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Cent. Eur. J. Biol. • 8(12) • 2013 • 1250-1264
DOI: 10.2478/s11535-013-0244-3

Central European Journal of **Biology**

Vegetation diversity influences endozoochoric seed dispersal by moose (*Alces alces* L.)

Research Article

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Received 29 March 2013; Accepted 15 July 2013

Abstract: Research on moose-mediated seed dispersal is limited. However, its potential role in transferring seeds in patchy landscapes may be of great importance. In this work we examined how seasons and vegetation diversity influence the species richness and abundance of seeds dispersed endozoochorically by moose. Samples of moose faeces were collected year-round, fortnightly, from contrasting vegetation types, dominated by diverse, species-rich wetland or poor, dry pine forest. The viable seed content of dung was studied by the seedling emergence method. The mean number of emerged seedlings per 0.8 L sample and the mean number of plant species per 0.8 L sample were several times higher in the diverse wetland vegetation than in the poor pine forest vegetation. Maximum species richness and seed abundance was observed during the fructification period, and the minimum during spring. The species richness of samples did not differ between winter and the growing season, although the composition of plant species was different. The results of this study suggest that moose are efficient seed vectors, especially of grasses typical for grasslands and wetlands. The species richness and abundance of dispersed seeds coincides with the diversity of the vegetation of the animal's habitat.

Keywords: *Herbivores • Seed dispersal • Seedling emergence • Species richness • Ungulates • Wetland*

1. Introduction

The seeds of many plant species are morphologically adapted to long distance dispersal by specific vectors (*e.g.* wind, water, birds), but most plant species are in fact polychoric, *i.e.* they are dispersed by multiple vectors [1]. Animals are the most important dispersal vector for a vast number of terrestrial plants [2], with evidence of directed seed dispersal [3,4]. During the last two decades, endozoochoric seed dispersal has been reported to be mediated in the temperate zone of Europe by domesticated animals, *e.g.*: cattle [5,6], horse [5,7], sheep [8,9], reindeer [10], and many wild European herbivores: European bison [11], red deer [12,13], fallow deer [13,14], roe deer [13,15], hare [16], rabbit [17,18], and omnivorous wild boar [15]. All these studies have shown the great potential of endozoochoric plant dispersal and the possible role of this process in the recolonization of land after glaciation [19,20], as well as the possible use of animals as seed vectors during the process of habitat restoration [21-23].

The moose (*Alces alces* L.) is classified by theriologists as a generalist browser [24] and a concentrate selector [25]. Shoots of woody plants predominate in its diet, and, as a consequence of low proportion of herbaceous plants [26], one may expect a low number of seeds deposited in its dung. This is probably the reason why the largest European cervid has so far been little researched in relation to ungulate-mediated plant dispersal. Heintze [27] noted that moose faeces include viable seeds of several plant species, Pastor *et al.* [28,29] pointed out the potential importance

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of moose in plant dispersal, but without any detailed information, and Seefeldt *et al.* [30] proved the survival in moose gut of the seeds of two plant species invasive in Alaska: *Melilotus albus* Medik. and *Crepis tectorum* L. There is also evidence that moose dung contributes to the biodiversity of bryophyte flora, although evidence that moose disperse the moss *via* endozoochory is lacking [31]. Moose-mediated endozoochoric seed dispersal is poorly studied, but taking into account the considerable patchiness of the wetland ecosystems inhabited by this ungulate in the temperate zone, its role in transferring seeds between isolated plant subpopulations may be of great importance. The moose is also a potentially good long distance seed vector: it occupies large ranges (larger than other European ungulates with the exception only of the European bison) and occasionally undertakes long migrations, exceeding 100 km [32], which increases the chances for seed to be deposited far from its mother plant.

Moose forage mostly on the shoots of trees and bushes, whose share in their winter diet can exceed 98% [26,33]. The diet of moose in Eurasia includes approximately 250 plant species, but only about 25-30 plant species make up the animal's basic food within an individual's range [26]. In Poland the only studies on moose diet, carried out in Augustów Forest, reported 32 plant species foraged during autumn, and only 16 during winter [34,35]. Heptner and Nasimovich [26] report that the diversity of the moose diet on a geographical scale is correlated with the plant diversity of their habitats: low in the northern and high in the southern parts of the animal's natural range.

In this study we examined endozoochoric seed dispersal by moose, with the aim to assess the potential role of this large herbivore in plant dispersal. Specifically, we tested how the species richness and abundance of seeds dispersed endozoochorically by moose are influenced by season and by the vegetation diversity of its habitat.

2. Experimental Procedures

2.1. Study area

We conducted our study in north-eastern Poland, in two areas lying approximately 120 km apart: at the Piekielne Wrota range (approximately 3,000 ha) of Biebrza National Park (53°36'N; 22°43'E), and at the Jelonka range (approximately 1,200 ha), in the vicinity of Białowieża Primeval Forest (52°36'N; 23°23'E). The vegetation of the Piekielne Wrota range consists of diverse and species-rich plant communities ranging from xerothermic grasslands, through forests and forest-meadow mosaics, and water plant communities. Plant species richness in the limits of the Piekielne Wrota range has not been estimated. Its forest cover is 6% of the total area, and is lower than average for the surrounding Biebrza National Park (23%). A large part of this range (44%) is covered by willow and birch scrub. The non-forest vegetation of the range is very diverse, with a high share of wet meadows (21%), a mosaic of wet meadows with willow-birch scrub (12%), sedge communities (7%), and some intensively used meadows (6%; Biebrza National Park's data resources; Table 1). The study site is surrounded by a similar mosaic vegetation as the Biebrza National Park, which protects the largest (close to 100,000 ha) and most well- preserved wetland in Central and Western Europe, lying in the valley of the Biebrza river. It is the main refuge of moose in Poland, inhabited by a population estimated in 2005 of approximately 600 individuals (Biebrza National Park's data).

The diversity of the flora (slightly over 130 species) and vegetation cover at the Jelonka range [36] is low in comparison to Piekielne Wrota, located in the Biebrza valley (Table 1). The study area is part of 12,000 ha of previous agricultural land abandoned after the two World Wars due to its infertile sandy soils [36], and is surrounded by farmland. Approximately 64% of the area is covered by nutrient- and species-poor pine stands, and 23% by a mosaic of heathers and pine-aspen-juniper scrub. The non-forest vegetation covers only 13% of the area, including three small transitional fens fed by local springs (12.0 ha, 1.5 ha and 0.3 ha), situated at the eastern edge of the range [36,37]. The moose population does not exceed a dozen animals.

Vegetation type	Piekielne Wrota	Jelonka
Pine forest	0	64
Pine-aspen-juniper scrub	0	23
Xerothermic grassland	1	2
Willow-birch scrub	44	4
Sedge communities	7	6
Birch-spruce forest	0	1
Birch-alder forest	6	0
Mosaic of forest and meadow	12	0
Water communities	2	0
Intensively used meadows	6	0
Wet meadows	21	0
Reed communities	1	0

Table 1. Percentage of the land covered by broad vegetation types at the study sites: Jelonka range (vicinity of Białowieża Forest) and Piekielne Wrota range (Biebrza Marshes), north-eastern Poland.

2.2. Methods

2.2.1. Dung collection and treatment

Moose dung samples were collected approximately fortnightly from September 2007 to September 2008 in Biebrza National Park, and from January 2008 to January 2009 in the Jelonka range. The matching period of sampling in both sites was January 2008 to September 2008 (Figure 1), and we limited most of the comparative analyses to these nine months in order to avoid the influence of possible differences in fruit availability between years. There was also a few days' difference between the sites in the dates of sampling. However, the influence of this was minimised by the fact that seeds pass through animal gut at different speeds depending on seed traits [38]. Although the mean food retention time for moose is only 53.6 hours [39], the last viable seeds can still be present in dung egested up to 11 days after feeding [30].

We sampled year-round along the same widely-separated transects across all major vegetation types at each study site. The transects were set not accounting for different vegetation types but run randomly across the site as moose are highly mobile and defecation can take place far from the feeding site [26,33]. A high attention was paid to collect only fresh pellet groups (looking wet and intact). Any surface material that might contaminate the sample was carefully removed. Pellet groups (2-3 per sample, male and female without differentiation) were pooled to tightly fill a 1 L container. Next, we calculated actual volume of each sample

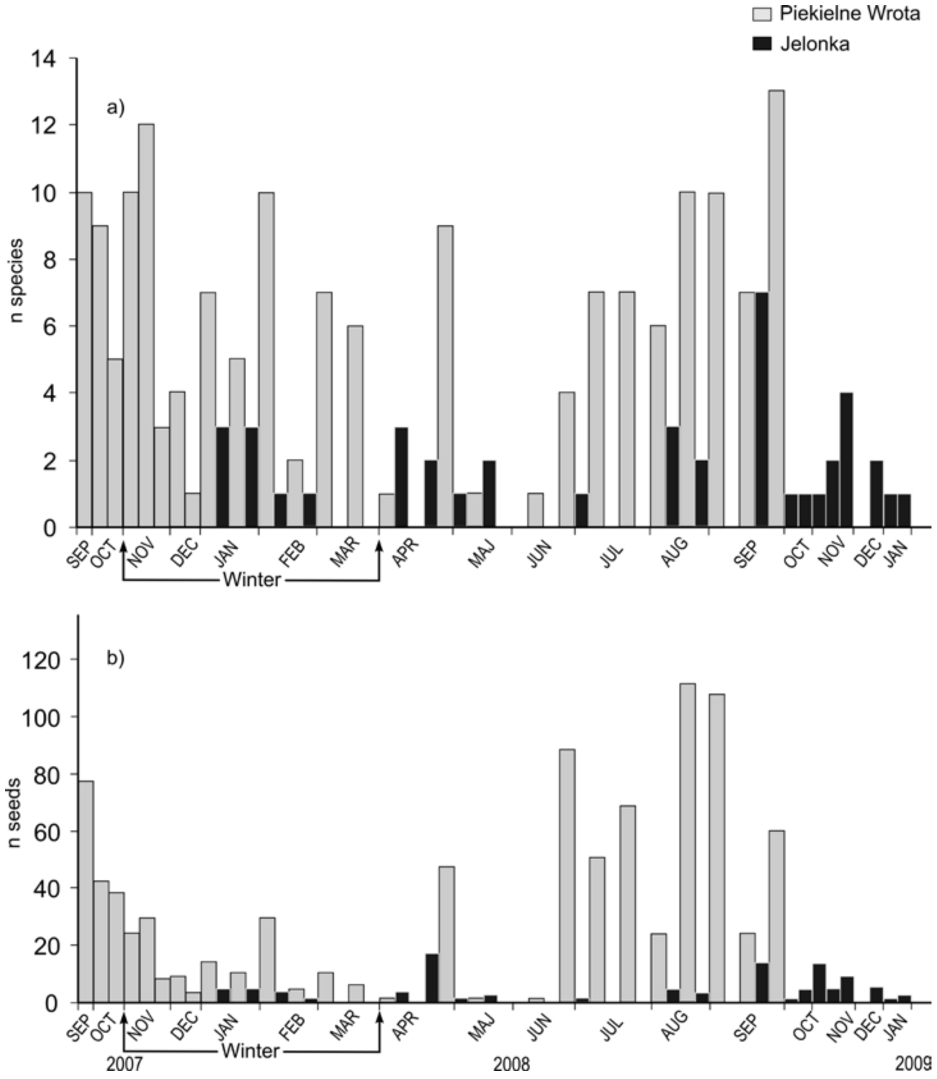

Figure 1. The temporal distribution of plant species richness (a) and viable seed abundance (b) in moose (*Alces alces* L.) dung samples collected in the Piekielne Wrota range (Biebrza Marshes; September 2007 – September 2008; n = 28) and in the Jelonka range (the vicinity of Białowieża Primeval Forest; January 2008 – January 2009; n = 28), north-eastern Poland. Each column represents one sample comprising 2-3 pellet groups.

by deduction of the volume of water poured into the container with the sample from the container's volume. Mean sample volume was 0.8 L ± 0.098 (SD). Fresh faeces immediately after collection and transfer to the laboratory were mixed, in a ratio of 1:3, with sand sterilised for 48 h at 110ºC and poured onto trays (30 cm x 40 cm x 10 cm) in an approximately 4-cm-thick layer. The control trays (containing pure sterilised sand) and sample trays were kept in a greenhouse and watered. Stratification samples were left for wintering in the greenhouse to create conditions for seed. Samples were not watered during the winter to avoid premature germination. Moreover, the tray substratum was stirred each time seedlings were removed during observations.

2.2.2. Estimation of viable seed content

To estimate the species composition and number of viable seeds in moose faeces, seedlings emerging from dung samples were counted and removed from trays as soon as they could be identified. Seedling monitoring was continued over 36 months. Individual seedlings that could not be identified during two to three consecutive observations were replanted into pots and grown until their identification could be verified. For simplicity, we refer to all taxa as species, including those seedlings that could only be identified to the genus (*Betula* spp., *Carex* spp., *Oenothera* spp., *Prunus* spp., *Rumex* spp., *Veronica* spp.). Undetermined graminoid seedlings (< 0.1% of the total seedling number) that died before accurate determination were excluded from analyses. Plant nomenclature follows Mirek *et al.* [40].

2.2.3. Statistical analysis

We assessed the vegetation type of origin for each plant species following Matuszkiewicz [41]. According to the vegetation type of their origin, plant species were divided into five groups: grassland (all non-forest habitats excluding fields and wetland habitats), forest (all types of forest), forest-grassland (species occurring in both previously-defined habitats), wetland (all non-forest wetland communities, *e.g.* sedge communities, wet meadows, rushes, reeds) and synanthropic (fields, roadsides, paths, ruderal sites, cultivated species, species alien to north-eastern Poland).

Winter was defined for the purposes of this paper as the period between the beginning of November and the end of March, when the shoots of woody plants become the basic moose diet [33,34]. The rest of the months are called hereafter 'the growing season'.

The differences in the number of seeds and the number of species between series (study areas and seasons during the nine-month overlapping period) were tested using the Mann-Whitney pairwise test (data distribution non-normal). To find (dis)similarities in species composition between series we used the Jaccard coefficient. Only plants identified at species or genus level were taken into consideration during statistical analyses, since those allocated to taxa of the family level were of little diagnostic value. Species richness of dung samples from different sites was compared by sample based rarefaction. All analyses were performed using PAST 1.58 software [42].

We used indicator species analysis to determine which of the dispersed plant species were significantly associated with studied sites (Piekielne Wrota vs. Jelonka) and/or seasons (winter vs. growing season). This analysis was performed only for samples collected during the nine-month period when sampling overlapped at both sites, using R [43] packages: 'labdsv' version 1.5-0 [44] and 'indicspecies' version 1.6.2 [45].

3. Results

3.1. Emerged seedlings

A total of 979 seedlings, comprising 74 plant taxa (overall 24 plant families), emerged from 56 moose dung samples (Table 2) and none from the control (sterilised sand). Sixty-nine taxa identified to species level accounted for 96.8% of all seedlings (Appendix A). The mean (±S.E.) number of seedlings per dung sample (0.8 L) was 17.5±3.7, while the mean number of emerged plant species per sample (0.8 L) was 3.7±0.5. Majority of plant species (85.1%) emerged in fewer than 10 seedlings. High number of species occurred with low frequency, with 23.2% occurring in one sample only. (*Urtica dioica* L., *Poa subcerulea* Sm., *P. pratensis* L., *Glyceria fluitans* (L.) R. Br., *Deschampsia caespitosa* (L.) P. Beauv.) accounted for 72.5% of all seedlings. However, they were abundant only in samples from the Piekielne Wrota range, where they constituted 79.3% of seedlings. Of these five species, only *U. dioica* and *P. subcerulea* emerged from samples from the Jelonka range, with seven seeds and one seed, respectively. The top five abundant species in the Jelonka range were *Molinia caerulaea* (L.) Moench, *Rorippa palustris* (L.) Hull, *Calluna vulgaris* (L.) Besser, *U. dioica* and *Juncus effusus* L., constituting 60.6% of seedlings (Appendix A).

Seedlings of forest and grassland species dominated, constituting 42.2% and 36.2% of overall seedlings emerged from moose dung samples, respectively, but most of the seedlings of forest species were those of *U. dioica* (39.3% of overall seedlings). Wetland species had a 12.5% share, while those of the synanthropic and forest-grassland groups were below 5% (Appendix A).

One-third (32.4%) of the species dispersed endozoochorically by moose were grasses (Poaceae), with none of the other families exceeding a proportion of 10%. Poaceae were also the most numerous (44.7%) among the emerged seedlings. However, their number was comparable to Urticaceae, represented by only one species with a share at 39.3% (Table 2; Appendix A). Limiting analyses to the nine-month period of overlapped sampling limited the number of emerged seedlings to 709 and the number of dispersed species to 55, but did not influence the species dominance structure of dispersed plants (Appendix A).

3.2. Temporal variability

Species richness and the number of seedlings per 0.8 L sample varied over time in both study populations. The number of species and the number of seeds per sample (0.8 L) in Piekielne Wrota reached their maximum between the beginning of July and the end of November (species; Figure 1a), and between the beginning of June and the end of September (seeds; Figure 1b). At the Jelonka range, the number of species peaked in September, and the maximum seed number was not well expressed (Figure 1a and 1b respectively). At both sites, the species richness and the seed density also peaked at the turn of January and February, and at the turn of April and May. Both characteristics reached their minimum at the beginning of the growing season: between the beginning of May and the middle of June in the Piekielne Wrota range, and the beginning of May and the beginning of August in the Jelonka range (Figure 1).

The number of plant species dispersed per dung sample (0.8 L) did not differ between winter and the growing season (Figure 2). However, there were different species sets in each of the seasons (the Jaccard coefficient of similarity $J < 0.2$). At the Piekielne Wrota range, the mean number of dispersed seeds during the growing season was three times higher than during winter (the Mann-Whitney test; P = 0.01). At the Jelonka range, however, the mean number of dispersed seeds did not differ (P = 0.92) between the seasons (Figure 2).

3.3. Differences between series

The mean number of seedlings emerged per sample (0.8 L) and the mean number of plant species per sample (0.8 L) were several times higher at the Piekielne Wrota range than at the Jelonka range (the Mann-Whitney test P<0.0001 in both cases; Table 3). Over a quarter (28.6%) of the samples collected year-round from the Jelonka range and 7.2% of those collected year-round from the Piekielne Wrota range did not contain any seeds.

Most of the plant species recorded in the dung of moose were exclusive for the Jelonka range or the Piekielne Wrota range. Only eight species out of 74 dispersed (*four out of 55 for the nine-month period) were common for both sites ($J = 0.11$): **Agrostis canina* L., **A. stolonifera* L., *Betula* sp., *Cerastium holosteoides* Fr. emend. Hyl. *Frangula alnus* Mill., **Molinia caerulaea*, *Poa subcerulea* and **Urtica dioica* (Appendix A). Cumulative species richness curves (Figure 3) showed that a number of infrequently dispersed species may not have been detected in the study. At both sites the highest number of year-round dispersed species belonged to Poaceae (33.0% and 46.0% of seedlings emerged from samples from the Jelonka range and the Piekielne Wrota range, respectively). The proportion of species from different plant families dispersed by

Family	Data series		
	Piekielne Wrota	Jelonka	Total
Poaceae	20	8	24
Caryophyllaceae	6	1	6
Asteraceae	5	1	6
Onagraceae	4	1	5
Rosaceae	1	3	4
Juncaceae	1	2	3
Brassicaceae	2	1	3
Lamiaceae	2	1	3
Cyperaceae	1	1	2
Polygonaceae	1	1	2
Scrophulariaceae	1	1	2
Ranunculaceae	2	0	2
Rubiaceae	1	0	1
Apiaceae	1	0	1
Chenopodiaceae	1	0	1
Betulaceae	1	1	1
Geraniaceae	1	0	1
Lythraceae	1	0	1
Plantaginaceae	1	0	1
Rhamnaceae	1	1	1
Solanaceae	1	0	1
Urticaceae	1	1	1
Campanulaceae	0	1	1
Ericaceae	0	1	1

Table 2. List of plant families ordered according to the total number of species that emerged from 56 moose dung samples collected year-round in 2007-2008 at the Piekielne Wrota range (Biebrza Marshes) and the Jelonka range (the vicinity of Białowieża Primeval Forest), north-eastern Poland

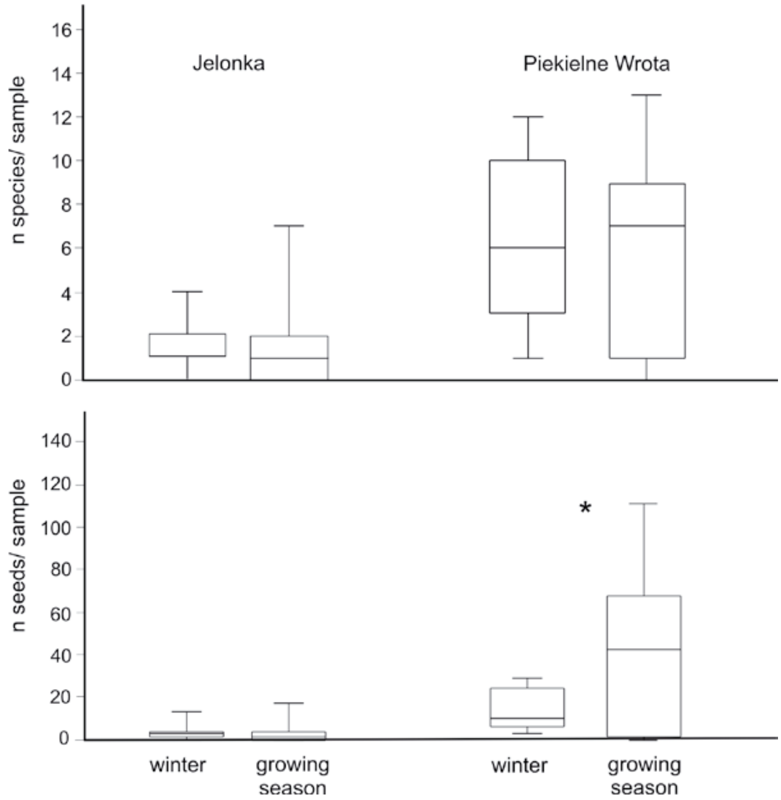

Figure 2. Number of seeds and number of plant species dispersed during the period from January to September 2008 by moose (*Alces alces* L.) in the Piekielne Wrota range (Biebrza National Park; 20 samples) and in the Jelonka range (the vicinity of Białowieża Primeval Forest; 20 samples), north-eastern Poland; a statistically significant difference is shown by an asterisk (the Mann-Whitney pairwise test; P=0.01); the 25-75 percent quartiles are drawn using a box; the median is shown with a horizontal line inside the box; the minimum and maximum values are shown by 'whiskers'.

	Year-round			January-September 2008		
	Series of samples		Total	Series of samples		Total
	Piekielne Wrota	Jelonka		Piekielne Wrota	Jelonka	
Total n seeds	885	94	979	656	53	709
Mean n seeds /sample	31.6±6.28	3.4±0.84	17.5±3.66	32.75±8.20	2.85±1.00	17.8±4.73
Maximum n seeds	111	17	111	111	17	111
Minimum n seeds	0	0	0	0	0	0
Total n plant speciesa	56	26	74	40	19	55
Mean n species /sample	6.0±0.72	1.5±0.30	3.7±0.49	5.6±0.83	1.5±0.39	3.55±0.56
Maximum n plant species	13	7	13	12	7	12
Minimum n plant species	0	0	0	0	0	0
Number of samples	28	28	56	20	20	40

Table 3. The total number (n) of seedlings and plant species that emerged from moose (*Alces alces* L.) dung samples, the mean (±S.E.) and the minimum/maximum values for seedling abundance and the number of species in samples collected in the Piekielne Wrota range (Biebrza Marshes) and in the Jelonka range (the vicinity of Białowieża Primeval Forest), north-eastern Poland.

[a] *Also considering as species those seedlings that could only be identified to the genus (Batrachium spp., Betula spp., Carex spp., Prunus spp.)*

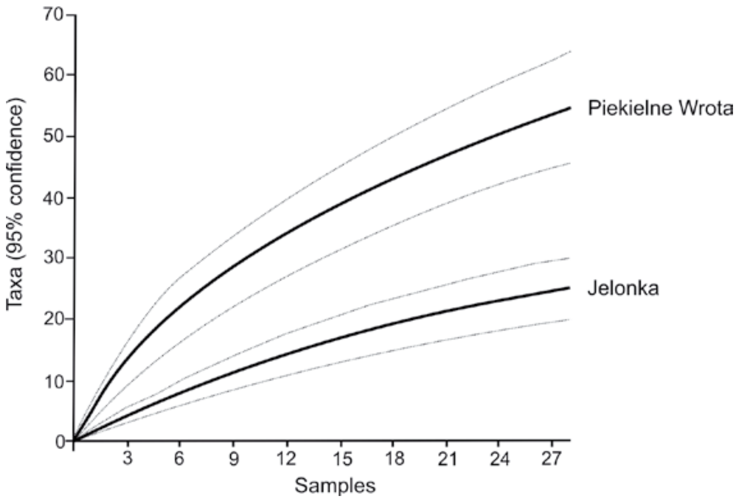

Figure 3. The cumulative number of plant species dispersed by moose (*Alces alces* L.), with increasing sample size (from sample-based rarefaction) in the Piekielne Wrota (Biebrza National Park) and the Jelonka (the vicinity of Białowieża Primeval Forest), north-eastern Poland; for both curves 95% confidence limits are shown; the mean sample volume is 0.8 ± 0.098 (SD) liters.

moose did not differ between the Jelonka range and the Piekielne Wrota range (the Mann-Whitney test; P = 0.072). Also, the share of species representing different habitat groups did not differ significantly between the series. The species of grasslands and wetlands had the highest shares in both studied series (Appendix A), in contrast to the different habitat cover of the sites (*Chi2*=169.74; P<0.001; Table 1), with high forest cover (close to 64%) and low cover of wetland communities (6%) in the Jelonka range, and the opposite situation in the Piekielne Wrota range (forest cover 6% and wetland communities cover close to 50%; Table 1).

The indicator species analysis identified 6 plant species as indicators of site and season at a significance level of $\alpha < 0.05$, with each species being positively associated with Piekielne Wrota as a site (three species) and to the growing season at this site (three species), while no species were associated to the Jelonka range (neither to growing season nor to winter) nor to winter at Piekielne Wrota. *Poa subcerulea* (a meadow grass species) and species with high water and nitrogen demands, *Urtica dioica* and *Glyceria fluitans*, were positively correlated with the site. High indicator values were also assigned to two other meadow grasses, *Poa pratensis* and *P. trivialis*, and to pioneering *Betula* sp. as indicators of the growing season at the Piekielne Wrota range (Table 4).

4. Discussion

In recent years, several attempts have been made to identify the importance of large herbivores for plant dispersal, but the second largest European ungulate (and the largest European cervid), the moose, has not been investigated. Our results demonstrate that this herbivore is, in the temperate zone of Europe, an endozoochoric vector for at least 74 plant taxa. This is more than the number of plant species reported to be dispersed by any other wild or domestic large herbivore in any other place in Europe [*e.g.* 5,7,14-16] with the exception of red deer/fallow deer in England [13] and European bison in Białowieża Forest [11]. The European bison was also characterised by over two times higher seed densities per 1 L of dung [11] than we found for moose. All studied species of vectors were reported to play some role in plant dispersal, although it is difficult to estimate the relative importance of each disperser without studies carried out for all compared species in similar habitat and vegetation conditions. Such studies are rare and have yet to include moose. In our opinion, comparing the dispersal efficiency of vectors studied in different sites is not proper because it does not allow one to distinguish between site effect (plant species richness, seed abundance, interactions among animals inhabiting the site) and vector species effect (food preference, physiology, behaviour).

The number of plant species dispersed by moose is surprisingly high for a generalist browser [24] and concentrate selector [25]. The number of plant species recorded in our study from moose dung is two times higher than the number of species registered as being foraged by this ungulate during autumn in Poland [35], and close to the number of species observed as constituting the moose diet in the whole of Belarus [33]. Therefore, it is very likely that the moose diet

Site/season and indicator plant species	*IndVal*	*rpb*	*P*
Jelonka; 0 species			
Piekielne Wrota; 3 species			
Urtica dioica	0.764	0.416	0.005
Glyceria fluitans	0.742	0.386	0.015
Poa subcerulea	0.671	0.431	0.030
Jelonka winter; 0 species			
Piekielne Wrota winter; 0 species			
Jelonka growing season; 0 species			
Piekielne Wrota growing season; 3 species			
Poa pratensis	0.750	0.408	0.005
Betula sp.	0.665	0.460	0.010
Poa trivialis	0.655	0.468	0.005

Table 4. Results of the indicator species analysis on the plant species dispersed by moose (*Alces alces* L.) in the Jelonka range (vicinity of Białowieża Forest) and the Piekielne Wrota range (Biebrza Marshes), north-eastern Poland. For each habitat and season, we indicate the species that obtained the highest value of the association (*IndVal*), the correlation (*rpb*) and the statistical significance of the association (*P*). The analysis was carried out for samples collected at both study sites during an overlapping sampling period from January 2008 to September 2008 (20 samples at each site). None of the plant species was associated with the Jelonka range at a significance level of $\alpha = 0.05$

includes many more plant species than is reported in the literature [26,33,34]. In our opinion, some seeds could also be ingested by animals as a consequence of serendipitous contamination of their forage. Indeed, the species most commonly emerging from dung samples were also among the most common at the study sites, *e.g.*: *Urtica dioica*, *Poa pratensis* and *Deschampsia caespitosa* at Piekielne Wrota, and *Molinia caerulea* and *Calluna vulgaris* at Jelonka [36]. The high proportion of species (85%) which produced fewer than 10 seedlings, and close to one quarter of species present in only one dung sample, also suggests the fortuitous origin of some seeds in moose faeces. This suggests that only about 15% of the plant species that emerged throughout the study with ten or more seedlings benefit highly from dispersal by moose, while for the rest of the plant species, endozoochory may be less important. It should be noted that our study indicates only the potential role of moose in plant dispersal. It shows sets of species and numbers of seeds dispersed endozoochorically in different habitats and seasons, omitting factors influencing seed ingestion and their chances of germinating from dung in the field and the chances of establishing themselves in new areas. These problems need to be addressed in future research projects.

Grasses contributed a high proportion of seeds in moose faeces, although only Danilov [46] reported that plants of the Poaceae family have a significant importance in the moose diet. Hofmann [25] holds the opposite opinion on this subject. According to him, the moose is rather poorly adapted to digest the rough fibre components of grasses. Dzięciołowski and Pielowski [34] share Hofmann's opinion and limit moose forage mainly to tall grasses of the genera *Calamagrostis*, *Agrostis*, *Poa* and *Deschampsia*. Our results are in line with the latter statement: the grasses of these four genera constituted the majority of grass seeds in dung samples in our study.

Unexpectedly, no Fabaceae species were recorded from moose dung, in spite of the good adaptation of their seeds to pass undamaged through the gut of herbivores. Many species of this family are frequently reported as dispersed endozoochorically by large ungulates [5,11,30,47]. Based on published data we expected that moose would serve as a good seed vector of the Fabaceae, which are well represented in both study sites. Werpachowski [48] reported 48 species from this family from Biebrza National Park, and Faliński *et al.* [36] 10 species from the Jelonka range. However, in our study, no Fabaceae emerged from the dung samples. Do moose avoid grazing legumes, or feed on them mainly before the fructification period? This question needs to be carefully addressed in a future study.

The lack of differences in the mean number of dispersed species per dung sample (0.8 L) between the winter months and the growing season was unexpected. Seed accessibility during winter is much lower than in the growing season, especially during the peak of fructification [49]. Data on the moose diet also acts against this result: during the growing season it is more diverse, with up to 30% of non-woody plants, while during the winter the share of tree shoots and bushes can exceed 98%, and the species diversity of foraged plants decreases [33,34]. These seasonal changes were well expressed by the species composition of dispersed plants at both study sites. However, the seed number expressed seasonality only at Piekielne Wrota, and the indicator species analysis revealed indicator species of the growing season only at this site, but none associated with the winter season. In our opinion, at the Jelonka range the lack of differences in the number of dispersed seeds between seasons and lack of indicator species for seasons can be explained by low vegetation diversity, which probably forces moose to feed year-round on woody plants. In effect, species richness and the number of seedlings emerged from moose dung from Jelonka was very low year-round. There was a different situation at the Piekielne Wrota range, where during the growing season moose utilize diverse vegetation patches of open marshland and wet meadows, foraging mainly on woody plants only during winter [50]. This seasonal change was expressed by a significant difference between seasons in the number of dispersed seeds per dung sample (0.8 L) at this location and by indicator plant species associated with the growing season (grasses of fresh meadows) but none to winter. Seed accessibility during the winter is generally much lower as it depends on plant phenology [51] and thickness of snow cover [11]. Some effect of snow cover was expressed in our study by the small peak in seedling number and the species number in dung samples at the turn of January and February, which coincided with a snowless period. The influence of seed accessibility is expressed only at the Piekielne Wrota range, where owing to high habitat and vegetation diversity, moose diet preferences can change according to season.

The number of emerged seedlings and the number of species per 0.8 L dung sample were lower, and the proportion of dung samples not containing any viable seeds was higher on the pine-forest-dominated, poor habitat of the Jelonka range in comparison to the diverse and species-rich fens of the Piekielne Wrota range. These differences are of similar character to the correlation between the plant diversity of the habitat and the diversity of the moose diet on a geographical scale. Heptner and Nasimovich [26] report that the species richness of the moose diet is low in the northern and high in the southern parts of the moose's range. Our results show a dependence between the species richness of endozoochorically dispersed seeds and the diversity of the studied habitats: the higher the habitat diversity, the higher the vegetation diversity (and plant species richness) and the higher the species richness and abundance of seeds in moose dung, which corroborates our hypothesis. It might be argued that faeces collected in the studied area could have come from food eaten by the animals outside of its limits. This seems likely but does not influence our results as long as the surrounding landscape and vegetation are similar to those in the study site, which is the case in the Piekielne Wrota range. In Jelonka, the comparatively small forest complex is surrounded by agricultural land, which could potentially serve as a source of seeds. However, the germination experiment showed that the share of synanthropic species (*i.e.* associated with farmland, ruderal, and alien for the area) is very low, and they occurred in low numbers, which suggests that moose foraged mostly within the limits of the study area.

The moose is the only large herbivore in the temperate climate living in fen ecosystems. Seefeldt *et al.* [30] and Schwartz *et al.* [39] documented that seeds can be retained in its gut up to 11 days after their ingestion. Moose also regularly undertake local (between habitat patches), and occasionally interregional, migrations [33,34,51,52]. Therefore we found moose to be a significant potential plant vector. Knowledge on the moose's endozoochoric dispersal capability allows for a better understanding of its role in the shaping of the vegetation of wetland and forest ecosystems. The moose is not just a factor altering the succession of woody plants [53], generating spatial patterns in boreal forests [29], or mediating the rates of nutrient cycling in its habitats [28,54]; it is also an efficient endozoochoric seed vector dispersing a considerable number of plant species, especially grasses typical for grasslands and wetlands. In our opinion, moose help to maintain the herbaceous plant diversity of the wetland mosaic landscapes, where species-rich mineral soil islands are isolated by surrounding fens, limiting plant dispersal [55].

Acknowledgements

We are grateful to A. Wiktoruk for her field and laboratory assistance, and to A. Dobrychno for help in the collection of dung samples in the field. Biebrza National Park granted us permission to collect samples and gave access to a digital map of vegetation. This research project (no. N N304 021737) was financed by the Polish Ministry of Science and Higher Education in 2009–2012.

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Appendix A

List of plant species ordered according to total seed number obtained from moose (*Alces alces* L.) dung samples collected in Biebrza Marshes (Piekielne Wrota) and in the vicinity of Białowieża Primeval Forest (Jelonka) in north-eastern Poland. Values for the year-round series and for the nine-month period of sampling that overlapped for both sites are given. Habitats of origin were assigned to plant species following Matuszkiewicz (2001): Gra – grassland; For – forest; ForGra – species occurring in both: forest and grassland habitats; Wet – non-forest wetland habitats; Syn – synanthropic plants occurring in human made habitats: fields, roadsides, pathways, ruderal sites and species not native to north-eastern Poland.

Species	Series of samples				Total		Habitat
	Piekielne Wrota		Jelonka				
	year-round	nine-month	year-round	nine-month	year-round	nine-month	
Urtica dioica L.	378	239	7	7	385	246	For
Poa subcerulea Sm.	128	113	1	0	129	113	Gra
Poa pratensis L.	114	104	0	0	114	104	Gra
Glyceria fluitans (L.) R. Br.	51	48	0	0	51	48	Wet
Deschampsia caespitosa (L.) P. Beauv.	31	27	0	0	31	27	ForGra
Molinia caerulea (L.) Moench	5	1	20	20	25	21	Gra
Betula sp.	20	18	3	0	23	18	NC
Poa trivialis L.	22	19	0	0	22	19	Gra
Rorippa palustris (L.) Besser	0	0	15	2	15	2	Wet
Lythrum salicaria L.	13	12	0	0	13	12	Wet
Poa annua L.	12	8	0	0	12	8	Syn
Calluna vulgaris (L.) Hull	0	0	10	2	10	2	For
Agrostis canina L.	8	7	1	1	9	8	Wet
Solanum dulcamara L.	8	3	0	0	8	3	Wet
Cerastium holosteoides Fr. emend. Hyl.	5	0	3	3	8	3	Gra
Holcus lanatus L.	7	7	0	0	7	7	Gra
Stellaria nemorum L.	6	1	0	0	6	1	For
Agrostis stolonifera L.	4	3	2	2	6	5	Wet
Frangula alnus Mill.	2	1	4	0	6	1	For
Epilobium obscurum Schreb.	5	4	0	0	5	4	Wet
Festuca rubra L.	5	1	0	0	5	1	Gra
Juncus effusus L.	0	0	5	2	5	2	Gra
Artemisia vulgaris L.	4	4	0	0	4	4	Syn
Poa compressa L.	4	4	0	0	4	4	Gra
Poa palustris L.	4	3	0	0	4	3	Wet
Alliaria petiolata (M.Bieb.) Cavaria&Grande	3	3	0	0	3	3	For
Carex sp.	3	3	0	0	3	3	NC
Poa angustifolia L.	3	3	0	0	3	3	Gra
Poaceae	3	0	0	0	3	0	NC

Species	Series of samples				Total		Habitat
	Piekielne Wrota		Jelonka				
	year-round	nine-month	year-round	nine-month	year-round	nine-month	
Corynephorus canescens (L.) P. Beauv.	0	0	3	0	3	0	Gra
Rubus idaeus L.	0	0	3	2	3	2	ForGra
Agrostis gigantea Roth.	2	2	0	0	2	2	ForGra
Cardaminopsis arenosa (L.)Hayek	2	2	0	0	2	2	Gra
Epilobium ciliatum Raf.	2	2	0	0	2	2	Syn
Epilobium palustre L.	2	1	0	0	2	1	Wet
Lychnis flos-cuculi L.	2	2	0	0	2	2	Gra
Sagina procumbens L.	2	1	0	0	2	1	Syn
Spergula arvensis L.	2	1	0	0	2	1	Syn
Jasione montana L.	0	0	2	2	2	2	Gra
Lycopus europaeus L.	0	0	2	2	2	2	For
Phleum pratense L.	0	0	2	0	2	0	Gra
Rumex acetosella L.	0	0	2	1	2	1	Gra
Alopecurus geniculatus L.	1	1	0	0	1	1	Gra
Angelica sylvestris L.	1	0	0	0	1	0	ForGra
Atriplex patula L.	1	0	0	0	1	0	Syn
Batrachium sp.	1	1	0	0	1	1	Wet
Bidens connata Muhl. ex Willd.	1	0	0	0	1	0	Wet
Bidens tripartita L.	1	0	0	0	1	0	Wet
Dactylis glomerata L.	1	0	0	0	1	0	Gra
Epilobium lamyi F. W. Schultz	1	1	0	0	1	1	ForGra
Festuca ovina L.	1	1	0	0	1	1	Gra
Galeopsis tetrahit L.	1	0	0	0	1	0	ForGra
Galium mollugo L.	1	1	0	0	1	1	Gra
Geranium robertianum L.	1	0	0	0	1	0	For
Holcus mollis L.	1	1	0	0	1	1	ForGra
Hypochoeris radicata L.	1	0	0	0	1	0	Gra
Juncus articulatus L. Emend. K. Richt.	1	0	0	0	1	0	Wet
Melandrium album (Mill.) Garcke	1	0	0	0	1	0	Syn
Plantago major L.	1	1	0	0	1	1	Syn
Polygonum hydropiper L.	1	0	0	0	1	0	Wet
Potentilla anserina L.	1	0	0	0	1	0	Syn
Ranunculus repens L.	1	1	0	0	1	1	Gra
Scrophularia umbrosa Dumort.	1	0	0	0	1	0	Wet
Scutellaria galericulata L.	1	0	0	0	1	0	Wet
Taraxacum officinale F. H. Wigg.	1	1	0	0	1	1	Gra

Species	Series of samples						Habitat
	Piekielne Wrota		Jelonka		Total		
	year-round	nine-month	year-round	nine-month	year-round	nine-month	
Agrostis capillaris L.	0	0	1	0	1	0	Gra
Carex hirta L.	0	0	1	1	1	1	Gra
Conyza canadensis (L.) Cronquist	0	0	1	1	1	1	Syn
Digitaria ischaemum (Schreb.) H. L. Mühl.	0	0	1	1	1	1	Syn
Epilobium parviflorum Schreb.	0	0	1	0	1	0	Wet
Juncus bufonius L.	0	0	1	1	1	1	Wet
Potentilla argentea L.	0	0	1	1	1	1	ForGra
Prunus sp.	0	0	1	1	1	1	Syn
Veronica chamaedrys L.	0	0	1	1	1	1	Gra
Total seed number	885	656	94	53	979	709	

References to Appendix A

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