Distribution, Population Structure, and Social Organization of Moose in the Biebrza Valley, Poland

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Between 1976 and 1985 the dispersion and distribution of moose *Alces alces* Linnaeus, 1758 were studied in a complex of swamp environments in the Biebrza Valley of northeast Poland. Changes in the social organization of groups between autumn and spring were analyzed using hunting statistics and aerial surveys. Prior to 1980, moose were expanding their range. We observed seasonal changes in the number of moose using sedge areas, willow-birch shrubland, and alder swamps. As well, moose migrated from summer range (swamps and marshes) to winter range composed 16.4% of the animals in various herds. The birth rate in population was 19.2%; twins accounted for 12.4% of births, and the mean number of calves born per breeding female was 1.13 (SE∓0.017). In spring, 80% of moose observed were either single animals or two-animals groups. In late autumn and winter 40% of moose formed groups consisting of three or more animals. Groups size of moose in autumn and winter was 2.04 (SE∓0.10) and 1.95 (SE∓0.06), respectively, and these values were not statistically different. However, the spring groups of moose were significantly smaller (1.49, SE∓0.08, $p < 0.01$).

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1. INTRODUCTION

The Biebrza Valley is a 200,000 ha post-glacial river valley located in Northeast Poland (Fig. 1). Since 1945, the population of moose *Alces alces* Linnaeus, 1758 in this area has grown from a small remnant population. Tomek (1977) estimated that no more than 4 to 6 moose survived in the inaccessible swamps of the Biebrza Valley. However, it is probable that the initial group was much more numerous (Chyliński, pers. comm.). Under complete protection from hunting in the 1960's, the number of animals increased rapidly. In this same period the similar process was observed in the territories of the adjacent Lithuanian and Byelorussian republics of the U.S.S.R. This probably led to the natural exchange

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of some animals and migration of moose from the East to the Biebrza Valley. This increase in the number of moose in Poland (about 850 in 1968; see Tomek, 1977) and in the Biebrza Valley (390 animals) resulted in damage to several pine forests, and in 1967 it was decided to resume moose hunting throughout Poland, including the Biebrza Valley. Presently, moose are dispersed throughout the entire country (Pielowski, 1984), but the Biebrza Swamps continue to be its main refuge.

The population of moose in northeast Poland has not yet been the subject of any detailed ecological studies. Certain data, especially on the dynamics of population were reported by Dzięciołowski and Pielowski (1975) and Tomek (1977). Habitat selection and food studies were conducted by Morow (1975, 1976).

The objectives of this study were (1) to document the distribution and movement of moose in the Biebrza Valley, (2) to determine changes in the population size, and (3) to document the age and sex structure and social organization of moose.

2. STUDY AREA

The Biebrza Valley is clearly divided into a northern, middle and southern (lower) basin (Fig. 1). There is a natural longitudinal shape to the river valley and a clear transverse arrangement of zones that differ in vegetation types (Okruszko, 1973). This study did not include the northern basin because it was very narrow and it connected directly to the extensive complex of the Augustów Forest.

The central basin is approximately 25 by 40 km in size with an area of 793 km²; 436 km² is classified as peatbogs. A large part of the central basin are peatbogs that are progressing towards a later successional stage of birch and willow shrubs. The Czerwone Bagno comprises a 2000 ha section of this basin and is classified as a high peatbog, with a swampy pine forest in its centre surrounded by mesotrophic types of bog forest. The Czerwone Bagno is surrounded by alder, willow, and birch shrubs (Czerwiński, 1983). Other types of bog forests in the central basin include two large complexes of birch woods called Brzeziny Ciszewskie and Brzeziny Kapickie. The open areas are primarily sedge-grass and grass communities overgrowing decomposing peatbogs. The swamp areas are mostly unused but some parts are mowed for hay production by local farmers. Patches of mineral soil within the central basin and more extensive areas on the margins of the middle basin are made up of pine forests. Forests surrounding the basin are primarily young pine plantations, 10—20 years of age growing on former fields. A more detailed description of vegetation complexes and their spatial arrangement of the middle basin can be found in Pałczyński (1975).

The southern basin is a broad valley 455 km² in area situated in a north-south direction. Two hundred thirty- six square kilometers are classified as low peatbogs, and 72 percent of the entire area is covered by swamps. The southern basin has a zonal arrangement of biotopes including reeds on river banks and old river beds, rushes composed of canary grass (*Phalaridetum arundinaceae*) and manna grass,

Glycerietum maximae extensive areas covered with sedges and mosses, willow-
-birch shrubs, birch swamps, and typical alder swamps (Oświt, 1973). The largest
alder swamp in Poland (approximately 2000 hectares) is found in this basin. Pine
forests primarily are found on mineral soil (often as dunes) around the perimeter
of the lower basin. Numerous hummocks (mineral soil above the level of the
peatbog) are present and often are overgrown with willow and birch srubs
which serve as seasonal resting and feeding areas for moose.

Fig. 1. Study area divided into hunting grounds. Hatched area — Biebrza refuge.
Broken line divides the upper (1), middle (2) and lower (3) basins.

The central and southern basins with surrounding areas (total area of 2090 km²)
are considered the main concentration area of moose in the Biebrza Valley. The
two basins contain 31 hunting areas. Population trends and age and sex structure
were determined from hunting statistics. Aerial censusing for moose was conducted
over a 50 thousand hectare area consisting of open expanses of sedge, interspersed
with shrubs and deciduous bog forests. Hunting statistics from the Biebrza Valley
were compared to 281 hunting areas that comprised a large portion of northeast
Poland; 166 from the Province of Białystok, 106 from the Province of Łomża and
9 hunting areas from the Province of Suwałki. All of these areas together, inclu-
ding the study area were considered to be part of the same population.

Climatic conditions in the Biebrza Valley are similar to those documented for the North Podlasie Lowlands (Kondracki, 1972). The mean annual temperature is about 1 to 2°C lower than in central Poland ranging between 6.4 and 7.0°C. Average temperatures for January range from –4.5°C to +4.5°C which are 1.5 to 3.0°C lower than in central Poland. The winter periods last 187—206 days. Annual precipitation in the Biebrza Valley is 550 to 600 mm and snow is present for 76 to 104 days each year (Kaczorowska, 1958; Krzywonos, 1965).

3. METHODS

Aerial observations for moose were conducted in winter, spring and autumn, 1980-86, (Table 1), when leaves of deciduous shrubs and trees did not interfere with observations. The study area was divided into sections during observation periods using defined landmarks in the area. Sections were flown at altitudes of 60 to 80 m above ground using fixed-wing aircraft and an area 300 metres wide was observed on both sides of the aircraft. The locations of all moose observed were recorded on 1:25000 scale maps. To determine and verify sex and age of moose and the composition of groups that were observed, the aircraft circled low over the animals. In spring, aerial censuses were conducted during the last two weeks of May immediately following the calving period, and the number of adults, yearlings, and females with calves were recorded. In winter, only total number of animals were recorded because of the difficulty of sexing moose and distinguishing calves from older age classes. For all observations, group size, distribution on the ground, and behavioral reactions to the aircraft were documented.

Aerial censusing was done by using either the multipurpose Wilga PZL-104 with a pilot and two observers or a Gawron PZL-101 aircraft which offered poorer observation conditions and required three observers to be effective. Both of these

Table 1

Number of moose observed by aerial surveys.
[1] Countings not including the whole area of the basin; [2] Countings including also pine plantations and young pine forests.

Year	Winter	Spring	Autumn
Middle basin			
1980	183	81	—
1981	178	169	—
1982	—	—	243
1984	—	161	—
1985	150	210	154[1]
1986	165	—	183
Lower basin			
1980	45 [2]	90	83
1981	61 [2]	125	35[1]
1982	—	—	101
1983	—	—	71
1984	—	89	84[1]
1985	25 [1]	146	77
1986	51	—	137

aircraft are high-wing monoplanes capable of minimum speeds of 100-120 km/hour. The entire study area was censused during 6 flights which required 15 hours of flight time (including ferrying to and from base). Winter and autumn aerial censusing occurred around noon, whereas in spring, flights occurred in the early morning and afternoon periods. Censusing during the winters of 1985 and 1986 was conducted with a Mi-2 helicopter. The total number of moose observed during the study is shown in Table 1.

Moose locations were recorded on 1:25000 scale phytosociological maps of the Biebrza Valley (A. Pałczyński, unpublished). These maps depicted detailed plant communities (49 in the Middle Basin and 29 in the Lower Basin), however moose locations were assigned to only a few generalized plant cover-types:

1. Sedge communities and sedge-moss communities containing complexes of *Magnocaricion* and *Caricetalia* species. These were open sedge communities with shrubs less than 10 years old and not dense enought to be considered bruswoods.

2. Bog willow-birch shrubs were complexes of *Salix cinerea* and *Betula pubescens* in various stages of succession. These were considered brushwoods when they occurred in compact patches of early successional stages. Birches were not sufficiently numerous to classify these patches as birch groves.

3. Bog alder forests and bog birch forests were forest complexes of *Carici elongate-Alnetum* and *Betuletum pubescentis verrucosae*. These two types of bog forest were combined because of their similar wet soil.

4. Meliorated meadows and pastures. This group consisted of plant communities of the genus *Molinietalia* and arable land near villages that were used for cattle grazing.

5. Bog pine forests were communities of *Vaccinio uliginosi-Pinetum* that were found exclusively in the Czerwone Bagno complex.

6. Pine forests supporting rich undergrowth, pine plantations 1-20 years of age, were communities of *Dicrano-Pinion*. This group included all pine forests situated on mineral soil including young pine plantations established on former fields, waste land and clearings. During 1980 and 1981 these forests were carefully surveyed for moose but were later ignored during aerial surveys because of poor observability due to dense forest structure.

7. Other atypical biotypes such as pits that remained following peat harvesting and boundary lines between forest and meadows.

Moose that were located in small distinct plant communities not included in the categories described above, were assigned to the predominant type in the area.

The official hunting statistics recorded for the period 1976—1984, inclusive, were used in this study. Generally, these data were gathered by hunting groups using the various individual hunting grounds in the region. Data were recorded such as number, sex, and age of moose observed by a hunting group on 31 March, number of bulls, cows and calves harvested, and the total area surveyed and proportion forested.

4. RESULTS

4.1. Territorial Expansion

The expansion of moose range was documented by recording the number of hunting grounds used by moose during the period 1976—1984. A
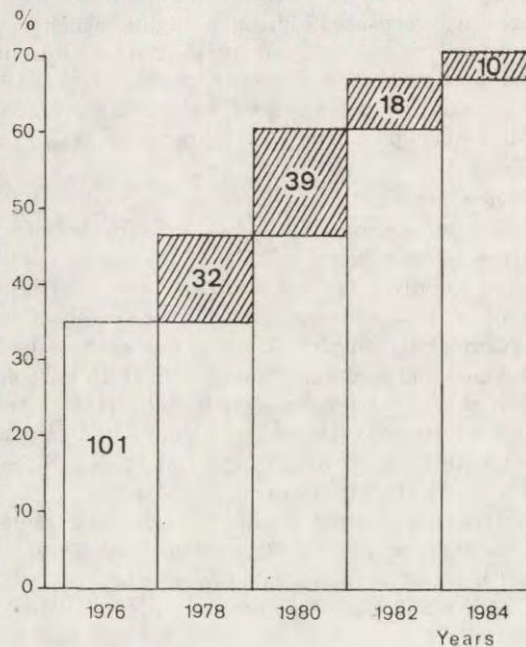
Fig. 2. Increase (in percent) of hunting grounds occupied by moose in northeast
Poland. (N=281 hunting grounds=100%. Numerals indicate the number of occupied
hunting grounds.

sharp increase in colonisation was noted in the period 1978—1980 (Fig. 2).
Of 281 hunting grounds studied in northeast Poland, only 69 percent
have been occupied by moose.

Moose first occupied areas that were considered prime habitat, mostly
swamp areas and areas with large part of swamps. During this study
most territorial expansion was directed to areas that contained significant
proportions of forests. To determine whether forested areas influenced
territory expansion by moose, we examined the relationship between
moose density and the proportion of forests in an area (Fig. 3). Swamps
were excluded from the analysis because of their known preference by
moose.

Areas with a low proportion of forest cover (0.5-30 percent) (Fig. 3)
showed a significant positive correlation with moose density ($p<.01$;
$r=0.35$, $y=0.04x+0.16$, $n=107$). No significant correlation was found in
areas with higher proportions (31-100 percent) of forest cover ($r=-0.03$,
$y=-0.001x+1.55$, $n=68$).

Areas of high moose density (>2 animals/1000 hectares) and exhibiting forest cover ranging from 10 to 60 percent are shown in Fig. 3. These areas were situated at the perimeter of the Biebrza Valley near the Augustów Forest and in the Narew Valley. All of these areas were in the vicinity of the main concentration areas for moose in the Biebrza Valley, and contained patches of pine forests or larger isolated forest complexes
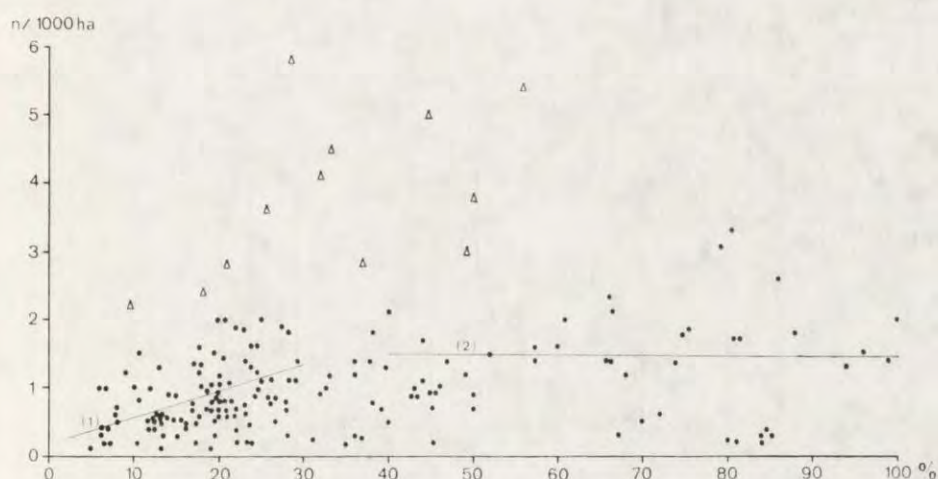

Fig. 3. Correlation of moose population density with the proportion of forest in the area of a hunting grounds. Regression lines: 1 — 0-30% of forest-covered area (n=107); $r=0.35$, $y=0.04x+0.16$ (significant at $p<0.01$); 2 — 31-100% of forest--covered (n=68); $r=-0.03$, $y=-0.001x+1.55$ (not significant); $\triangle$ — swamp hunting grounds are excluded from the calculation.

Areas containing a high proportion of forest cover (>60 percent) were usually part of the main forest complexes in northeast Poland, the Augustów Forest, the Knyszyn Forest, and the Białowieża Forest. Deer, not moose, are the predominant species of *Cervidae* in these forests.

4.2. Habitat Selection

Habitat selection by moose was determined by aerial observations of animals. Comparisons of preference for various habitat types (1-7) were based on the frequency of encounters with moose each season. Both basins of the valley were considered as separate territorial units (see Gębczyńska & Raczyński, 1984).

In spring, sedge-covered patches (1) were preferred by moose in the middle basin, where about half the animals (up to a maximum of 65 percent) were observed grazing. Many fewer sightings of moose (mean = 22 percent) were in bog willow-birch shrub types (2) and bog alder forest (3) (mean = 13 percent) (Fig. 4). Since the spring is a period of rapid growth for meadow plants and leaves of trees, it may be postulated that a similar pattern of habitat use occurs later in the vegetative season. In
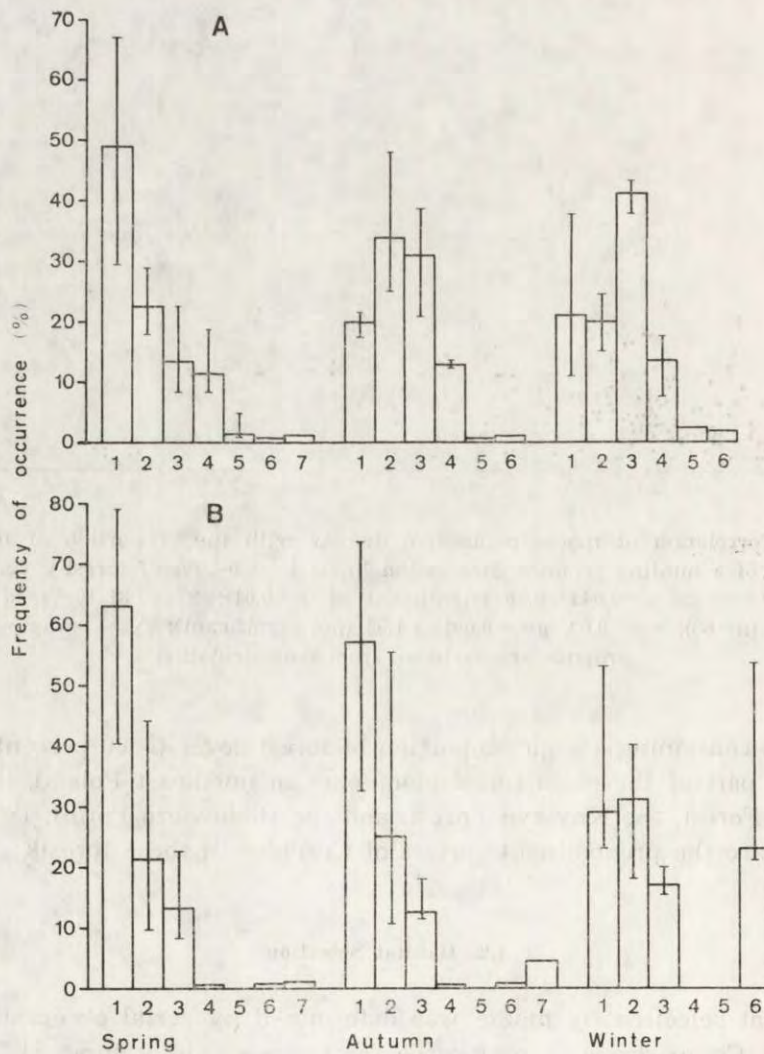

Fig. 4. Utilization of various habitats by moose in the Middle (A) and Lower (B) Basins. Numbers (1-7) indicated habitats (see Chapter 3). Vertical line shows the range (min. — max.).

autumn, moose prefer bog-alder forests (3) and shrubs (2), whereas the number of moose recorded in sedge-covered areas (1) declined. In winter, many moose were located in groups in bog-alder forests (3) while approximately 20 percent of animals remained in each of the sedge communities (1) and shrub types (2). It is worthy to note that the prime winter habitat occurred in the bog-alder forests (3) of the middle basin near the border of the Czerwone Bagno complex. Whereas, the large expanses of bog birch forests (3), *i.e.* Brzeziny Kapickie (4122 ha) and Brzeziny Ciszewskie (980 ha) were not utilized during winter.

Similar patterns of habitat use by moose were observed in the lower basin. In spring, up to 78 percent of all moose observed were in sedge communities (1). In autumn, up to 65 percent of moose were located in sedge communities (1). Bog-alder forests (3) played a lesser role as moose habitat in winter in the lower basin where less than 20 percent of moose were present.

Pine forests (6) appeared important to moose only in the winter season. During the winters of 1980 and 1981 in the lower Biebrza basin, 64 percent and 21 percent, respectively, of moose were observed in pine forests. Censusing of moose in pine forests was not continued in subse-
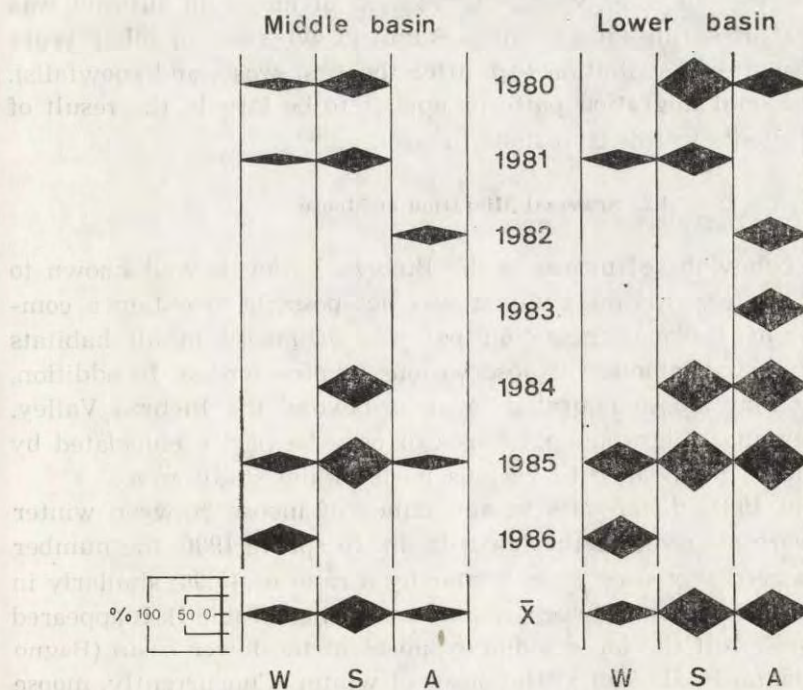

Fig. 5. Percent of moose observed in sedge communities during various seasons. W — winter, S — spring, A — autumn.

quent years, therefore these two values are probably not representative of forest habitat utilization. The importance of pine forests for moose is discussed in chapter 4.3. — Seasonal migrations.

Differences between the middle and lower basins in utilization by moose were particularly evident for sedge-covered habitat types (1) which were heavily used in spring in both basins but rarely occupied in winter in the middle basin (Fig. 5). The presence of moose in sedge patches during persistent snow cover may be explained by the presence of patches of scattered shrubs which were used as food. Sedge patches were used to a similar extent in both spring and autumn in the lower basin, whereas in the middle basin the autumn utilization by moose was similar to that found in winter (Fig. 4). To interpret these differences between the middle and lower basins, the patterns of seasonal migrations must be considered for each basin. The middle basin exhibits a relatively uniform mosaic of habitat types. This results in limited seasonal migration by moose. However, the lower basin is clearly divided into swamp and mineral sections, the latter containing pine forests. Most moose migrate to the pine forests in winter in this basin.

Differences in moose utilization between autumn and winter, varied from year-to-year. In some years, distribution of moose in autumn was similar to that of spring (and perhaps summer), whereas, in other years it resembled winter distribution (e.g. after the first frosts and snowfalls). Therefore, seasonal migration patterns appear to be largely the result of phenological events in this transitional season.

4.3. Seasonal Migration of Moose

Migratory behaviour of moose in the Biebrza Valley is well known to rangers and hunters. In this study it was not possible to obtain a complete picture of seasonal migration patterns of moose in all habitats because of the small amount of observations in pine forests. In addition, it was likely that moose migrated to areas beyond the Biebrza Valley. Therefore, seasonal migration patterns can only be partly elucidated by comparing moose abundance in various parts of the study area.

In 1980 and 1981, differences in abundance of moose between winter and spring were observed in the lower basin. In spring 1980, the number of moose observed increased from winter by a ratio of 45:90; similarly in 1981 this ratio was 61:125 between winter and spring (Table 1). It appeared that most moose left the large sedge expanses in the lower basin (Bagno Ławki and Bagno Podlaskie) at the onset of winter. Concurrently, moose density in young pine forests and pine plantations increased. Damage caused by moose in winter were recorded annually by the Forest Admi-

nistration Units. Aerial estimates of moose density in various habitats indicated considerable differences among years. For example, in the Brzeziny Ciszewskie bog birch forest (approximately 980 ha) winter moose density ranged from 1.0 animals per 1000 hectares in 1981 to 20.4 moose per 1000 hectares in 1985. In a similar complex of bog birch forest (Brzeziny Kapickie, 4122 ha) moose density in 1985 was estimated to be only 0.83 animals per 1000 hectares, yet at the same time in a nearby young pine forest (Przychody village region) moose density estimated by drives (Pucek *et al.*, 1975 Bobek *et al.*, 1984) was 190 per 1000 hectares (unpublished data). These examples indicate that seasonal migration occurs among various habitat types in the Biebrza Valley but primarily between areas abounding in summer food (sedge patches) and areas containing abundant winter food (young pine forests and pine plantations). The high year-to-year variability in moose population estimates within various habitat types suggests that the degree of migration depends on several factors. Some of these factors have been addressed in previous studies (Gębczyńska & Raczyński, 1984).

4.4. Moose Population Structure and Recruitment of Young

Patterns of age and sex structure of moose were studied using data from hunting records. Hunting clubs recorded three categories of animals: bulls, cows, and calves (up to 1 year old).

During 9 successive years (1976—1984) cow moose were predominant in the population and the proportion of bulls (per 100 cows) ranged from 73.0 to 85.5 (Table 2). With the exception of 1977 and 1982, the difference in sex ratios were significant ($p < 0.05$).

To determine the proportion of calves in the population, data from

Table 2

Sex ratio in the moose population in the Biebrza Valley. * $p < 0.05$.

Year	n ♂♂	n ♀♀	% ♂♂	χ^2	♂♂/100 ♀♀
1976	230	282	44.9	5.28 *	81.6
1977	290	338	46.2	3.67	85.8
1978	296	355	45.5	5.35 *	83.4
1979	288	364	44.2	8.86 *	79.1
1980	292	366	44.4	8.32 *	79.8
1981	276	333	45.3	5.33 *	82.9
1982	243	288	46.8	3.81	84.4
1983	224	304	42.4	12.12 *	73.7
1984	206	282	42.2	11.84 *	73.0
Total	2345	2912	44.6	61.15 *	80.5

hunting records were compared with results from aerial censusing. Data from spring calf counts were used because of the ease of identifying newborn calves which improved the reliability of results. Hunting statistics comprised data up to March 31 of each year, thus the number of calves includes the number born the preceding year minus the number that died or were shot during hunting seasons. In the years 1976—1979 approximately 20 percent of calves were shot each year (unpublished data) and in 1980—1981 this proportion increased to approximately 30 percent. Natural or other mortality of calves was not known.

Table 3

Proportion of calves in herd (N). Data from hunting records and aerial counts in spring. Column N contains all animals (with calves).
[1] Autumn data.

Year	Hunting statistics			Aerial counts		
	N	Calves		N	Calves	
		n	%		n	%
1976	667	155	23.2			
1978	831	180	21.7			
1979	803	151	18.8			
1980	824	166	20.1	171	27	15.8
1981	771	162	21.0	297	46	15.5
1982	681	150	22.0	347	55	15.8[1]
1983				71	13	18.3[1]
1984				252	44	17.5
1985				361	57	15.8
Total	4577	964	$\bar{x}=21.1$	1499	242	$\bar{x}=16.1$

Aerial censusing revealed that calves comprised 16.1 percent of moose in a herd (Table 3). This percentage was similar in successive years indicating a stable calf cohort in the population and reliable aerial censusing methodology. Estimates of proportions of calves in herds using aerial censusing techniques showed that hunting statistics overestimated calf ratios (Table 3).

Aerial surveys indicated an increase in the proportion of young moose in a herd (juvenile: adult+subadult) (Table 4). Data were insufficient to provide a proper comparison within years between spring and autumn. However, we observed more young animals in autumn records. There may be several explanations for these differences: (1) during spring, all calving may not have been completed, (2) killing of adults before autumn censusing, since hunting of bulls begins 1 month earlier than hunting for cows and calves, (3) possible misclassification of yearlings as calves when

isolated cow-calf pairs were encountered. These last two points could have resulted in an increased calf proportion in autumn.

Spring census values were accepted as the annual increase in the number of young animals in the population. These values were based on representative samples and showed low annual variability. The annual increment in number of calves was estimated at 19.2 percent for the entire population (Table 4).

Table 4

Recruitment of calves in moose population in the Biebrza Valley. Data from aerial counts. Column N contains animals aged over one year.

Year	Spring			Autumn		
	N	Calves		N	Calves	
		n	%		n	%
1980	144	27	18.8	69	14	20.3
1981	251	46	18.3	—	—	—
1982	—	—	—	292	55	18.8
1983	—	—	—	58	13	22.4
1984	208	44	21.5	90	24	26.7
1985	304	57	18.8	185	48	25.9
Total	907	174	19.2	694	154	22.2

The twinnig rate for cows with calves (291 individuals) was determined by combining observations from 1980—1985 for both spring and autumn. The proportion of twins in the population was 36:291 or 12.4 percent.

The mean number of calves accompanying cow moose was 321:291 or 1.13 calves per cow (SE ± 0.017). Fluctuations in this index among years and between spring and autumn ranged from 1.08 to 1.23.

4.5. Formation of Moose Groups

Group sizes and structures were recorded during aerial censusing. Groups were identified when there were only short distances between individual moose, and low flying aircraft effected in aggregation of animals. The analysis included: (1) the number of groups, including single animals (no. of groups=100%), (2) the distribution of all observed animals in various groups (the total number of moose was considered 100 percent), (3) the mean grup size by season, and (4) the social composition of two-animal groups, including cow with calf grups.

In spring, single animals represented approximately 60 percent of observations, while two animal groups represented 30 percent of sightings.

Larger size groups were primarily composed of three animal groups (7 percent). Grouping patterns of moose in autumn and winter were similar with single and two-animal groups representing about 60 percent of all observations. Ten percent of sightings were groups of three moose, and larger groups represented 5 percent of observations (Fig. 6).
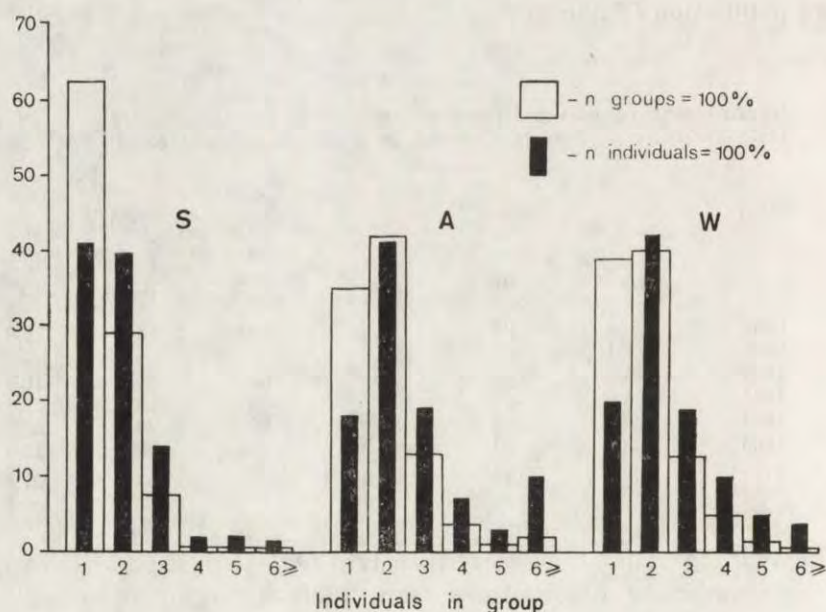

Fig. 6. Seasonal changes in group size. S — spring, A — autumn, W — winter.

In spring, about 80 percent of moose were living alone or in two-animal groups. Approximately 15 percent were found in three-animal groups. This pattern was similar in autumn and winter with most animals (40 percent) in groups of two, approximately 20 percent in three-animal groups, and about 20 percent were found alone. In autumn and winter a greater proportion of large groups (4-21 moose) were seen compared to spring.

The mean group sizes in autumn and winter were similar ($p < 0.01$, t-test). However, average sizes of groups found in spring were significantly lower ($p < 0.01$) than other seasons (Table 5).

The proportion of two-animal groups was similar in all seasons, repre-senting about 40 percent of the entire moose population (Fig. 6). During aerial censusing in spring and autumn, it was possible to determine the number of cows with calves of the year. Of two-animal groups, cows

Table 5

The mean group size of moose (± S.E.).

Year	Spring	Autumn	Winter
1980	1.5	2.2	—
1981	1.6	—	1.9
1982	—	2.1	—
1983	—	1.9	—
1984	1.4	2.4	—
1985	1.5	1.8	1.9
1986	—	—	2.1
$\bar{x}$	1.49±0.04	2.04±0.10	1.95±0.06

with calves represented 57.5 percent of spring observations and 53.2 percent of autumn sightings ($x^2 = 1.43$; 1 df, $p < 0.01$).

The following conclusions can be drawn from these results:

(1) The proportion of cows with calves was similar between spring and autumn, indicating that calves remain with their cows during this period. This bonding probably extends over the winter season, since the proportion of two-animal groups in winter was similar to autumn. It is speculated that between spring and autumn there are no changes in moose behaviour to alter the proportion of two-animal groupings, and this idea can probably apply through the winter season as well.

(2) Changes in group dynamics in winter probably accounts for significant differences in patterns of single moose and two-animal groups observed within herds. In spring, the number of single animals increases. These were probably calves born the previous year (yearlings) that were driven away by their cows prior to spring calving.

(3) The absence of any differences in group sizes between autumn and winter indicates that observations in late autumn (after leaf drop) occur after the formation of new groups for the winter.

In autumn and winter the proportion of three-animal groups increases. This may be due to a seasonal grouping of moose or to yearlings rejoining cows with calves. This social composition of groups was noted occasionally during aerial surveys in autumn and winter.

5. DISCUSSION

Since the 1940's throughout much of northern and eastern Europe there has been a sudden rise in moose populations. With this expansion of range, moose have occupied new ecological niches (Rajakoski & Koivisto, 1970; Marcström, 1978; Nymmsalu, 1973; Filonov & Zykov, 1974).

Studies conducted between 1976 and 1984 in northeast Poland have documented range expansion by moose (Fig. 2). The expansion of moose populations in the study area coincided with the extension of moose range throughout the region (unpublished data). Towards the end of this study (1981—1982), the rate of range expansion by moose declined pro bably because most suitable habitats had been occupied. Since 1982, range expansion has also been limited by hunting (Gębczyńska & Raczyński, in press). However, the critical factor that appears to be limiting further expansion of moose populations is suitable habitat and food abundance. The increase of food availability for moose resulting from forest harve-sting and silviculture was stressed by Marcström (1978).

The type of terrain and vegetative cover plays an important role in the ability of an area to support moose. In hunting grounds moose density increases only where there is a medium proportion (up to 30 percent) of forest cover (Fig. 3). This is particularly evident on former fields where trees were planted during the last 15 to 20 years. In large forest complexes, despite regular harvesting of trees and large clearcuts, moose populations are not increasing probably because of competition with other ungulates (particularly red deer).

The observed tendency of declining moose populations associated with large forested areas was not observed in areas adjacent to marshes; here, moose populations were positively correlated with increasing forest cover up to a level of 60 percent coverage (Fig. 3). This is probably because moose exhibited a pattern of seasonal migration between the two adjacent habitats. The summer refuges (marshes) and winter habi-tats (pine forests) exhibited the highest population densities of moose in this study, up to 10 animals per 1000 hectares (Gębczyńska & Raczyń-ski, in press). The work published by Glushkov (1982) in Estonia agree with results found in this study where moose populations is related to the degree of forestation. The highest moose densities (>5 moose per 1000 ha) were found in areas of approximately 30 percent forest cover, whereas the lowest density estimates (1-2 animals per 1000 ha) were in areas of extensive forest cover (90 percent).

The habitat types preferred by moose in various seasons of the year correspond to habitat selection observed by other moose populations in Europe and North America. There types of habitat are preferred: (i) marshy areas with peat vegetation, sedge communities and boggy forests, (ii) areas with wet soil covered with willow shrubs, and (iii) mixed or coniferous forests. In the Biebrza Valley, the first two habitats are associated with peatbog (hygrophilous soil) vegetation and the third type is found on patches of mineral soil that support pine forests.

Habitat use by moose is characterized by seasonal shifts in use of

areas, especially between winter and other seasons. In the Biebrza Valley, winter habitat selection by moose of willow shrubs and pine forests was confirmed by ground observations of tracks and scats left by moose (Fedyk *et al.*, 1984).

Willow shrubs, which are preferred by moose, are found in several geobotanical zones. Areas of willow shrubs and meadows partly shrub covered were used to a similar degree throughout the entire year in the Berezina reserve (Kozlo, 1983). In northwest Minnesota (U.S.A.), 84 percent of moose were found in willow shrubs and similar biotypes (Berg & Phillips, 1974). In the Biebrza Valley, shrubs were utilized by moose throughout the entire year (Fig. 4). Pertinent here, is that the only areas used by moose year-round in the peatbogs of the lower basin were compact sites of shrubs that covered approximately 600 hectares. In winter, moose migrated from the sedge-covered areas of this region to adjacent pine forests. In the middle basin, where shrubs cover a greater area, winter migration of moose is less pronounced. The local pattern of habitat types appears to influence the extent of seasonal migration (Gębczyńska & Raczyński, 1984). This confirms the general observation that bogs having adjacent forest-covered uplands with mineral soil are optimal habitats for moose (Berg & Phillips, 1974). Therefore, seasonal migration is an adaptive strategy employed by moose to ensure that they are in areas of abundant food supply (Coady, 1982). In North America, early successional stages of forest attract moose (Peterson, 1977).

According to many authors, habitat selection and seasonal movements by moose are associated with the amount of food availability and its accessibility, at least as it relates to shifts from summer to winter ranges. This is illustrated by the use of sedge areas by moose in this study (Fig. 5). The degree of migration by moose in both basins of the Biebrza Valley depends on winter severity (Gębczyńska & Raczyński, 1984). Cederlund *et al.* (1980) identified snow depth of 105 cm as critical for moose, while Thompson and Vukelich (1981) considered 65 cm as critical for cow moose with calves. During winter 1979 when snow cover was approximately 100 cm deep, moose were not evident in marshy areas of the lower Biebrza basin (Fedyk *et al.*, 1984), while in 1986 when snow cover was shallow yet frost conditions severe, 51 moose were censused in the basin (Table 1).

Several habitat types found in the Biebrza Valley appeared to be avoided by moose. This was especially noticeable in the old bog forests of the Czerwone Bagno Reserve where no moose have been recorded. Two bog birch complexes, *Betuletum pubescentis-verrucosae*, are not frequented by moose. These are forests situated on wet soil and containing old birch forests. Moose are usually only found along the perimeter of

these complexes during spring. The feeding conditions of these forests are less rich to moose than the typical bog-alder forests *(Carici elongate--Alnetum)* (Raczyński *et al.*, 1983, 1986).

Sex ratios of moose determined in this study showed a consistent predominance of cows in the population (mean=45:55 or 80.5 bulls per 100 cows). This may be the result of higher mortality of bulls because of selection by hunters (unpublished data). Studies of sex ratios of moose in other areas indicate a prevalence of bulls, cows, or equal numbers of both sexes. The prevalence of females is usually a result of excessive killing of males in a population. An extreme example of a preponderance of females in a population occurred in the Matanuska Valley, Alaska, where the ratio of bulls to cows was 4-20:100, and this ratio persisted during a 20 year period (Bishop & Rausch, (1974). Peterson (1955) compared sex ratios of moose from Ontario nad Newfoundland which showed nearly 1:1 ratios, and from Alaska where cows were predominant. Peterson (1955) also mentioned observations from British Columbia where bulls represented 25 percent of adult moose. Kozlo (1983) stated that in the Byelorussia sex ratios of moose embryos and adults depended largely on changes of population size. Thus, for example, during the period 1961—1980 bulls accounted for 34.6 to 68.2 percent of the entire population. During the population increase, the proportion of bulls was 61.7 percent, whereas in the decline phase cow moose represented 59.6 percent of the herd. He concluded that a high proportion of adult cows in a population results in disorganization of herd structure. This view contradicts data from Bishop and Rausch (1974) and Hutter as quoted in Peterson (1955), showing that a small proportion of adult bulls in a population had little effect on reproductive results. This observation is surprising in light of the limited published knowledge of polygamy in moose. Jazan (1972 quoted by Bromlej & Kučerenko, 1983), stated that one bull can service 2 to 3 cow moose during the rut. Markgren (1969) considered moose not to be completely polygamous.

When interpreting population growth, the proportion of calves and yearlings in a herd are usually considered, especially in populations exhibiting high over-winter calf mortality *(e.g.*, 56 percent in Alaska; Bishop & Rausch, 1974; Peterson, 1977; Le Resche, 1968). In this study, the yearling cohort was not determined, but the number of newborn calves in a given year was recorded in both spring and autumn. The moose population rate of growth was calculated as 19 percent in the Biebrza Valley. Moose population growth rates in two regions of Alaska ranged from 14.4-23.4 percent to 18.5-32.6 percent (Bishop & Rausch, 1974). The mean number of calves per adult cow was estimated as 1:1.3 in this study. In Byelorussia, the index of the number of embryos in

pregnant cow moose ranged from 1.22 to 1.58 during various phases of population growth (Kozlo, 1983). In eastern U.S.S.R. the number of calves per lactating cow was 1.46 (Bromlej & Kučerenko, 1973) and on Isle Royale, Michigan, it was as high as 1.9 (Mech, 1966). Data from the Biebrza Valley moose population indicate a relatively low fertility rate and suggest that European moose have a lower reproductive rate than North American moose.

Growth rate estimates in this study (derived from the proportion of calves) should be considered with caution because of unknown calf mortality rates .In many areas, predators (mainly wolves) are important mortality factors on calf moose (e.g., on Isle Royale; Peterson, 1977). However, in the Biebrza Valley, wolf population is considered low (1-2 families; Trokowicz, 1980) and predation on moose calves may be negligible.

Kozlo (1983) recorded higher twinning rates of adult cows (60 percent) during periods of population growth, whereas, during declines or periods of population stability, the rate of twinning was approximately 30 percent. During a moose population increase phase on Isle Royale, 34 percent of cows had twins, while during a decline in moose population, only 14 percent of cows had twins. However, the lowest proportion of twinning (6 percent) occurred during a peak population period (Peterson, 1977). Similar trends were noted by Coady (1974) in Elk Island. In the Biebrza Valley, the twinning rate calculated during a period of high population growth was 12.4 percent. Perhaps the high moose density was responsible for the relatively low reproductive parameter.

Social structures of moose populations can be interpreted from the various groupings of animals throughout the year. Grouping behaviour has been interpreted in two ways by various authors: (1) group composition is influenced by the physiological state of the individuals, the type of interspecfic behavioral relationships in a group, and by seasonal changes in habitats (Stringham, 1974; Rounds, 1978; Mytton & Keith, 1981). (2) groups are relatively stable structural units in a natural population, and are influenced only by seasonal variability and changes in population size (Kozlo, 1983).

Aerial surveys in the Biebrza Valley showed that only cow-calf groups were incorporated in groupings of 2-3 moose. Occasionally, groupings of cow-calf-yearlings were identified, while during autumn surveys it was possible to differentiate bulls with antlers. Despite the limited data on sex and age classifications, it was possible to draw indirect conclusions concerning group composition and changes in group dynamics over reasons. We consider that grouping by moose is the result of at least two population processes: interspecific social interactions and spatial distri-

bution of moose. The latter factor is closely related to seasonal changes in habitat use by moose, which is largely influenced by food supply and its availability. In this context, moose groups are not a stable structural element of the population and their composition is independent of social structure. The exceptions are cow-calf and cow-calf-yearling groups which are largely determined by behavioral and physiological factors. The bonding of a calf moose to its mother occurs for a prolonged period and is not interrupted at the time of weaning (Stringham, 1974). Observations by Altmann (1960, 1963) show that some yearlings remain with their cows until the autumn rut, when they are driven away by adults of the same sex, which consider them rivals (Stringham, 1974). Our observations show that the proportion of single moose is greatest in spring (see empty columns in Fig. 6). During spring aerial survey, cows had recently calved, and the increase in lone moose may have been the result of cows driving away their previous years calf just prior to calving (Stringham, 1974; Rounds, 1978). Another factor to consider is the feeding strategies employed by moose in spring, since it coincides with migration to spring habitats. The tendency of large herds or groups in winter may be the result of a restricted available food base on their winter range.

From observations during this study, large winter herds occurred in areas of abundant preferred food (willow shrubs). If available food is significant in winter grouping behaviour by moose, then these groups probably exhibit low stability. This has been confirmed by observations of Kozlo (1983) and Sweanor *et al.* (1986).

Summarizing our observations of moose group dynamics in the Biebrza Valley, we recorded high variability in groupings of animals. Observed aggregations are related, at least in part, to social structure (mother-offspring), and at times the feeding strategy of moose in various habitats and at different times of year. The importance of changes in social composition of groups and its influence on the rate of moose population change requires further research of discrete populations of moose.

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Zofia GĘBCZYŃSKA i Jan RACZYŃSKI

DYNAMIKA ROZMIESZCZENIA, STRUKTURA I ORGANIZACJA POPULACJI ŁOSIA W KOTLINIE BIEBRZAŃSKIEJ

Streszczenie

W badaniach nad dynamiką populacji łosi w Kotlinie Biebrzańskiej (Ryc. 1) wykorzystano urzędową statystykę łowiecką z lat 1976—1985. Własne obserwacje łosi z

ıpowietrza (1980—1986) z terenu środkowego i dolnego basenu doliny Biebrzy (Tabela
ı1), posłużyły do prześledzenia rozmieszczenia zwierząt w środowiskach oraz wiel-
ıkości i składu ugrupowań. Stwierdzono wyraźną ekspansję terytorialną łosi do
ı1980 r. (Ryc. 2). Zbadano zależność między stopniem lesistości obwodu a zagęszcze-
ıniem populacji łosi (Ryc. 3). Dodatnią korelację stwierdzono przy lesistości wzra-
ıstającej do 30%. Przy wyższym stopniu zalesienia obwodów, istotnej zależności już
ınie ma.

Stwierdzono sezonowe różnice w preferencji najważniejszych środowisk między
ıbasenem środkowym i dolnym (Ryc. 4). Turzycowiska są miejscem przebywania
ıłosi głównie w sezonie wegetacyjnym, natomiast w zimie frekwencja spotkań w
ıtym środowisku maleje (Ryc. 5).

Wykazano sezonowe zmiany ostoi zwierząt, z preferencją środowisk bagiennych
ıod wiosny poprzez sezon wegetacyjny, a suchych, mineralnych części doliny po-
ırośniętych młodnikami sosnowymi w zimie.

Struktura płci w populacji w ciągu 9 kolejnych lat, wykazuje dominację klęp,
ızaś udział byków w proporcji do 100 klęp ıwaha się w zakresie od 73,0 do 85,5
(Tabela 2). Udział łoszaków w stadzie, wyliczony na podstawie obserwacji lotni-
ıczych, wynosi średnio 16,4%, natomiast szacowany przez myśliwych — 21,1% (Ta-
ıbela 3). Przyrost młodych w populacji biebrzańskiej, obliczony z kilkuletnich
ıwiosennych i jesiennych taksacji, kształtuje się na poziomie 19,2% (wiosna) i 22,2%
(jesień) (Tabela 4).

Wskaźnik klęp prowadzących bliźnięta, z lat 1980—1985, wynosi 12,4% (36:291).
Średnia liczba młodych, przypadających na jedną klępę prowadzącą, wynosi 1,13
(SE±0.017).

Skład liczebny grup łosi określano podczas obserwacji zwierząt z samolotu. Na
wiosnę dominują w populacji osobniki pojedyncze i dwuosobnicze grupy, stano-
wiące odpowiednio ok. 60% i 30%. Skupiają one łącznie około 80% zwierząt. Po-
dobnie sytuacją wygląda w jesieni i w zimie, kiedy to analogiczne grupy stanowią
razem ok. 80% grup i skupiają 60% zwierząt (Ryc. 6). Średnie wielkości grup w
jesieni i w zimie wynoszą odpowiednio 2,04 (SE±0,10) i 1,95 (SE±0.06) i nie
różnią się od siebie statystycznie. Na wiosnę średnia grupa liczy 1,49 (SE±0,08)
i jest istotnie mniejsza (Tabela 5). Udział klęp z cielętami w grupach 2-osobni-
czych w jesieni i w zimie, wskazuje na trwałość związku matka-cielę.