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THE IMPACT OF THE DIFFERENT PERIOD OF OCCURRENCE OF THE EUROPEAN BEAVER POPULATION ON ITS FEEDING BEHAVIOR AND IMPACT ON THE ENVIRONMENT*

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Abstract

The aim of the study was to determine the influence of the period of occurrence of the European beaver (*Castor fiber* L.) population on foraging strategies and on the diversity of the species of cutting trees and shrubs. Two beaver populations at different stages of development – a younger (42yr) population from the Kampinos National Park and an older (72 yr) population from the Wigry National Park were studied. Both populations foraged according to the Optimal Foraging Theory (OFT), according to which the distance to available food depends on its size and the distance to reach it. The dominant factors modifying the foraging behavior of beavers and their foraging ranges were the presence of a dam, the availability of preferred species. The greater diversity in the areas where beaver are found may be the result of both beaver activity and the selection of more attractive areas for dam construction.

Introduction

The first beavers were introduced into Poland in the second half of the 1940s in the northeastern part of the country (ŻUROWSKI 1984, KASPERCZYK 1990, JANISZEWSKI, MISIUKIEWICZ 2012, RAKOWSKA, STACHURSKA-SWAKOŃ 2021). From the population established in this area, the species

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was reintroduced to other areas of the country. Between 2000 and 2020, the population size of this species in Poland increased 5 times (GUS 2021). Although the population continues to increase nationally, in northeastern Poland the Wigry National Park Service is beginning to observe a decline in the beaver population. When expanding into new areas, beavers primarily colonize areas rich in deciduous species. A beaver family colonizing sections of rivers rich in preferred plants initially can occupy as much as a 200m section of a watercourse. With the depletion of the food supply, the length of the section of the watercourse penetrated by beavers increases (DVORNIKOVA 1987). In extreme cases, the section of the river occupied by can reach several kilometers (DEZHKIN et al. 1986). Beavers show a preference not only for species, but also for the diameter of gnawed trees. The most common diameter reported in the literature is less than 10 cm (ŻAK 2001, MARGALETIĆ et al. 2006, BRATCIKOV 2007, MISIUKIEWICZ et al. 2016, MAHONEY and STELLA 2020, JACKOWIAK et al. 2020, JUHÁSZ et al. 2023).

There have been a number of studies and observations in Poland and around the world related to changes in bite intensity with increasing distance from the edge of a reservoir or watercourse. In Poland, the species in search of which beavers moved furthest from the water was poplar, and the average distance of movement for this species was 62 m. The animals also traveled relatively far in search of hazel and willow, for which the average distance was 34 and 25 m, respectively. Beavers traveled the shortest distance (4 m) to forage on alder (BOROWSKI and BORKOWSKI 2003, 2004). In the Wigry National Park, which has one of the oldest beaver populations in Poland, beavers used to roam up to several hundred meters from the shore in search of aspen (BOREJSZO and SKÓRZYŃSKA 1991). According to STOFFYN-EGLI and WILLISON (2011), 95% of trees are cut within 50 meters of the shore. FRYXELL (2001) showed that more than 50% of gnawed stems were within 10 meters of the water. BARNES and DIBBLE (1988) show that beavers penetrate an area up to 60 meters from the water in search of food.

Many researchers are attempting to develop a model to predict the foraging behavior of animals based on the theory of the central foraging site. In the case of beavers, this theory is related to foraging in terms of not only the species of trees and shrubs but also their size, distance, energetic inputs in felling trees and transport of food to water (ORIAN and PEARSON 1979, SCHOENER 1979, MCGINLEY, WHITHAM 1985, FRYXELL and DOUCET 1991). According to this theory, animals should be more selective near the center of their stand, and in order to maximize the profit associated with the energy expended, beavers should reach for thicker trees at distances farther from their feeding and burrows. According to GALLANT et al. (2004), food selectivity depends on the quality of the habitat. In fertile habitats (with a higher proportion of deciduous species), beavers show greater selectivity than in poorer habitats (with less deciduous species). According to these studies, in high-quality areas, as the distance from the pond increased, beavers cut fewer trees but the trees were larger. Some authors suggest that the relationship between size and distance should be inverse, especially when "the prey is larger than the predator" (JENKINS 1980). A number of studies have documented a decrease in the thickness of gnawed plants as distance from shore increases (JENKINS 1980, BELOVSKY 1984, BUSHER 1996, HAARBERG and ROSELL 2006, RAFFELA et al. 2009). The results of these studies are consistent with the optimal foraging theory (OFT), which states that the distance from the available food, and the time spent acquiring it, depends on the size of the food and the distance that must be traveled to reach it. In the literature, one can also find studies that indicate that there is no correlation between the diameter of felled trees and the distance from the water (BRATCIKOV 2007). Other factors such as habitat richness (GALLANT et al. 2004), predator pressure (BASEY and JENKINS 1995, MYSŁAJEK et al. 2019) or humans (JACKOWIAK et al. 2020) can also influence selectivity.

The purpose of our study was to indicate whether the different period of colonization of the areas influences the selective foraging of rodents near the center of their habitat, and what differences exist between the parks' vegetation, especially in terms of species diversity of woody vegetation in beaver sites.

Material and Methods

Research works were located in the Wigry National Park (WNP) and Kampinos National Park (KNP). A population from the WNP established in the 1950s and a population from the KPN established from individuals brought from the KPN in 1980 (ŻUROWSKI 1984, KASPERCZYK 1990, JANISZEWSKI, MISIUKIEWICZ 2012, RAKOWSKA, STACHURSKA-SWAKOŃ 2021). The KPN population is classified as stabilizing (younger population, 42 years since introduction), while the WPN population is classified as aging (older population, 72 years since introduction).

Within each park, six experimental plots (banks of rivers, canals and lakes) were selected where traces of beaver foraging were found, and an additional three research plots (with beaver dams) were selected (Figure 1).

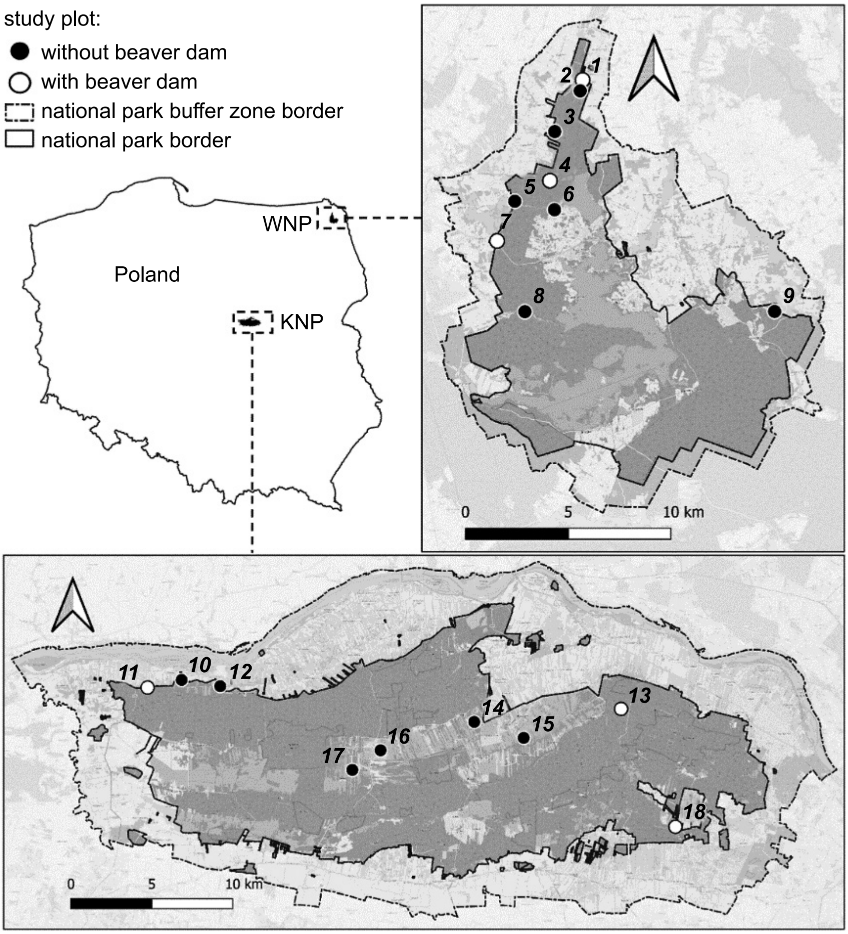

Fig. 1. Location of survey plots in Wigry National Park (WNP, older population, 72 years) and Kampinos National Park (KNP, younger population, 42 years)

Research plots from the area of the Wigry National Park were mainly located in the northern part of the Park (Wiatrołuża, Kamionka, Maniówka, Samlanka, Kamionka and Czarna Hańcza rivers). One plot was located in the eastern part of the WNP (Gremzdowka river). One survey plot was also located in the WPN area near the Suchar I water reservoir. Inside KNP, the plots were drowning located in northwestern (Kromnowski canal), central and eastern (Łasica, Ł9, Wilcza Struga canals) and south-eastern (Struga canal) parts of the Park.

Plots were drawn from historical databases and current information provided by the park managers. From the presence of watercourses, the most common habitats in the survey plots were wet and marshy habitats.

The most common plant communities were Fraxino-Alnetum (WNP) and Carici elongatae-Alnetum (KNP). More detailed descriptions of the measurement plots are included in the Appendix (Table 1.1).

Ten transects located perpendicular to the axis of the watercourse were established along the river in each study plot. The transects were distanced 20 meters apart from each other (Figure 2). Each transect was divided into 10-meter sections 4 meters wide. The number of sections per transect was determined by the presence of traces of beavers. If occlusions or damage to trees and shrubs were not present no further measurements were made on a given transect. In the plots with a beaver dam present, transects 5 and 6 were located near the dam, while the remaining transects were located in the area upstream of the dam, transects 1–4, and downstream of the dam, transects 7–10.

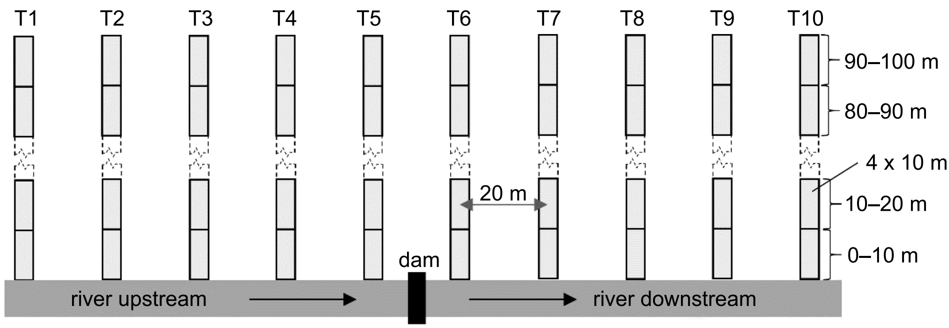

Fig. 2. Sampling scheme for assessing beaver foraging and floristic characteristics of sample plots. Arrow water flow direction

The measurements mainly used the methodology proposed by O'CONNELL et al. (2008), with some modifications, including the height at which tree and shrub thicknesses were measured. In each subplot, woody plants were inventoried by species, divided into three degrees of damage: *S* – stumps after trees and shrubs, *D* – damaged standing trees, and *U* – undamaged trees or shrubs. Thickness was measured at a height of 20 cm from the ground level, divided into three classes: 1 (<10 cm), 2 (11–30 cm) and 3 (>31 cm).

Data on the dimensions of the dam – length, thickness and height – were collected on measuring plots where beaver dams occurred. Information about the width of the river (the section behind the dam) and the beaver pond (the section before the dam) was also recorded. Information on the width of the river or canal was collected at each transect.

The collected data was analyzed in terms of the beaver's foraging range from the riverbank, preference for gnawed species, and diversity of trees and shrubs. Preferences were analyzed in terms of the number of stumps gnawed and damaged trees, but also in terms of the basal area of gnawed trees and shrubs. The basal area reflects the volume of felled trees relatively well and is commonly used in Polish forestry as a volume index equivalent. In describing the results, there were also used the sum of the diameters of gnawed or damaged trees in the survey plot and the average diameter of gnawed wood.

There were compared the effects of population age (WNP – older population vs. KNP – younger population) and the dam on foraging range, number and diameters of gnawed and damaged trees, and species diversity of trees and shrubs. We performed the same analysis for the immediate vicinity of the dam (Upstream, Dam, Downstream). The Margalef (R) and Shannon-Wiener (H) diversity indices and Simpson's Dominance (C) were used to assess species diversity of trees and shrubs (Table 1). As beaver populations differed significantly in terms of foraging range, comparisons were made for the entire length of the transect and for the section in the immediate vicinity of the river or channel (0–10 m).

Table 1

Ecological indices

Index	Equation	Legend
Margalef (R)	$R = \frac{S_1}{\log N}$	S_1 – number of species N – number of all trees, shrubs on plot, transect n_i – number of trees, shrubs of a given species on plot, transect
Shannon-Wiener (H)	$H = -\sum (pi) \cdot (\log pi)$ $pi = \frac{n_i}{N}$	
Simpson (C)	$C = \sum \left(\frac{n_i}{N}\right)^2$	

The analyses used non-parametric tests – Mann-Whitney U test for two independent samples and Kruskal-Wallis ANOVA with Dunn Bonferroni post-hoc test for comparisons of more than two variants. Spearman's rank correlation coefficient was used in correlation analyses. Data were processed using an Excel spreadsheet and the PQ Stat statistical package.

Results

It was found no differences between the characteristics of the dams between analysed populations of beaver (Table 2). It was also shown that the rivers and channels on which the dams were built were also characterized by a similar width in both experimental parks (3.7–4.0 m), and beaver pond had a similar surface area too (450.0–666.7 m^2).

Table 2

Main features of the river and the dam

Feature	Younger population	Older population	Total
	average		
Width of dam [m]	7.7^{A}	10.3^{A}	9.0
Height of dam [m]	1.0^{A}	0.7^{A}	0.9
Thikness of dam [m]	1.3^{A}	1.2^{A}	1.2
Volume of dam [m^3]	14.2^{A}	9.6^{A}	11.9
Width of river upstream over a distance of 50 meters from dam [m]	13.3^{A}	9.0^{A}	11.2
Width of river downstream over a distance of 50 meters from dam [m]	3.7^{A}	4.0^{A}	3.8
River surface over a distance of 50 meters upstream from dam [m^2]	666.7^{A}	450.0^{A}	558.3
River surface over a distance of 50 meters downstream from dam [m^2]	183.3^{A}	200.0^{A}	191.7

The same capital letters of the alphabet indicate no statistically significant differences between beaver populations, while different letters indicate significant differences (Mann-Whitney *U* test, $a = 0.05$)

Animals from the younger population foraged on 20 species of trees and shrubs, while those from the older population fed on 18 species (Table 3). Five species of trees and shrubs were mainly browsed or damaged by beavers from KPN: *Corylus avellana* L. (14.6%), *Alnus glutinosa* (L.) Gaertn. (15.2%), *Quercus robur* L. (17.4%), *Tilia cordata* Mill. (9.6%) and *Prunus padus* L. (13.4%). In terms of basal area, these were mainly: *Quercus robur* L. (41.5%), *Alnus glutinosa* (L.) Gaertn. (23.2%) and *Betula pendula* Roth. (11.0%). The beavers from older population, in terms of number of gnawed trees, foraged mainly on *Corylus avellana* L. (91.7%). In terms of basal area, foraging was spread out among three species: *Alnus glutinosa* (L.) Gaertn. (34.4%), *Corylus avellana* L. (21.2%) and *Tilia cordata* Mill. (10.6%). Beavers from both populations almost entirely used *Populus tremula* L. – from the older population, they fed on almost 100% of the trees of this species occurring near the rivers.

The analysis of the proportion of undamaged tree and shrub individuals (*U*) shows that the foraging base of the Wigry population is shrinking. Coniferous species – *Picea abies* (L.) H. Karst and *Pinus sylvestris* L. – dominate in the surroundings of the beaver's lodges. In terms of basal area, these species account for almost 45% of the share along the length of the entire transect and more than 30% of the share along the 0–10 meter section. It should be noted that cases of damaged individuals of these species were encountered in the area of the older population. The Kampinos population existed in more favorable conditions. Among the undamaged trees, the species preferred by beavers were *Prunus padus* L. and *Alnus glutinosa* (L.) Gaertn. in terms of number, and *Quercus robur* L., *Alnus glutinosa* (L.) Gaertn. and *Betula pendula* Roth. in terms of basal area.

Table 3

Percentage of woody plant species by number and basal area divided into preferred by beavers (*S* + *D*) and undamaged trees and shrubs (*U*). Bold values indicate the three species with the highest share. Numbers in the anvias refer to the 0–10 m section. In the younger population area, species shares for the total and for the 0–10 m section were the same

Gatunek	Younger population (KNP)				Older population (WNP)			
	number		basal area		number		basal area	
	S + *D*	*U*	*S* + *D*	*U*	*S* + *D*	*U*	*S* + *D*	*U*
	%							
Corylus avellana L.	**14.6**	7.0	0.2	0.1	**91.7 (90.8)**	**38.2 (27.8)**	**21.2 (18.2)**	2.2 (1.2)
Alnus glutinosa (L.) *Gaertn.*	**15.2**	**9.3**	**23.2**	**30.3**	**1.9 (2.3)**	8.2 **(12.0)**	**34.4 (39.2)**	**35.8 (48.5)**
Quercus robur L.	**17.4**	5.7	**41.5**	**20.4**	0.1 (0.1)	0.6 (0.1)	0.5 (0.5)	2.1 (2.1)
Tilia cordata Mill.	9.6	3.4	5.4	4.3	**2.5 (3.0)**	5.4 (5.6)	**10.6 (11.5)**	7.1 (9.1)
Betula pendula Roth	5.0	2.8	**11.0**	**16.0**	0.6 (0.6)	0.4 (0.5)	7.8 (6.4)	1.0 (1.3)
Prunus padus L.	13.4	**26.6**	3.6	3.7	1.5 (1.8)	**9.1 (13.7)**	1.2 (0.9)	0.9 (1.2)
Populus tremula L.	5.9	0.1	5.0	1.4	0.1 (0.1)	0.01 (0.02)	1.7 (2.0)	0.01 (0.01)
Sorbus aucuparia L.	0.0	1.6	0.0	0.1	0.3 (0.2)	2.2 (1.6)	5.7 (6.4)	1.0 (0.9)
Picea abies (L.) *H. Karst*	1.2	0.0	0.1	0.0	0.3 (0.4)	**9.3** (8.2)	5.3 (5.5)	**24.2 (18.6)**
Fraxinus excelsior L.	0.3	0.3	0.4	0.0	0.2 (0.3)	1.3 (1.9)	3.9 (4.4)	1.1 (1.5)
Pinus sylvestris L.	1.9	1.5	1.6	10.9	0.1 (0.0)	1.8 (1.2)	1.7 (0.0)	**20.4 (11.3)**
Frangula alnus Mill.	0.3	**23.7**	0.4	0.6	0.0 (0.1)	3.7 (4.6)	0.0 (0.03)	0.2 (0.2)
Other*	15.2	18.0	7.6	12.2	0.7 (0.4)	19.8 (22.6)	6.0 (5.0)	4.0 (4.1)
All	100	100	100	100	100	100	100	100

* **Younger population (*S* + *D*):** *Acer platanoides* L.*, Malus sylvestris* L.*, Malus domestica* Borkh.*, Ulmus minor Mill., Pyrus communis* L.*, Acer negundo* L.*, Salix caprea* L.*, Prunus domestica* L.*, Crataegus monogyna Jacq*. **Younger population (*U*):** *Euonymus verrucosus Scop., Euonymus europaeus* L.*, Carpinus betulus* L.*, Rhamnus cathartica* L.*, Prunus myrobalana (L.) Loisel, Juglans regia* L.*, Ribes nigrum* L.*, Robinia pseudoacacia* L.*, Salix cinerea* L.*, Salix aurita* L.*, Sambucus nigra* L.*, Viburnum opulus* L.*, Acer pseudoplatanus* L.*, Larix decidua Mill., Padus serotina (Ehrh.) Borkh, Cornus sanguinea* L.

* **Older population (*S* + *D*)**: *Acer platanoides* L.*, Euonymus verrucosus Scop., Carpinus betulus* L.*, Acer negundo* L.*, Rhamnus cathartica* L.*, Ulmus laevis Pall., Lonicera xylosteum* L. **Older population (*U*):** *Salix caprea* L.*, Crataegus monogyna Jacq., Ribes nigrum* L.*, Daphne mezereum* L.*, Sambucus nigra* L.*, Viburnum opulus* L.*, Acer pseudoplatanus* L.*, Juniperus communis* L.

The dwindling food supply in the WNP may also be indicated by the foraging range and the diameter and number of trees gnawed (Table 4).

Table 4

Foraging ranges and the diameter and number of trees gnawed

Specification	Younger population (KNP)			Older population (WNP)		
	average	median	max	average	median	max
Beaver foraging ranges						
All rivers or canals	5.7^{B}	5.5	26	20.0^{A}	16.0	97
Rivers or canals without a beaver dam	6.0^{aB}	5.5	15	17.0^{bA}	15.2	75
Rivers or canals with a beaver dam	5.9^{aB}	5.6	25	26.6^{aA}	32.7	95
Beaver foraging ranges in relation to the dam						
Upstream	6.0^{Ba}	5.6	15	27.8^{Aab}	25.7	75
Dam	9.0^{Ba}	7.4	25	18.1^{Ab}	16.1	45
Downstream	5.0^{Ba}	4.7	6	35.1^{Aa}	28.4	97
Diameter and number of damaged and cut trees						
Number of gnawed trees and shrubs (*S* + *D*) per location	35.8^{B}	38	61	456.1^{A}	293	2330
Sum of diameters of gnawed trees and shrubs (*S* + *D*) per location	367.8^{A}	270	730	455.6^{A}	320	1270
U diameter	16.9^{bA}	16.6	40	13.5^{bB}	15.6	40
S diameter	15.1^{bA}	14.6	40	10.5^{bB}	8.7	40
D diameter	29.9^{aA}	29.5	40	28.0^{aA}	30	40

Explanations: *U* – undamaged trees and shrubs; *S* – stumps; *D* – damaged standing trees. The same uppercase letters mean no differences between columns, different letters mean statistically significant differences (Mann-Whitney *U* test, $a = 0.05$). The same lowercase letters indicate no differences between row averages, different letters indicate statistically significant differences (Mann-Whitney *U* test, $a = 0.05$ for differences between foraging range in plots with and without a dam, and Kruskal-Wallis ANOVA, Dunn-Bonferroni post-hoc test, $a = 0.05$ for other analyses in the table)

Beavers from the older population foraged much farther from the axis of the watercourse to compare with beavers from the younger population. Beavers from the WNP made the farthest wanderings at a distance of almost 100 meters. With 43% of gnawed or damaged trees located within 10 meters of the river, more than 90% of gnawed trees or shrubs within 40 meters of the river. In the case of the younger population from the KNP, the maximum foraging range did not exceed 30 meters, and we recorded

92% of the gnawed trees or shrubs up to 10 meters from the channel. Beavers from the older population migrated significantly farther in plots where beaver dam were present – 26.6 m with dam and 17.0 m without dam. In the case of the younger population, beavers migrated similar distances in both plots with and without a dam (about 6.0 m). Within the plots with dams, beavers from the older population migrated significantly further on transects located behind dam (downstream – 35.1 m) compared to sites near dams (18.1 m) and before dam (upstream – 27.8 m). In the area inhabited by the younger population, beavers migrated similar distances regardless of the transect's location relative to the dam (5.0–9.0 m). In terms of the sum of diameters of gnawed or damaged trees and shrubs, both populations had similar conditions. The younger population gnawed an average of 367.8 cm in diameter per location, while the older population gnawed 455.6 cm in diameter per location. However, the older population had to acquire more than 10 times the number of trees and shrubs (456.1 per location) than the younger population (35.8 per location). The diameter of undamaged trees (*U*), damaged trees (*D*) and stumps (*S*) indicates that the younger population had a greater availability of thick trees. Interestingly, both populations damaged and left trees (*D*) with similar diameters. In WNP, beavers damaged mainly alder (63% of damaged trees) and pine (9% of damaged trees), while in KPN beavers damaged mainly oak (44%) and alder (17%). Within both parks, damaged trees tended to be thicker than trees that were cut down (stumps – *S*). Within each park, the diameters of stumps and undamaged trees did not differ significantly from each other.

Damaged trees (*D*) were mainly found in the immediate vicinity of the river. The younger population damaged and left trees up to 20 meters from the river or channel, while the older population damaged trees up to 40 meters from the river. The number of damaged trees was negatively correlated with the distance from the river bank (Table 5). The number and diameter of stumps from felled trees and shrubs decreased with increasing distance from the river. We showed significant correlations in this aspect for the number of stumps at the site of the younger population (r = -0.85) and for the diameter of stumps at the site of the older population (r =-0.45). The diameter of the stumps of undamaged trees did not change significantly in the WNP and was about 15 cm in diameter along the entire 100-meter transect. In the case of the KNP, the diameter of undamaged trees and shrubs successively increased from 15 to 20 cm on the 0–30 m section. This was a statistically significant increase (r = 0.42). Analysis of correlations between the number and diameter of gnawed trees and distance from the river or canal bank showed no significant relationship for most species. The only correlation was shown for *Corylus avellana* (L.) in the WNP – as the distance from the river increased, the number and diameter of gnawed hazel trees decreased (r = -0.18 for diameter and r = -0.14 for number). Examining correlations between other traits, there were found that dam volume was positively correlated with gnawed wood diameter and negatively correlated with foraging range.

Table 5

Correlation between the number and diameter of trees and distance from the river or canal bank (Spearman's monotonic relationship, a = 0.05)

Feature	Population	Uundamaged (*U*)	Damaged (*D*)	Stumps (*S*)	All
Number	younger	-0.38	-0.48*	-0.85*	-0.37
	older	0.25	-0.53*	-0.24	0.11
Diameter	younger	0.42*	0.13	-0.22	0.39
	older	-0.05	-0.74*	-0.45*	-0.24

Due to that the beaver populations differed significantly in terms of foraging range, the comparison in terms of diversity was carried out on the whole material, i.e. the entire foraging range, and for the section located in the immediate vicinity of the river or channel (0–10 m). The KNP showed significantly higher species diversity of woody vegetation measured by the R and H indices and lower species dominance measured by the C index, both for the whole material and for the 0–10 m section (Table 6).

Table 6

Indicators of biological diversity of trees and shrubs by population

Wariant	Simpson's dominance index (*C*)	Shannon-Wiener diversity index (*H*)	Margalef diversity index (*R*)
All			
Younger population (KPN)	0.43^{b}	1.04^{a}	1.39^{a}
Older population (WPN)	0.58^{a}	0.73^{b}	1.05^{b}
First 10 metres of transect (section 0–10 m)			
Younger population (KPN)	0.46^{b}	1.03^{a}	1.39^{a}
Older population (WPN)	0.56^{a}	0.72^{b}	1.07^{b}

The same lowercase letters indicate no differences between the row, different letters indicate statistically significant differences (Mann-Whitney U test, a = 0.05)

The analysis of correlation between the foraging range and values of ecological indicators showed that in the younger population's area, the dominance index *C* decreased and diversity indices *H* and *R* increased as the distance from the river or channel was longer (Table 7). In the area of the older population, an inverse relationship was shown. However, the correlations for this population were statistically insignificant. The diameter of gnawed trees and shrubs was usually not correlated with the values of the indices. The exception was the index of dominance in the older population's area. This index decreased as the diameter of gnawed trees increased.

Table 7

Correlation between foraging range and diameter of gnawed trees and shrubs and biodiversity indicators

Feature	Population (Park)	Biological indicator		
		Simpson's dominance index (*C*)	Shannon-Wiener diversity index (*H*)	Margalef diversity index (*R*)
Beaver foraging range	older (WPN)	0.26	-0.35	-0.12
	younger (KPN)	-0.81*	0.80*	0.82*
Diameter of gnawed trees and shrubs	older (WPN)	-0.54*	0.10	0.08
	younger (KPN)	-0.05	-0.05	0.32

* Correlation significant at $\alpha = 0.05$ (Spearman's monotonic relationship)

In the case of the analyses for the area with the current beaver dam, it was shown that in the vicinity of the dam the tree and shrub layer is richer in species than the areas upstream and downstream of the dam (Table 8). In most cases, these differences were not statistically significant. We showed the only significant differences for the dominance index C in the area occupied by the younger population, and for the Margalef index *R* in the section of the first 10 meters in the area occupied by the older population.

Table 8

Values of indices of woody vegetation diversity depending on the location of the transect in relation to the dam in the variant for the entire transect and for the first 10 meters of the transect

Population (Park)	Variant	Simpson's dominance index (*C*)	Shannon-Wiener diversity index (*H*)	Margalef diversity index (*R*)
All				
Younger (KPN)	upstream	0.44^a	1.02^a	1.38^a
	dam	0.27^b	1.10^a	1.60^a
	downstream	0.45^a	1.03^a	1.43^a
Older (WPN)	upstream	0.62^a	0.65^a	0.98^a
	dam	0.59^a	0.70^a	1.25^a
	downstream	0.57^a	0.68^a	0.92^a
First 10 metres of transect (subplot 0–10 m)				
Younger (KPN)	upstream	0.42^a	1.05^a	1.40^a
	dam	0.35^a	1.19^a	1.58^a
	downstream	0.45^a	1.03^a	1.43^a
Older (WPN)	upstream	0.62^a	0.59^a	1.01^b
	dam	0.43^a	1.02^a	1.37^a
	downstream	0.51^a	0.62^a	0.94^b

Same lowercase letters indicate no differences between row, different letters indicate statistically significant differences (Kruskal-Wallis ANOVA, Dunn-Bonferroni post-hoc test, $\alpha = 0.05$)

Discussion

The results of the study indicate foraging behavior of European beaver according to the optimal foraging theory (OFT) for younger and older populations, thus confirming the studies of JENKINS 1980, BELOVSKY 1984, BUSHER 1996, HAARBERG and ROSELL 2006, RAFFELA et al. 2009. Both populations presented similarly feeding behaviour, despite differences in foraging range away from the river or channel. As the distance from the river or canal increased, the number and diameter of trees and shrubs felled decreased. Thus, the age of the population did not affect foraging strategy in this case. The younger population inhabited more fertile habitats (with a higher proportion of deciduous species) than the older one (lower proportion of deciduous species) hence it also did not confirm the theory of GALLANT et al. (2004) according to which in richer habitats beavers show selectivity consistent with the central foraging theory. The beavers did not move further away from the river to search for specific species of trees or shrubs. Beavers of both populations gnawed almost 100% of aspen poplar, but this species was found in close proximity to rivers and canals. The species that were gnawed farthest from the river on the KNP were: pine, apple and oak, while on the WNP were: hornbeam, linden and hazel – the choice of species was not dictated by foraging preference, but rather reflected the local habitat layout. The decrease in diameter and number of stumps with distance from the river may also be due to the presence of predators and humans. A study by Mysłajek et al. 2019 realised in the WNP showed that beaver make up almost 10% of the wolf's diet. In the KNP area, the wolf is less numerous, but it is one of the most populous parks in Poland.

The own study shows that the dominant factors modifying the foraging behavior of beavers and their foraging ranges in the analysed populations were: the presence of the dam, the availability of food and its spatial variation. The older population migrated farther in plots with a current dam – this may be due to the need to obtain more raw materials for dam construction. It should be noted that the volume of the dam was positively correlated with the diameter of the gnawed trees and negatively correlated with the foraging range. At the same time, within the plots with dams, beavers migrated to the shortest distances on transects located next to the dam - this in turn may indicate the selection of the species-richest area for dam construction. This was confirmed by biodiversity analyses – we tended to find higher richness (H, R) and lower dominance (C) of tree and shrub species on transects next to the dam. Beavers from the younger population moved similar distances in both plots with and without the dam. In the case of the younger population, we showed a little further range of migration for trees and higher biodiversity on transects located next to the dam. The lack of comparison plots makes analysis in this aspect difficult. It is difficult to find sites unaffected by beaver activity, especially in the WNP. In previously research in the Polesie National Park, was managed to find plots that beavers have not yet colonized (Piętka and Misiukiewicz 2022). On the beaver-inhabited rivers, it has been showed greater variation in tree layer than in areas that beavers have not yet colonized. Although the compositions of the tree stands in the beaver-occupied and comparison plots were very similar they were not identical – for example, in the beaver-occupied areas we showed a higher proportion of aspen – 6.8% in the beaver-occupied river area and 1.4% in the comparison plots, respectively. This already indicates that the greater diversity in beaver-inhabited areas may be both a result of beaver activity and the selection of more attractive areas for dam construction. Most studies in this area indicate that beavers increase the species richness of the areas they inhabit (Gaywood 2016).

There are also studies indicating that beavers are selective in terms of, and in the first instance, beavers populate areas that are most attractive to them (DVORNIKOVA 1987). In order to determine which factor plays a greater role, it is necessary to move away from comparative plots to cyclic surveys within these parks.

Analysis of damaged trees provided interesting results. Damage usually consisted of ringing the tree. It was noticed that beavers usually damaged very thick trees and, importantly, we encountered them mainly within 30 meters of the river or canal bank. We know from stump analysis that further away from the river thick trees were not cut down, and we also know that thick live trees were quite common further away from canals and rivers. It can be assumed that due to their thickness, the beavers did not complete the felling of these trees due to energy conservation, or the felling process is still ongoing. The thickest stumps were found just off the river bank. In our surveys, however, we encountered many trees damaged in an advanced stage of decay that were ultimately not cut down, mainly alder. One might be tempted to say that the goal was not to cut down a tree, but to create conditions for the renewal of a new generation of trees by allowing more light into the forest floor. Numerous studies and the results of our research show that beavers mainly harvest small-diameter trees and shrubs. Killing a tree creates a niche for smaller sized trees and shrubs such as hazel. At the same time, felling trees with large dimensions would involve a large energy expenditure. Thus, ringing was a way to expand the foraging base at the lowest possible cost. It should be noted that beavers have damaged species such as pine and spruce – species they do not prefer in their diet.

Conclusion

Beavers from the older population moved farther away from the water bank than beavers from the younger population. This could be the result of a shrinking foraging base or an overcrowded population in the Wigry National Park. The study did not confirm the theory of central foraging. According to this theory, beavers, in order to maximize the profit associated with the energy expended, should reach for thicker trees at distances further from the river. Both the younger and older populations foraged according to the theory of optimal foraging, according to which the distance from the available food, and the time spent to reach it, depends on its size and the distance to be traveled to reach it. Our study shows that the dominant factors modifying the foraging behavior of beavers and their foraging ranges were the presence of a dam and the availability of preferred species. Greater diversity in the areas where the beaver is present may be the result of both its activities and the selection of more attractive areas for the construction of the dam.

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Appendix 1

Table 1.1

Location and brief description of survey plots

Number	Park (population)	Near river, canal, lake	Beaver dam presence	Coordinates WGS 84		Plant community*
				x	*y*	
1	WNP (older)	Wiatrołuża river	yes	54,15257405	23,08446543	1, 2
2	WNP (older)	Wiatrołuża river	no	54,14787708	23,08224792	1, 2
3	WNP (older)	Maniówka river	no	54,13080822	23,06159436	1, 3
4	WNP (older)	Samlanka river	yes	54,10953227	23,05589423	1, 4
5	WNP (older)	Kamionka river	no	54,10146956	23,02890188	1, 4
6	WNP (older)	Kamionka river	no	54,09678799	23,0580681	1, 4
7	WNP (older)	Suchar I lake	yes	54,08461992	23,01411128	1
8	WNP (older)	Czarna Hańcza river	no	54,0531611	23,0317406	1
9	WNP (older)	Gremzdówka river	no	54,04688593	23,21697512	1, 2
10	KNP (younger)	Kromnowski canal	no	52,37289914	20,34984958	5
11	KNP (younger)		yes	52,36899707	20,3188032	5, 6
12	KNP (younger)		no	52,36902899	20,38481193	5, 6
13	KNP (younger)	Wilcza Struga canal	yes	52,35149243	20,7482574	7
14	KNP (younger)	Ł9 canal	no	52,34615397	20,61470229	7
15	KNP (younger)	Łasica canal	no	52,33661303	20,65928257	7
16	KNP (younger)	Ł9 canal	no	52,33144887	20,52919234	7
17	KNP (younger)	Łasica canal	no	52,32081006	20,50320054	3, 7
18	KNP (younger)	Struga	yes	52,28501501	20,7949335	5

*plant community (Matuszkiewicz and Wolski 2023): 1 – *Fraxino-Alnetum* (=*Circaeo-Alnetum*) – Lowland alder and ash-alder forest on the periodically swamped ground-water soils; 2 – *Tilio--Carpinetum* – Subcontinental lowland lime-oak-hornbeam forest; subboreal vicariant with spruce, eutrophic („rich") communities; 3 – *Tilio-Carpinetum* – Subcontinental lowland lime-oak-hornbeam forest; subboreal vicariant with spruce, mesotrophic („poor") communities; 4 – *Pino-Quercetum* (=*Querco-Pinetum* + *Serratulo-Pinetum*) – Continental mesotrophic oak-pine mixed forest; 5 – *Pino-Quercetum* (=*Querco-Pinetum* + *Serratulo-Pinetum*) – Continental mesotrophic oak-pine mixed forest; 6 – *Ficario-Ulmetum typicum* – Lowland ash-elm floodplain forest; occasionally flooded; 7 – *Carici elongatae-Alnetum* (=*Ribeso nigri-Alnetum* + *Sphagno squarrosi-Alnetum*) – Middle-European alder fen forest