COMPETITION BETWEEN MOOSE AND RED DEER IN THE AUGUSTOW FOREST

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Abstract: A study of food habits, range use, and relationships of moose (Alces alces) and red deer (Cervus elaphus) was carried out in the Augustow Forest (north-eastern part of Poland). Winter diet of moose consists of 16 plant species, and the most important one is pine (Pinus silvestris) - 92.6 percent, Pine, trembling aspen (Populus tremula), and dog-wood (Evonymus europaea) altogether amount to 63 percent of red deer winter diet, while dwarf shrubs - to 32 percent. Pine provides winter food preferred by moose on sites of fresh coniferous, bog coniferous, fresh mixed coniferous, and moist mixed coniferous forests. Shoots of pine are preferred over other browse plants on sites of fresh coniferous and moist coniferous forests by stags of red deer only. Day consumption of food was calculated as a result of tracking after moose (57 individuals) and red deer (38). The extent of the utilization of forest site types by both animal species shows a high seasonal variation. Competition between moose and red deer for pine, the main component of their winter diet, was observed only on areas with a deep snow which impeded red deer from using dwarf shrubs, their most preferred food. The importance of interspecific relations in spatial distribution of both populations was determined by the index of association (Dice, 1945). Moose and red deer avoid each other in most coniferous, fresh mixed coniferous forests, ash alderwood, and alderwood. They show mutual tolerance in fresh coniferous and moist mixed coniferous forest. In the case of an intensive penetration of sites attractive for red deer respecting food (niche overlapping with moose) there occurs a shift of feeding activity by moose or temporal succession or spatial penetration of those sites. Here one deals with competition model in which mechanisms of interaction between these two species occur at an individual level.

Interspecific competition denotes every interaction between two or among more than two populations, which adversely affects their growth and survival. Competition leads to ecological separation of closely related or similar in other respects species (Hardin 1960).

Mutual competitive interaction between two species may refer, e.g., to space and food. As it is known, no matter which type of interaction it represents, interspecific competition causes adequate adaptation of one species to the other or it brings about the substitution of one population by other or else, finally, it forces the population to occupy another place in space or to use other forage plants (Odum 1971).

If related organisms which are similar in behaviour or life form appear to occur together, then, in principle, they use different forage, their activities do not coincide or in a different way they occupy rather different niches. Intense competition also occurs when the niches partly overlap.

Investigations on moose and red deer food uses indicate certain differences in the composition of their diet; yet they were carried out in different phytogeographic and climatic regions (Peterson 1955, Swift 1946, Ahlen 1975, Kearney and Gilbert 1976). Conclusions of those investigations cannot be reliable with respect to differences in food habits and in direct food competition between species.

In Canada (Peterson 1955) gen. Odocoileus being predominant in some areas and having a higher biotic potential impeded the growth of moose populations.

Ahlen (1975), in his comparative study on moose and red deer ecology has put forward two questions: Is the competition for food with moose an important factor likely to bring about a decrease in red deer populations in an area densely inhabited by moose? Do the two species differ in their feeding behaviour in severe winter conditions? A partial dietary overlap occurs in some plant species, but none of those species is important for red deer or for moose. Moose utilize the shrub stratum (98 percent of their diet), and other food available during the whole winter. Red deer, while benefiting from adaptations for using food from under the snow, feed on dwarf shrubs and the herb stratum (91 percent of their diet).

Dorn (1976), from studies of range use, food habits, and competition between moose and cattle in north-west Montana, concluded that competition for food has no importance in his study conditions. *Salix wolfii*, which comprised above 50 percent of the cattle diet, was rarely browsed by moose. The abundance of three willow species counterbalanced the reduction by cattle of plant species important in the moose diet.

In Nova Scotia, Telfer (1967) found out that in spite of moose and deer population concentrations on southwest slopes, deer occur on higher elevations.

The above-mentioned studies, their results as well as a number of other studies concerning interactions between moose and other big ruminants, do not indicate the existence of competition (e.g., Prescott 1974, Stevens 1974).

Investigations presented in this study were conducted in the Augustow Forest during 1971-1978. The purpose of the present work was to examine interactions between moose and red deer inhabiting the area under investigation.

Both populations spread over this area at the turn of 1950-1960. They demonstrated a dynamic growth and attained food carrying capacity in the second-half of the decade of the 1970's (unpubl. data).

Availability of winter forage is a factor limiting the number of herbivorous animals and influencing food capacity. It was assumed that competition for food or for preferred habitats may take place during winter. Therefore, it was considered to be particularly important to elaborate data regarding food habits and range use during winter.

STUDY AREA

Studies were carried out in the Augustow Forest (53°40'-54°10', 22°40'-23°32') on the area of above 7,700 ha. Podzol (46 percent of the area), brown forest (25 percent), and red soils (20 percent) developed from the older facies of glacial and fluvioglacial sediments.

Climatic conditions are characterized by low mean temperature (6.1°C), short vegetative season (192 days), and a long period of snow cover prevalence (135 days).

The forest site types, which were formed as a result of the natural conditions mentioned, are illustrated by Table 1. A characteristically high percentage of moist habitats was observed on the study area. Alderwood, ash alderwood, bog coniferous, and moist coniferous forests altogether occupy 37.7 percent of the study area.

Table 1. Comparison of forest area according to forest site types

Forest Site Type	Size (%)	% of Total
Fresh coniferous forest	2,526.17	32.8
Moist coniferous forest	313.23	4.1
Bog coniferous forest	380.17	4.9
Fresh mixed coniferous forest	757.00	9.8
Moist mixed coniferous forest	924.49	12.0
Mixed deciduous forest	435.31	5.6
Fresh deciduous forest	52.19	0.7
Moist deciduous forest	109.67	1.4
Ash alderwood	916.74	12.2
Alderwood	1,269.87	16.5
Total	7,704.84	100.0

Forest stands consist of: pine - 51.5 percent, alder (*Alnus glutinosa*) - 19.4, birch (*Betual pubescens*) - 18.4, spruce (*Picea excelsa*) - 8.7, and ash (*Fraxinus excelsior*),oak (*Quercus robur*), trembling aspen - 2 percent. It should be stressed that the above-mentioned species are

prevailing but not the only ones. Thus, for instance, spruce occurs together with predominant pine and with the admixture of birch, trembling aspen and oak, while in alder stands there occurs birch with the admixture of ash and spruce.

METHODS

Composition of diet, its variation and food selection, were studied with the aid of analysis of rumen content samples and tracking in snow after animals (Morow 1976).

Studies on the extent of utilization of forest site types by moose and red deer in annual cycle were carried out with the aid of direct observations and tracking in snow (Morow 1975).

RESULTS

Moose and Red Deer Food Habits during Winter

Moose Diet

Composition of diet was determined on the basis of tracking of 128 moose and analysis of five rumen samples (Table 2). In the course of tracking 86,588 bites were recorded. For the sake of the comparison of results bites were converted into grams of dry matter (Morow 1976).

Table 2. Composition of moose diet during winter as determined on the basis of tracking (128 individuals) and of 5 rumen content samples.

Samples	% Weight of Diet
Trees and shrubs	
Pinus silvestris	92.6
Betula pubescens	3.0

Table 2 (Cont'd)

Samples	% Weight of Diet
Salix cinerea	1.6
Populus tremula	1.3
Frangula alnus	0.8
Sorbus aucuparia	
Tilia cordata	
Evonymus europaea	0.1
Padus avium	
Rubus idaeus	
Carpinus betulus	
Subtotal	99.4
Swarf shrubs	
Vaccinium myrtillus	
Vaccinium vitis-idaea	0.6
Calluna vulgaris	
Total	100.0

Shoots of trees and shrubs constituted the most important group of plants in the moose diet. The most important tree species: pine, birch, and trembling aspen comprised 97 percent. Gray willow (*Salix cinerea*) and alder buckthorn (*Frangula alnus*) take the first place among shurbs. Dwarf shrubs provided only 0.6 percent of diet.

Moose diet during winter consisted of 16 species, among which pine provided 92.6 percent in respect to weight.

Food preferences of moose

Data on food preferences in relation to palability and availability were obtained in the course of 128 trackings after moose in feeding places. This way of determining preferences is more reliable than those used in other methods (Morow 1976).

Research results indicate that one cannot agree with assumptions of certain researchers who suggested that the consumption of conifers (pine under our conditions) by moose during winter is of compulsory nature.

Pine provided a preferred winter food for moose on sites of fresh coniferous, moist coniferous, fresh mixed coniferous, and moist mixed coniferous forests. Numerous observations of moose feeding grounds in these forest site types indicated that pine is a prime browse species in relation to gray willow and alder buckthorn. In numerous cases the daily diet of moose consisted of shoots and bark of pine only. Pine bark was stripped most willingly in the fresh coniferous forest.

Gray willow, alder buckthorn, and trembling aspen provide a secondary winter food (Morow 1976).

Daily consumption of food during winter

Table 3. Daily consumption of food during winter in g of dry matter.

Species	Bull(15)	Cow(18)	Calf(24)
Pinus silvestris	2,760.8	2,714.3	2,335.0
Betula pubescens		796.8	658.1
Populus tremula	144.7	212.9	198.7
Salix cinerea	95.0	85.1	78.5
Frangula alnus	78.4	104.8	63.6
Vaccinium myrtillus	39.8	36.6	59.3
Total	3,118.5	3,950.5	3,393.2

Table 3 illustrates the daily consumption of food. Pine constitutes 85 percent of the diet of bulls, 67.7 - in cows, and 68.8 percent - in calves. After conversion these percentages amount to 6 kg, 5.9, and 5.1 kg of fresh shoots per day and night, respectively.

Red deer diet

Composition of diet was determined on the basis of tracking 101 red deer and analyses of 22 rumen samples (Table 4).

Table 4. Composition of red deer winter diet as determined on the basis of tracking (101 individuals) and of 22 rumen content samples

Species	% Weight of Diet
Trees and shrubs	
Pinus silvestris	45.2
Evonymus europaea	8.8
Populus tremula	8.6
Betula pubescens	0.5
Salix cinerea	0.5
Frangula alnus	0.1
Fraxinus excelsior	0.1
Tilia cordata	0.1
Subtotal	64.1
Dwarf shrubs	
Calluna vulgaris	18.6
Vaccinium vitis-idaea	7.4
Vaccinium myrtillus	6.2
Subtotal	32.2
Grasses, rushes	
Scirpus silvaticus	2.6
Sieglingia decumbens	0.3
Nardus stricta	0.3
Indetermined grasses	0.2
Subtotal	3.4

Table 4. (Cont'd)

Species	% Weight of Diet
Pteridophytes	
Pteridium aquilinum	0.1
Polystichum sp.	trace
Subtotal	0.1
Moses, lichens	
Cladonia sp.	0.1
Entodon Schr.	trace
Dicranum sp.	0.1
Sphagnum sp.	trace
Subtotal	0.2
Total	100.0

In the course of tracking 52,138 bites were recorded. One bite of pine weighed 3.000±0.056 g, trembling aspen - 0.970 ± 0.029g, dog-wood - 0.280± 0.014g, common juniper (*Juniperus communis*) - 0.145 ± 0.015g, limetree (*Tilia cordata*) - 0.110 ± 0.015g, while 10 twigs of cowberry (*Vaccinium vitis-idea*) - 0.900±0.020g, 10 twigs of heather (*Calluna vulgaris*) - 0.682 ± 0.027g, and 10 twigs whortleberry (*Vaccinium myrtillus*) weighed 0.362 ± 0.042g.

Shoots of trees and shrubs evidently prevailed in the diet and comprised 64.1 percent of it. The most important tree species: pine and trembling aspen contributed 54 percent to the diet. Dog-wood (9 percent) was a dominant species in shrubs. Dwarf shrubs provided 32.2 percent of diet; of greatest importance among them was heather (18 percent). Grasses participated in winter diet more than 3 percent.

In general, the winter diet of red deer consisted of 18 identified plant species.

Food preferences of red deer

As distinct from moose, pine is not a prime browse species for red deer. Shoots of pine were preferred over other browse plants on sites of fresh coniferous and moist coniferous forest by stags only. It is interesting to note that hinds with calves preferred bark of pine over shoots from 5-8 year old thickets on sites of fresh coniferous and fresh mixed coniferous forests. Trembling aspen, which is very easily available for red deer after thinning in alderwood and ash alderwood was an intensively browsed and preferred kind of forage. On sites of moist mixed coniferous forest alder buckthorn and dog-wood provided a prime browse in relation to other browse plants. When the depth of snow cover permited the grazing of heather, cowberry, whortleberry twigs, they were more willingly grazed on sites of fresh coniferous, and fresh mixed coniferous forests than pine. Limetree, and ash were seasonally preferred food by red deer during winter.

Daily consumption of food during winter

Table 5. Daily consumption of food during winter in g of dry matter.

Species	Stag(18)	Hind (13)	Calf(14)
Pinus silvestris	1,843.6	1,101.3	1,270.7
Populus tremula	532.2	620.3	480.8
Tilia cordata	120.0	90.0	76.2
Frangula alnus	119.5	152.1	30.7
Fraxinus excelsior	100.7	140.8	95.7
Salix cinerea	50.8	82.3	35.6
Evonymus europaea		480.5	98.7
Calluna vulgaris	381.7	270.7	330.1
Vaccinium vitis-idaea	215.2	220.3	112.7
Vaccinium myrtillus	180.7	110.2	90.2
Scirpus silvaticus		30.2	17.8
Total	3,543.9	3,298.7	2,639.2

Table 5 illustrates the daily consumption of food by red deer. Stags take most forage (3.5 kg dry matter) during day and night; hinds consume 3.3kg and calves 2.6kg. Pine constitutes 52 percent of diet of stags, 33 percent - in hinds, and 48 percent - in calves. Trembling aspen provided a high percentage of daily consumption. This kind of forage (shoots and bark) is obtained from trees after thinning.

Repartition of Forest Site Types

Moose

Repartition of the area into individual types of forest sites is given in table 6. Results were based on the observation of 560 moose, and of 128 trackings.

During 1971-1974 (low population numbers and density of moose and red deer per 100 ha of forest area), in spring moose utilized seven forest site types. The fresh mixed coniferous, alderwood, and fresh coniferous forest were the most preferred. During summer moose utilized seven forest site types among which mixed deciduous, and fresh coniferous forests were highly preferred. Nine forest site types were utilized during fall by moose - fresh coniferous, fresh mixed coniferous, and moist mixed coniferous forests were preferred the most. During winter moose utilized seven forest site types, and fresh coniferous and mixed deciduous forests indicated a higher degree of utilization.

During 1975-1978 (both populations attained food carrying capacity), in spring moose utilized eight forest site types - fresh coniferous forest and alderwood were the most preferred. A high preference for ash alderwood

and mixed deciduous forest was also noted. During summer moose utilized only six forest site types, alderwood was the most preferred. The mixed deciduous and fresh mixed coniferous forests were preferred too. It is interesting to note that moose were not seen using ash alderwood during this season. In fall eight forest site types were utilized. The alderwood and fresh coniferous forest were preferred to some degree. The use of fresh mixed coniferous forests in the fall showed little change from the pattern established during the summer. The moist mixed coniferous forest was much more preferred than during summer. In winter eight forest site types were utilized. The fresh coniferous and fresh mixed coniferous forests were the most preferred during this season. The alderwood use shifted abruptly which contrasted with the other seasons.

Towards the material contained in Table 6 there was formulated a question: whether the distribution of moose frequentation is concordant with the areal share of individual forest site types within the range of moose populations. The X^2 test was used, and it was found that differences between the areal proportion of forest site types in the range of moose populations and moose frequentation in these forest site types were significant (P 0.05).

In order to characterize better the extent of the utilization of individual forest site types, moose activity was divided into three kinds: moving, feeding, and bedding (Morow 1975). The X^2 test was used,

Table 6. Repartition of forest site types by moose in an annual cycle /in percent/.

Forest site type	Spring		Summer		Fall		Winter	
	1971-74	1975-78	1971-74	1975-78	1971-74	1975-78	1971-74	1975-78
Fresh coniferous forest	19.2	29.4	21.9	21.3	25.1	29.3	28.4	33.o
Moist coniferous forest	11.5	4.o		6.4	4.1	4.1	9.4	5.8
Bog coniferous forest	5.7	1.3	7.3		4.1		9.3	1.o
Fresh mixed coniferous forest	25.1	5.3	12.2	14.9	19.8	13.8	12.3	33.o
Moist mixed coniferous forest	13.5	5.3	9.8	8.5	16.5	11.4	1o.8	5.8
Mixed deciduous forest	3.8	13.3	24.4	17.o	9.4	6.5	2o.7	3.9
Fresh deciduous forest								
Moist deciduous forest			9.8		2.3	1.6		
Ash alderwood		17.3			6.9	2.4	14.1	7.8
Alderwood	21.2	24.1	14.6	31.9	11.8	3o.9		9.7

Table 7. Repartition of forest site types by red deer in annual cycle /in percent/.

Forest site type	Spring		Summer		Fall		Winter	
	1971-74	1975-78	1971-74	1975-78	1971-74	1975-78	1971-74	1975-78
Fresh coniferous forest	52.7	34.o	51.5	23.4	18.8	32.o	45.4	41.4
Moist coniferous forest		8.o		6.6	2.6	1o.5		7.2
Bog coniferous forest		4.o				o.6		
Fresh mixed coniferous forest	33.3	18.o	3o.3	6.6	18.2	22.2	12.9	4.8
Moist mixed coniferous forest		6.o		23.4	8.2	12.5	3.6	21.2
Mixed deciduous forest	14.o	16.o		3o.o	2o.1	9.2	8.1	8.6
Fresh deciduous forest								
Moist deciduous forest					3.8		2.4	
Ash alderwood		4.o	6.1		2o.1	5.8	13.7	9.6
Alderwood		1o.o	12.1	1o.o	8.2	7.2	12.9	7.2

and it was found that there was a significant differentiation (quite obvious when feeding is concerned) in the intensity of use of individual forest site types during comparison seasons.

The developmental stages of forest site are of prime importance in the selection of habitat by moose (Morow 1975). Forest site types utilized by moose were split into young plantations, thickets, and timber stands. Such a division gives better characteristics of the extent of the use of forest by moose (and red deer, too).

Moose use young plantations, thickets, and timber stands for moving in an equal degree (12-15 percent) throughout a year. During spring and fall moose mostly feed in young plantations (about 60 percent), twice as much as during winter. During this season young plantations are rich in food preferred by moose. During winter the increasing depth of snow cover in young plantations renders food in numerous cases inacessible for moose. The use of thickets as a potential food resource during winter doubles that from the fall. Thickets are used by moose during winter to a great extent as bedding places and shelter against adverse weather conditions (Morow 1975).

Red Deer

The distribution of red deer in types of forest sites is presented in Table 7. The results were based on the observations of 917 red deer, and of 101 trackings.

During 1971-1974, in spring red deer used only three, and during summer four forest site types. The most preferred was fresh coniferous forest. In fall they utilized eight forest site types, among which fresh coniferous, fresh mixed coniferous forests, mixed deciduous

forest, and ash alderwood were preferred to the same degree. The fresh coniferous forest was the most preferred during winter.

During 1975-1978, in spring red deer used eight forest site types. The most preferred was fresh coniferous forest, then fresh mixed coniferous, mixed deciduous forest, and alderwood. During summer red deer utilized only six forest site types, among which mixed deciduous forest was highly preferred. In fall, the use of fresh coniferous forest increased but without attaining the level of spring penetration. The fresh mixed coniferous forest had the maximum utilization over the year. In winter red deer used seven forest site types, fresh coniferous forest being the most preferred. During these years red deer avoided fresh deciduous forest.

The X^2 test was used, and it was found that (a) differences between the areal proportion of forest site types in the range of red deer population and red deer frequentation in these forest site types were significant, and (b) there was a significant differentation in the intensity of use (kind of activity) of individual forest site types during comparison seasons.

Red deer used young plantations, thickets, and timber stands for moving in an equal degree (15-21 percent). During spring red deer fed in young plantations and timber stands to the same degree (40 percent). In summer the utilization of young plantations as feeding places increased to 60 percent, and even attained 80 percent in fall. In this time red deer began intensive browsing in thickets. The thickets were used in fall by red deer to a great extent as bedding places and shelter against adverse weather conditions. During winter red deer

browsed mostly in timber stands (50 percent), the thickets were used for this purpose in 40, and young plantations in 10 percent. In that time, thickets and timber stands were utilized to the same degree as bedding places.

DISCUSSION

Food Habits

While comparing the composition of moose and red deer winter diets (Table 2 and 3) one can see that pine constitutes the main component of both diets. Moose browse on pine twice as much as red deer. For red deer, pine is a species rarely preferred over other browse plants. The observations show that stags can only compete for this kind of forage with moose. Things are different as far as bark stripping is concerned. Pine bark was stripped most willingly in the same forest sites, and in the same months during winter by moose as well as by hinds with calves. It has been observed that trembling aspen is the next species which can come to competition. It comprises about nine percent of red deer and more than one percent of moose diet. Moose and red deer browsed and stripped the trembling aspen after logging and thinning. However, it has been noted, that in this case there occurs a shift of feeding activity, for moose and red deer have interchanged in time of feeding on this browse species. At first moose were coming and browsing until red deer would appear which then browsed mostly the whole night. After they had finished (at daybreak or dawn) moose were browsing, and resting all day at logging woods. It should be stressed that the largest group of moose constitutes three individuals (cow with twins) and red deer - seventeen.

Dwarf shrubs provide above 32 percent of the red deer diet. I think that this group of plants is the most preferred by red deer during winter. Although they benefit from adaptations for using food from under the snow, they cannot graze on dwarf shrubs because often the depth of snow cover in the Augustow Forest is high. In this period red deer compete for browse, twigs and bark of both pine and trembling aspen, with moose.

Use of Habitat Types

An analysis was made to find the role of the interspecies relations in the formation of spatial distribution of individual species in a habitat during winter.

For this purpose the index, applied by Dice (1945) for analyzing the occuring-together of species, referred to as the index of association, informing about the avoidance or tolerance between individuals of two different species, has been used in this paper.

This index, is equal the quotient between numbers of observed animals of two different species and theoretically probable numbers.

When $0<S<1$, the species tend to avoid each other, when $S=1$, the species in question have a random distribution with regard to each other and when $S>1$ they show an association greater than that determined theoretically.

During 1971-1978 when both the population number and the density of both species were low, moose and red deer avoided each other in fresh mixed coniferous, moist mixed coniferous, moist deciduous forests and ash alderwood. They showed mutual tolerance in fresh coniferous forest.

During 1975-1978 when both populations attained food carrying capacity, moose and red deer avoided each other in moist coniferous, fresh mixed coniferous, moist deciduous forests, ash alderwood and alderwood. They showed mutual tolerance in fresh coniferous and moist mixed coniferous forests.

The forest area under study consists of 2,682 valuation units (of average size of 3.13 ha). Above 720 homogenous patches occur in the habitats of fresh coniferous forest. These units occupy small areas occuring usually in a mosaic pattern on the study area. A very similar situation occurs in mixed deciduous forest sites. In sites of ash alderwood and alderwood, about 280 homogenous patches have been found but they are usually situated along water courses where great acreages were created by them.

A comparison of the repartition of the area of individual types of forest sites between moose and red deer in question has shown that the interactions between these species depend on the degree of differentation of the habitat. A growth in the differentation of the habitat is followed by an increase in the reciprocal tolerance between individuals of moose and red deer.

In the case of an intensive penetration of sites attractive for red deer respecting food (niche overlapping with moose) there occurs a shift of feeding activity by moose or temporal succession or spatial penetration of those sites. Here one deals with a competition model in which mechanisms of interaction between these two species occur

at an individual level. This indicates a direct competition where results or intensification depend on intensity influences of individuals of another species on individuals of the given species. The effects of this phenomenon at the population level will be the result of frequency meetings between individuals in the competing species.

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