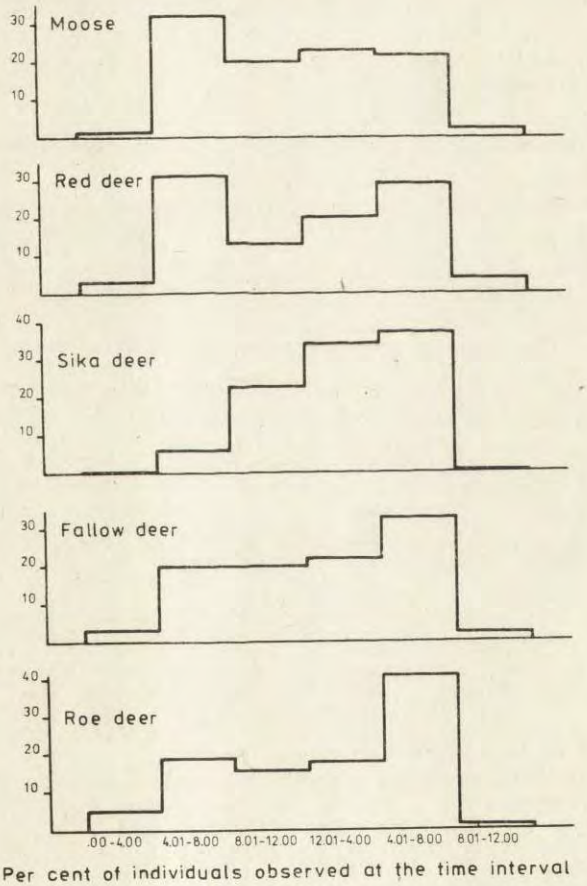

Fig. 1. Diurnal rhythm of activity of the five animal species studied.

3.3. Penetration of Different Habitats in an Annual Cycle

Table 9 compares actual versus expected frequentation of red deer in individual forest site types and certain non-forest sites (meadows, farmland) within individual forest tracts studied. The expected frequentation was calculated according to areal contribution of the site type within each of the forest tract, while the last column gives the

Table

Selection of habitats by red deer within

Forest site type	Acreage of habitat					
	Józefów			Kobiór		
	ha	a	e	ha	a	e
Fresh coniferous forest	2853.88	592	639	324.72	0	51
Fresh mixed coniferous forest	183.03	16	41	1087.76	90	170
Moist mixed coniferous forest	141.65	57	32	2354.52	501	368
Moist coniferous forest	646.09	210	149	218.27	4	34
Boggy coniferous forest and swamps	99.53	46	22	21.83	0	3
Fresh deciduous forest	—	0	0	761,16	0	119
Mixed deciduous forest	164.59	1	37	89.48	0	14
Moist mixed deciduous forest	—	0	0	330.43	12	52
Alderwood	63.31	7	14	205.03	1	32
Total forest area	4152.08	929	934	5393.20	608	843
Meadows and compartment lines	55.43	90	12	220.55	292	34
Farmland and other	395.73	12	89	280.14	22	44
Total non-forest area	451.16	102	101	500.69	314	78
Grand total	4603.24	1031	1035	5893.89	922	921

share of the site type in the total acreage of the four forest tracts compared [2]. For the calculation of farmland, 100 m wide belt of fields directly adjoining the forest studied was taken. It was arbitrarily determined that such a belt includes the area usually penetrated by deer leaving a forest.

Table 10

Selection of habitat by red deer, sika deer, fallow deer and roe deer within the Kobiór forest district.

Forest site type	Numbers of:							
	Red deer		Sika deer		Fallow deer		Roe deer	
	a	e	a	e	a	e	a	e
Fresh coniferous forest	0	51	0	12	0	28	0	36
Fresh mixed coniferous forest	90	170	0	40	53	95	62	120
Moist mixed coniferous forest	501	368	95	86	252	205	391	260
Moist coniferous forest	4	34	0	8	3	19	4	24
Boggy coniferous forest and swamps	0	3	0	1	0	2	0	2
Fresh deciduous forest	0	119	0	28	0	66	0	84
Mixed deciduous forest	0	14	0	3	0	8	0	10
Moist mixed deciduous forest	12	52	0	12	0	29	4	36
Alderwood	1	32	0	8	2	18	0	23
Total forest area	608	843	95	198	310	470	461	595
Meadows and compartment lines	292	34	121	8	198	19	170	24
Farmland and other	22	44	0	10	6	24	19	31
Total non-forest area	314	78	121	18	204	43	189	55

[2] This is why expected total frequencies differ from sums of expected frequencies in the four forest tracts.

9

each of the four forest tracts studied.

and numbers of red deer

Iława			Płaska			Total	
ha	a	e	ha	a	e	a	e
1611.16	807	742	4095.23	354	399	1753	2087
3646.74	1876	1680	1016.52	119	99	2101	1400
95.85	79	44	292.84	9	28	646	681
24.91	4	12	392.32	113	38	331	302
2.95	22	1	93.38	20	9	88	51
93.09	0	43	38.64	0	4	0	211
1181.42	79	544	352.39	53	34	133	422
6.90	3	3	7.73	0	1	15	81
178.00	37	82	1428.54	83	139	128	442
6841.02	2907	3151	7717.59	751	751	5195	5677
61.84	264	28	83.36	18	8	664	100
292.35	144	135	85.80	0	8	178	249
354.19	408	163	169.16	18	16	842	349
7195.21	3315	3314	7886.75	769	767	6037	6026

Observed and theoretical frequencies (corresponding with the areal proportion of definite site type) were compared with the aid of χ^2 test. Test indicated differentiation of the frequencies compared. Following values of χ^2 were obtained: for Józefów — 683.2 with 8 degrees of freedom, for Kobiór — 2,292.7 with 10 degrees of freedom, for Iława — 2,787.0 with 10 degrees of freedom, for Płaska — 239.3 with 10 degrees of freedom.

Data presented in Table 9 indicate that site types compared may be

Table 11

Selection of habitats by moose and red deer within the Płaska forest district.

Forest site type	Moose		Red deer	
	actual	expected	actual	expected
Fresh coniferous forest	270	318	354	399
Fresh mixed coniferous forest	90	79	119	99
Moist mixed coniferous forest	18	23	9	29
Moist coniferous forest	71	30	113	38
Boggy coniferous forest and swamps	24	7	20	9
Fresh deciduous forest	1	3	0	4
Mixed deciduous forest	44	27	53	34
Moist mixed deciduous forest	0	1	0	1
Alderwood	40	111	83	139
Total forest area	558	599	751	752
Meadows and compartment lines	53	6	18	8
Farmland and other	2	7	0	8
Total non-forest area	55	13	18	16

Table 12

Selection of forest associations by red deer within each of the three forest tracts studied.

Forest association	Acreage of association and number of red deer in forest districts								
	Józefów			Kobiór			Iława		
	ha	a	e	ha	a	e	ha	a	e
1. *Peucedano-Pinetum*	—	—	—	—	—	—	852.05	614	391
2. *Leucobrio-Pinetum*	162.71	27	75	285.16	—	131	—	—	—
3. *Dicrano-Pinetum*	1288.48	227	591	—	—	—	—	—	—
4. *Calamagrosti villosae-Pinetum*	9.75	—	4	1281.10	356	588	—	—	—
5. *Vaccinio uliginosi-Pinetum*	119.67	10	55	7.74	—	4	24.57	—	11
6. *Pino-Quercetum*	124.07	—	57	896.71	255	412	1196.21	898	549
7. *Fago-Quercetum*	—	—	—	—	—	—	1482.57	780	680
8. *Potentillo albae-Quercetum*	—	—	—	—	—	—	99.46	100	46
9. *Stellario-Carpinetum*	—	—	—	—	—	—	302.72	86	139
10. *Tilio-Carpinetum*	20.30	—	9	—	—	—	478.81	388	220
11. *Circeo-Alnetum*	—	—	—	36.23	—	17	39.37	6	18
12. *Salicetum pentandro-cinereae*	—	—	—	—	—	—	10.30	—	5
13. *Carici elongatae-Alnetum*	41.79	—	19	73.79	—	34	30.77	11	14
14. *Lycopodio annotini-Piceetum*	—	—	—	—	—	—	45.52	45	21
15. *Betuletum pubescentis*	—	—	—	—	—	—	4.30	2	2
16. *Pino-Betuletum*	35.87	28	16	—	—	—	—	—	—
17. *Sphagnetum medii pinetosum*	49.54	3	23	—	—	—	29.89	3	14
Total forest habitat	1852.18	295	849	2580.73	611	1186	4596.54	2933	2110
18. Association from the order *Ledetalia*	—	—	—	—	—	—	8.99	14	4
19. Association from the order *Phragmitetalia*	—	—	—	—	—	—	34.61	—	16
20. *Caricetum lasiocarpae*	9.15	—	4	—	—	—	—	—	—
21. Meadows, compartment lines, pastures	55.43	90	25	220.55	283	101	61.84	248	28
22. Farmland, plantations, forest nurseries, other	395.73	31	182	280.14	84	129	292.35	178	134
Total non-forest habitat	460.31	121	211	500.69	367	230	397.79	440	182
Grand total	2312.49	416	1060	3081.42	978	1416	4994.33	3373	2292

generally divided into three broad categories, namely: (1) those frequented more intensively by red deer than it would result from their acreage (fresh mixed coniferous forest, meadows and compartment lines), (2) frequented roughly in proportion to their areal share, and (3) those frequented less intensively than could be expected from their areal contribution (fresh coniferous forest, fresh deciduous forest, mixed deciduous forest, and alderwood).

So the red deer indicated a definite preference towards the fresh mixed coniferous forest (evidently so in Iława) and grassy areas (in all four forest districts). Interesting is the avoidance of the fresh coniferous forest and most deciduous forest sites.

Very interesting is the comparison of the frequentation of four cervid species in forest site types within one forest district (Kobiór), given in Table 10. All four deer species reveal a very uniform, general trend of preference for two types of site, namely moist mixed coniferous forest, the most important forest site type in this forest district, and grassy areas (meadows and compartment lines). All other site types were frequented less than it would result from their acreage share.

The χ^2 test calculated for data contained in Table 10 also indicated significant differentiation between observed and theoretical frequencies. Following value of χ^2 were obtained: for red deer — as in table 12, for sika deer — 2,000.0, for fallow deer — 1,865.3, for roe deer — 1,171.8, all with 10 degrees of freedom.

Similar comparison was done for moose and red deer inhabiting the same forest district (Płaska) (Table 11). It appears that both animals show exactly the same preference for definite forest site types. Fresh mixed coniferous forest, moist coniferous forest, boggy coniferous forest + swamps, mixed deciduous forest, meadows and compartment lines are obviously preferred by moose and red deer above the remaining types of habitat. This is a completely different result from that obtained by A h l é n (1965, 1975). Our results evidence a direct competition for habitat, and possibly for food.

Another classification of game habitats in our forests follows division into plant associations. These two classifications are rather similar, but do not coincide. Interesting is the general comparison of frequentation of red deer in forest habitat versus non-forest habitat. This is illustrated by table 12. Only in the richest environment of Iława the actual frequentation of red deer in forest habitats exceeded the value expected. At Józefów and Kobiór it was much less than the expected value. On the other hand, the actual frequentation of red deer in non-forest habitats was more frequent than expected at Kobiór and Iława, and less frequent at Józefów.

At Józefów only the boggy forest and grasslands were frequented by red deer to a greater extent than it would be expected. None of the forest associations was preferred by the deer at Kobiór. It was only at Iława, where several forest associations (*Peucedano-Pinetum, Pino--Quercetum, Fago-Quercetum, Potentillo albae-Quercetum, Tilio--Carpinetum, Lycopodio annotini-Piceetum*) were preferred by the red deer. From among non-forest habitats the association from the order *Ledetalia*, grassy areas, and farmland were intensively frequented by the red deer at Iława.

Previous work (Dzięciołowski), 1969), concerning red deer frequentation of forest association in the Iława forest, indicated a strong preference towards *Peucedano-Pinetum*, medium use of *Fago-Quercetum* and *Pino-Quercetum*, and an avoidance of *Tilio-Carpinetum*.

Interesting is the strong preference for grassy areas shown by deer from all the four forest tracts.

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STRUKTURA I ORGANIZACJA PRZESTRZENNA POPULACJI JELENIOWATYCH

Streszczenie

Badania nad strukturą i organizacją przestrzenną populacji łosi, jeleni szlachetnych, jeleni sika, danieli i sarn prowadzono w czterech środowiskach (Nadl. Iława, Płaska, Józefów i Kobiór) w latach 1964—1975. Zebrano materiał ok. 8,5 tys. obserwacji (Tab. 1) w tym 6,4 tys. obserwacji jeleni, szlachetnych. Dane o użytkowaniu środowiska przez zwierzęta oparto na klasyfikacji siedlisk leśnych oraz, w przypadku trzech spośród czterech obiektów terenowych, na fitosocjologicznej klasyfikacji zespołów roślinych. W przypadku obydwóch klasyfikacji wyodrębniono kategorię powierzchni trawiastych (łąki i linie oddziałowe). Dane liczbowe dotyczące struktury płciowo-wiekowej, stadności, dobowego rytmu aktywności oraz wykorzystania różnych środowisk w cyklu rocznych, opracowano w formie programu na maszynę liczącą.

Wszystkie badane populacje wykazywały liczbowy stosunek płci o przewadze samic (od 53% u jelenia szlachetnego do 75% u daniela (tab. 2)). Populacje łosi i danieli wykazywały duży wskaźnik zrealizowanej rozrodczości (28 i 27% cieląt w populacji). Długowieczne gatunki (łoś i jeleń szlachetny) wykazywały większy udział zwierząt starych w populacji niż gatunki krótkowieczne.

Wielkość ugrupowań tworzonych przez badane zwierzęta (tab. 4) dowodzi, że łosie i sarny należą do gatunków żyjących samotnie lub w małych grupach rodzinnych (do 3 osobników). Jelenie sika i daniele tworzą grupy 2—6 osobników a najliczniejsze stada sięgają 12 osobników. Jeleń szlachetny jest zwierzęciem stadnym, często zbierającym się w chmary liczące 10 osobników a najliczniejsze ugrupowania stwierdzane w niniejszych badaniach przekraczały 21 osobników.

Struktura ugrupowań jelenia szlachetnego (tab. 5 i 7) wykazała następującą zmienność czasową: a) procent samotnych samców jest większy od wartości oczekiwanych w okresie od listopada do marca, b) procent samotnych samic jest większy od wartości oczekiwanych zimą (listopad — styczeń) i wiosną (marzec — maj), c) obserwacje grup „łania — cielę" są najczęstsze w czerwcu, następnie spadają do listopada, gdy jelenie gromadzą się w chmary zimowe, d) grupy „łania — jednoroczniak" są najczęściej obserwowane wiosną (kwiecień — czerwiec), a zatem do czasu urodzenia następnego cielęcia przez łanię, e) grupy o składzie „łanie + potomstwo" były najczęściej obserwowane w okresie od listopada do marca, f) grupy o składzie „byk + łania" nie są typowe dla jelenia szlachetnego i występują liczniej niż można oczekiwać wyłącznie podczas rui (wrzesień — październik)

g) grupy o składzie innym niż wspomniano były obserwowane liczniej niż można oczekiwać również w okresie od sierpnia do października.

Struktura ugrupowań jelenia szlachetnego wykazuje również zmienność przestrzenną (tab. 6 i 8), zwłaszcza w zakresie częstotliwości spotykania zwierząt dorosłych i ugrupowań o składzie „łanie + potomstwo". Populacje zachodnie wydają się wykazywać większy przyrost zrealizowany niż populacje wschodnie.

Badane zwierzęta wykazywały dość jednolity rytm aktywności dobowej, (Fig. 1), chociaż łosie wykazywały szczyt aktywności w godzinach wczesnorannych, jelenie szlachetne wykazywały dwa szczyty aktywności (wczesny ranek i popołudnie), jelenie sika — szczyt w godzinach popołudniowych i wieczornych, daniele i sarny — szczyt aktywności o zmierzchu.

Jeleń szlachetny wykazuje zdecydowaną preferencję wobec boru mieszanego świeżego i wobec powierzchni trawiastych, jak łąki i linie oddziałowe (tab. 9).

Porównanie uczęszczania czterech gatunków (jeleń szlachetny, sika, daniel i sarna) w zbiorowiskach leśnych w obrębie jednego nadleśnictwa wykazuje podobne preferencje wobec określonych typów siedliskowych lasu (tab. 10).

Łoś i jeleń szlachetny, porównywane w innym nadleśnictwie (tab. 11), wykazywały niemal jednakowe preferencje wobec określonych typów siedliskowych lasu, co dowodzi bezpośredniej konkurencji o środowisko.

Wszystkie porównywane zwierzęta wykazywały silną preferencję wobec powierzchni trawiastych we wszystkich czterech terenach badań.