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# FEEDING BEHAVIOUR OF EURASIAN BEAVERS (*CASTOR FIBER*) ALONG SMALL STREAMS IN AN AGRICULTURAL LANDSCAPE

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## Abstract

In areas with high population density, the Eurasian beaver may be forced to utilise sparsely forested landscapes where living conditions may not be optimal for the species. Here, we examine the feeding strategy of Eurasian beavers along a number of small (mainly) forested streams in the Czech agricultural landscape. Diet availability in these sparsely forested landscapes is characterised by a lack of woody plants but a large supply of herbaceous vegetation, including agricultural crops grown close to the watercourse. The beaver has adapted to such conditions by building dams on low-water streams, allowing it to move between scattered diet resources. In winter, the main dietary component was woody plants (70% V), with species normally neglected in optimal sites (e.g. *Acer negundo, Prunus* spp.) taken in the absence of more favoured species (e.g. *Salix* spp., *Populus* spp.), the remaining 30%V consisting of herbaceous vegetation. In summer, however, the main component in the diet was herbaceous vegetation (90% F), which included agricultural crops (56% V). Where there were not enough trees, the beaver tended to leave its summer territory and move to stretches with denser tree stands. Thus, beavers in sparsely forested agricultural landscapes have adapted by utilising the diverse supply of herbaceous vegetation, though its continued presence in the landscape is still primarily dependent on sufficient stocks of woody plants, which the beaver needs to survive winter.

Keywords: adaptation, diet strategies, seasonal changes, summer diet, winter diet

## INTRODUCTION

In the Czech Republic, the Eurasian beaver (*Castor fiber*) is recognised as a protected herbivorous species and, as a result, it has spread over a large part of the country in recent decades, as in many other Central European countries (Nolet and Rosell, 1998; Halley *et al.*, 2012; Halley, Saveljev *et al.*, 2021). The widespread return of the beaver to the Czech countryside stands as just one example of the ongoing change in society's attitude toward nature protection, with increasing numbers supporting the presence of potential conflict species. This has led to the re-emergence of a number of other large mammal species formerly extinct in the Czech landscape, e.g. the Eurasian lynx (*Lynx lynx*), the grey wolf (*Canis lupus*) and the Eurasian moose (*Alces alces*). On the other hand, these species can all have a negative effect on human economic activities and, as such, their continued presence has become controversial and is now widely debated, with the interested parties (e.g. nature protection vs. forestry) often taking up antagonistic positions. In many cases, problems arise due to a lack of information on the ecology of problematic species, with non-reliable data preventing rational approaches to issue solving.

Through its habit of building large burrows and dams, and felling trees as a source of diet and building materials, the beave can significantly alter the environment, both at the habitat (Law *et al.*, 2017) and ecosystem level, by influencing the water regime in small and medium-sized streams (Rosell *et al.*, 2005; Janiszewski *et al.*, 2014; Pollock *et al.*,

2014) and significantly altering tree stands along water bodies (Nolet *et al.*, 1994; Donkor and Fryxell, 1999). The beaver is highly adaptable and can utilise a wide range of plants, though it tends to show distinct preferences through the year depending on the phenological phase of individual plants and their current nutrient content (Mikulka *et al.*, 2020). During the spring/summer growing season, the beaver consumes mainly herbs; however, during the autumn, as the supply of herbs decreases, beavers focus more on woody plants, which they can store and gradually consume over the winter when other resources are unavailable (Jenkins, 1979). Nevertheless, the proportions of herbs will remain high if they are available in high enough volumes and of good enough quality (Henker, 2009). The ability to obtain enough diet throughout the year, from sites close to water, is usually a limiting factor for the permanent occurrence of beavers (Severud *et al.*, 2013), particularly for populations living in areas with larger predators. Despite this, the beaver has shown a strong ability to adapt, successfully inhabiting landscapes subject to heavy anthropogenic alteration (Ulevičius *et al.*, 2011).

In the Czech Republic, the beaver finds an optimal environment in floodplain forests in the river basins of larger rivers, and it is in such habitats that the beaver has been present longest and in relatively high population densities (Vorel *et al.*, 2009; Mikulka, 2021 unpublished). As populations in such optimal habitats increase, however, the beaver is increasingly being forced to settle in new localities, particularly those in agricultural landscapes (Mikulka *et al.*, 2020) where it has settled along small streams lined with narrow bands of riparian woodland. Consequently, diet availability at such localities differs greatly from that in their optimal habitat, both during the vegetation period and winter. Despite their increasing occurrence in the agricultural landscape, relatively little is known of beaver biology in such environments. Thus, the main aim of the present study was to analyse beaver feeding behaviour on small streams in agricultural landscapes, where there is often a significant lack of woody plants, and to estimate the prospects of beaver survival in such landscapes.

## MATERIALS AND METHODS

### Study Area

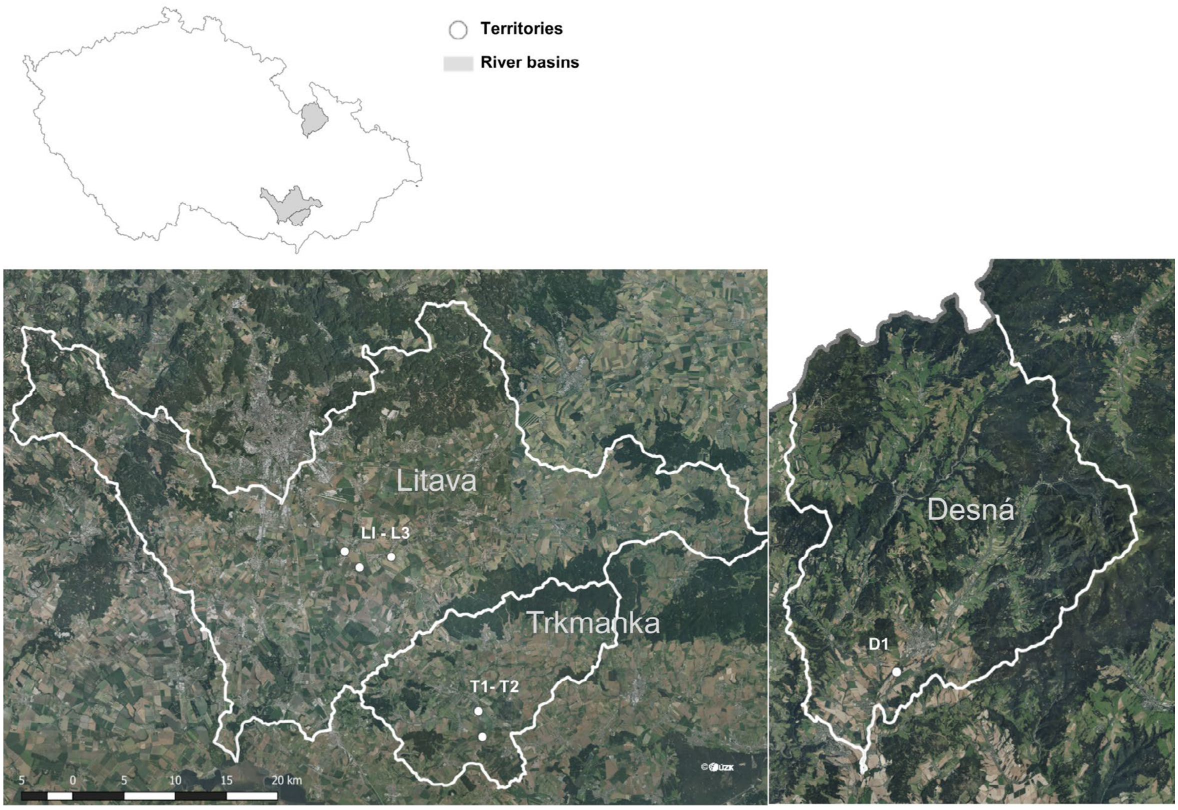
Beaver diet was assessed in six beaver territories along three small river basins (all within the Morava river basin) from autumn 2016/17 to winter 2018/19 (Fig. 1, Tab. I). Five of the territories were located in the south of the basin (Telnice L1, Újezd L2, Žatčany L3 [Litava river basin; Krumvíř T1, Terezín T2 [Trkmanka river basin]) and one approximately 100 km to the north on the river Desná (Šumperk D1). All territories were situated in open agricultural landscapes where woody plants only existed as narrow strips of riparian vegetation, with fields of wheat (*Triticum aestivum*), barley (*Hordeum distichon*), rape (*Brassica napus*) or maize (*Zea mays*) behind them (for further details, see Mikulka *et al.*, 2020). Most of the territories were inhabited by couples or individuals, with no young observed during the research period.

### Diet Availability

Diet availability in each territory was evaluated in a 5 × 10 m quadrat oriented with the shorter side along the riverbank, with one quadrat placed every 50 m along the bank. A total of 131 quadrats were processed in the summer and 75 in the winter over the six territories (numbers were lower in winter due to the seasonal reduction in area used by beavers). During the summer, coverage of herbaceous and shrub species was also included alongside tree species (note that the sum of layer coverage could be > 100% where layers overlapped). In each case, the area monitored was maintained at 5 × 10 m, even where woody riparian growth was < 10 m. In such cases, the area comprising field crops was assigned as 'without vegetation' as a) diet availability tended to change rapidly, and b) most fields had already been harvested in the middle of summer when evaluation took place. Cover of individual tree species was recorded separately, while coverage in the herbaceous layer was only quantified by species where coverage was 10% or higher. In winter, the number of each tree species was recorded in each plot, along with their trunk diameter (20 cm above ground).

I: *Basic characteristics of the beaver territories used to assess beaver diet in agricultural landscapes*

| Territory | Šumperk | Telnice | Újezd | Žatčany | Krumvíř | Terezín |
|---|---|---|---|---|---|---|
| Basin | Desná | Litava | Litava | Litava | Trkmanka | Trkmanka |
| Site code | D1 | L1 | L2 | L3 | T1 | T2 |
| Altitude (m a.s.l.) | 285 | 207 | 194 | 189 | 175 | 175 |
| Width of bank vegetation (m) | 7–10 | 5–6 | 9–10 | 9–10 | 4–5 | 4–6 |
| Average flow ($m^3/s$) | 3.8 | < 0.5 | 0.68 | 0.68 | < 0.5 | < 0.5 |




1: *Location of the Litava, Trkmanka and Desná river basins, with the beaver territories examined marked*

## Diet Analysis

Beaver diet composition was determined by directly monitoring traces of its feeding behaviour at each locality and by analysing the content of faeces. In addition, 44 stomachs were obtained from legally hunted individuals or those found dead within the territories. Beaver diet centres were visited regularly once or twice a month and any ingestion of woody vegetation registered. For herbs, we recorded the species and estimated the area grazed. This area was then categorised into three classes, i.e. 1 (up to 0.25 m$^2$), 2 (up to 0.5 m$^2$) or 3 (more than 0.5 m$^2$). For gnawed trees, we recorded the species and the trunk diameter 20 cm above ground.

Faecal and stomach samples were assessed under a 100× magnification microscope using preparations made from 1.0–1.5 mm plant fragments, with individual dietary components being identified using comparative material obtained from each diet centre. The relative volume (%V) of individual dietary categories was calculated based on 100–200 fragments taken from each sample. Where possible, dietary components were identified to genus level, though some of these were later merged into larger groups for subsequent analysis.

Handling of these specially protected animals was approved under exceptions granted JMK 107931/2020, PK-ŽP/29395/20, JMK 165016/2016, KUOK 60372/2017 and SR/0053/OM/2017-5.

## Data Evaluation

Evaluation of both diet availability and diet composition was performed using the importance index

$$\%I_i = (\%F_i + \%F_{vi})/2, \qquad (1)$$

where $F_i$ is the relative frequency of component $i$ ($\%F_i = F_i/\sum(F_{i\text{-}n}) \times 100$) and $\%F_{vi}$ is the relative volume index of that species. For tree species, the relative volume index was based on the diameter (cm) of each gnawed trunk 20 cm above the ground, and for herbs, the relative index of herb coverage grazed (see 'diet analysis' section).

This same index was then used to evaluate the proportion of woody plants available as diet and the proportion in beaver diet. Species preferences were then calculated using Ivlev's selectivity

$$E_i = (r_i - n_i)/(r_i + n_i), \qquad (2)$$

where $r_i$ is the proportion of component $i$ in the diet and $n_i$ is the proportion of the same component available in the environment. Preference was only assessed for those species taken by at least 30 individuals.

The community coefficient

$$CC = 2C/(A + B) \times 100 \qquad (3)$$

was used to assess species similarity in diet and diet availability, where $C$ is the number of components common to the compared sets and $A$ and $B$ are the numbers of components in sets $A$ and $B$, respectively.

To calculate the quantitative similarity, we used the similarity index

$$SI = \Sigma\%I_{min}, \tag{4}$$

where $I_{min}$ is the smallest value of $\% I$ in the pair of components compared. As the data did not show a normal distribution, even after transformation, we used the non-parametric Kruskal-Wallis test to assess vegetation structure.

Diversity in beaver diet and diet availability was expressed using the Shannon Wiener index

$$H' = p_i \times ln(p_i) \times -1, \tag{5}$$

where $p_i$ is the proportion of component $I_i$ in the diet (or diet available). Dietary component evenness was calculated according to

$$J' = H_{max}/\ln(p_i), \tag{6}$$

where $H_{max} = H'$. Differences in the representation of diet components were tested using the chi square goodness of fit test

$$\chi^2 = \Sigma(X_i - Np_i)^2/Np_i, \tag{7}$$

where $X_i$ is the value measured and $Np_i$ is the expected value.

All statistical analyses were performed using the STATISTICA 12 software package (StatSoft, 2013).

## RESULTS

### Diet Availability in Summer

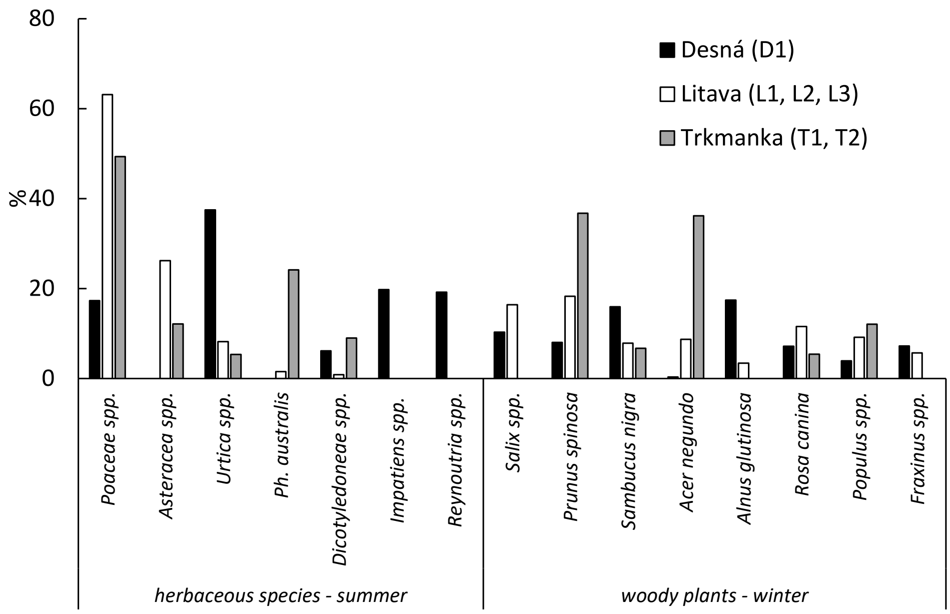
In the Trkmanka and Litavka river basins, the herbaceous layer was usually well developed outside shaded areas under woody plants between spring and summer, being comprised mainly of grasses and reeds (*Poaceae* spp.), with stands of Asteraceae, such as goldenrod (*Solidago* sp.) or astra (*Aster* sp.), also relatively abundant (Fig. 2). In comparison, the herbaceous layer at the site on the River Desná mainly comprised *Poaceae* spp., *Impatiens* sp. and *Reynoutria* sp. Of the other dicotyledonous herbs, nettle (*Urtica dioica*) was common in all territories.

Total vegetation layer coverage at T1 differed significantly from the other territories (Kruskal-Wallis, $P < 0.001$; $n = 6$), with woody plant coverage (e2 + e3 in Appendix 1) being 5- to 10-times lower than the other sites, and herbaceous coverage around half that at most other sites, being restricted to a 4–5 m strip along the bank bordered by arable land (Appendix 1).

Observations indicated that herbaceous vegetation along unmaintained banks gradually became less attractive to beavers over the course of the year, whereas on maintained banks mowed during the summer, vegetation regrowth in autumn provided attractive diet for the beaver up until winter.

### Diet Availability in Winter (Woody Plants Only)

Between 10 and 26 woody species were recorded in individual territories, with highest species diversity at D1 ($n = 25$; $H' = 2{,}565$), lowest at T2 ($n = 10$; $H' = 1{,}476$) and 13 to 20 species ($H' = 1{,}908$ to 2,348) recorded elsewhere (Fig. 2, Appendix 1).




2: *Relative proportion of the most important herbs and woody plants (tree and shrub layer together) available to beavers in each river basin*

The evenness of species representation had no effect on woody plant diversity ($J'$ = 0.74 - 0.78).

### Summer Diet Composition

A total of 21 wild herb species, six agricultural crop species and 13 woody plant species were recorded in the diet of beavers from the three river basins during the growing season (Appendix 2). Overall, herb species were most consumed (89.6%F), of which 55.9%F comprised agricultural crops (Fig. 3, Appendix 2). While free-growing dicotyledonous herbs were consumed at approximately the same frequency in all three river basins (Fig. 3), the proportion of other components differed significantly (woody plants $\chi^2 = 25.73$, $df = 2$, $P < 0.001$; grasses $\chi^2 = 6.15$, $df = 2$, $P < 0.05$; agricultural crops $\chi^2 = 8.96$, $df = 2$, $P < 0.05$). The largest deviation from the mean was in consumption of woody plants at Trkmanka, which were consumed 11-times less than expected. Furthermore, and contrary to expectations, the beaver consumed 3-times less grasses than expected in this area. At Litava, the beaver consumed 2.3-times more woody plants than expected, while grasses were consumed 1.8-time more than expected at Desná (Fig. 3).

Of the herbaceous species, beavers mainly grazed *Reynoutria* sp. and *Impatiens* sp. (together 21.6%F), with grasses also of importance on the Desná (12.4%F) (Fig. 4). At Litava and Trkmanka, Asteraceae (*Astra* sp. and *Solidago canadensis*) were also frequently consumed (12.6%F) and, to a lesser degree, grasses (4.5%F). Interestingly, a substantial part of beaver diet during the growing season was made up of agricultural crops, with cereals, especially *T. aestivum* and *Z. mays*, being grazed throughout the ripening period up until harvesting. *Brassica napus* was an important dietary component right up to the flowering stage in the spring, but was taken at a lower rate during the seed ripening period (for further details, see Mikulka *et al.*, 2020).

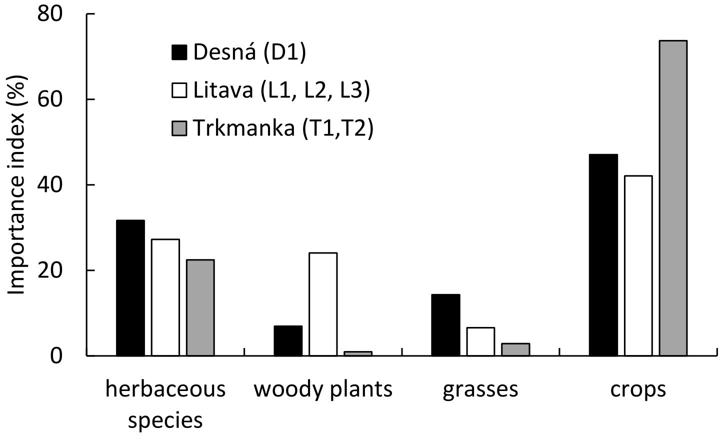
### Winter Diet Composition

Of the 27 woody plant species recorded at the monitoring sites, the beaver consumed 21 (77.8%), though only seven species represented > 10%F in at least one territory (Fig. 4).

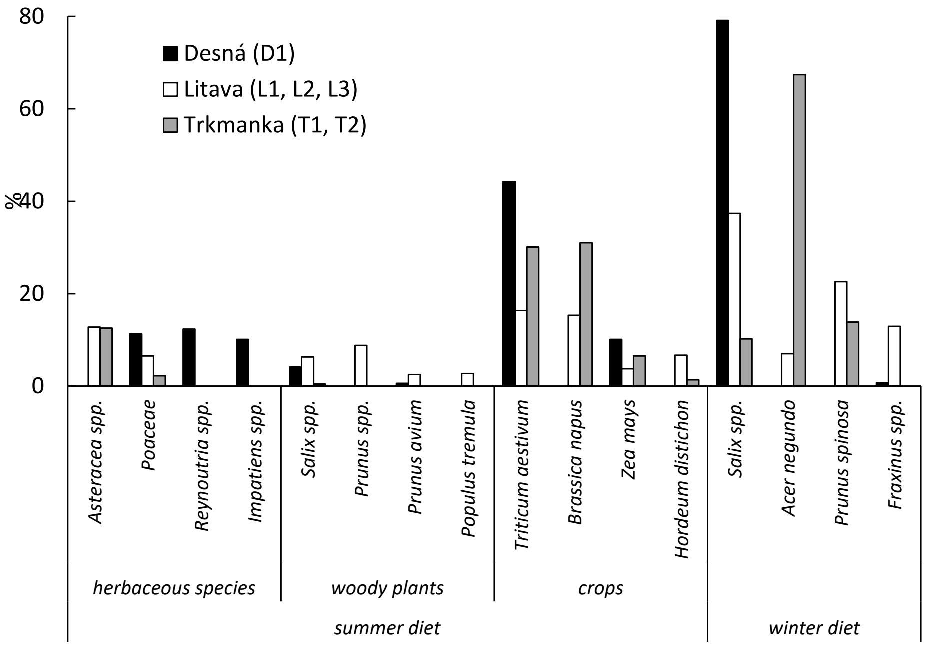
While the most important woody plant species in beaver diet, based on the damage observed, would appear to be willow (*Salix* spp.), European plum (*Prunus domestica*), Boxelder (*Acer negundo*) and European ash (*Fraxinus excelsior*), the frequency at which these occurred at each site differed significantly ($P < 0.001$). *Salix* spp., for example, were ingested 1.8-times more than the mean occurrence at D1, but 3-times less than the mean at T2. At L2, *P. domestica* was the dominant species in the diet, being taken 3.5-times more than the mean, but was taken 5-times less at L3 and 2.6-times less at L1, and not at all at D1. Finally, *A. negundo* was the dominant component in the diet at T2, but taken rarely or was absent at all other sites. Dietary diversity was significantly affected by both the number of components consumed and their balance (Spearman's rho $rs = 0.90$, $n = 5$, $P = 0.37$, in both cases), but not by sample size (Spearman's rho $rs = 0.10$, $n = 5$, $P = 0.873$). Overall, sites L3 and L1 had the most diverse diet, with beavers taking twice as many species than those at D1. The amount of diet diversity in the territory was not affected.

### Woody Plant Preferences

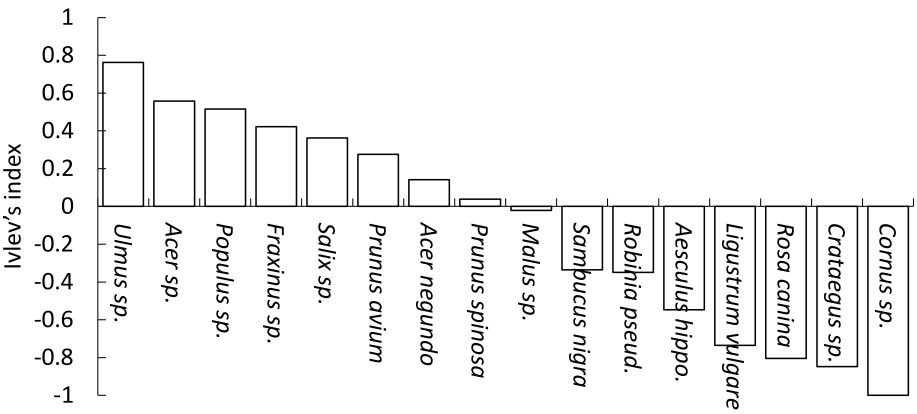
Only *Salix* spp. were clearly taken preferentially at all sites (Ivlev's index $Ie$ = 0.11 - 0.32). In comparison, both *P. domestica* and *A. negundo* were taken preferentially at L2 ($Ie = 0.32$), but were ignored or avoided at all other localities ($Ie$ *P. domestica* = -0.12 to -0.41; *A. negundo* -0.17 to -0.20). Likewise, there was a slight preference for European elder (*Sambucus nigra*) at L2, but the species was clearly avoided at other two basins ($Ie$ = -0.93 and -1.00). Other clearly unpopular species were dog rose (*Rosa canina*) and false acacia (*Robinia pseudoacacia*). Other woody plants formed




3: *The relative importance of dietary classes at the three river basins during the growing season*




4: *Relative frequency of the most important items in the summer and winter diet of Eurasian beaver*




5: *Woody plant species taken preferentially (+1) or avoided (-1) by beavers in winter (all territories combined)*

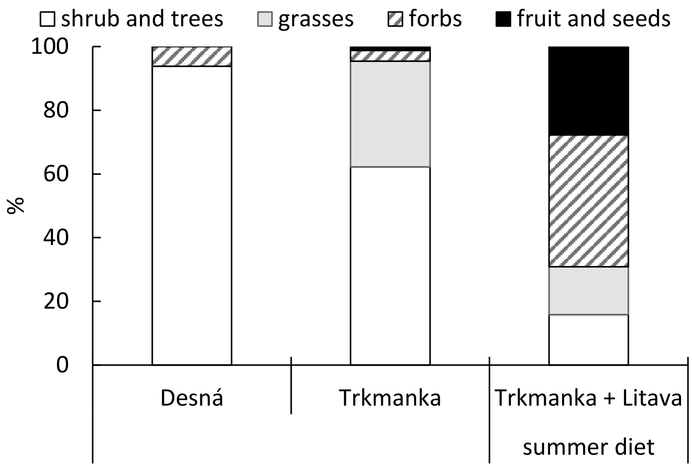
a relatively small proportion of the bank vegetation and preference/avoidance could only be calculated based on a relatively small sample (Fig. 5).

## Comparison of Winter and Summer Diet Based on Observations

Beaver consumed woody species far more often in winter (mean 70%F) than during the spring/summer growing season (mean 10%F), with the six most frequently taken woody species (> 5%F) accounting for > 80%F in both summer and winter and the remaining 20%F consisting of 15 species accounting for 0.1–3.6%F. In winter, the beaver consumed *A. negundo* (5×) and *F. excelsior* (10×) more than in summer but, in summer, consumed *Prunus* sp. (1.5×), common aspen (*Populus tremula*) (3×) and sweet cherry (*Cerasus avium*) (9×) more often than in winter. While more woody species were consumed in winter ($n = 21$) than summer ($n = 13$), the diversity of species consumed was greatest in summer ($H'l = 2.020$ compared with $H'w = 1.836$ in winter). Likewise, the balance of woody species consumed was greater in summer ($J's = 0.603$) than winter ($J'w = 0.787$). There was no correlation between the representation of individual woody species in the diet in summer and winter ($rs = 0.073$, $n = 7$, $P = 0.877$) and the similarity of representation between seasons was relatively low ($SI = 66.9\%$).

## Faecal Analysis

While faecal analysis indicated that woody plants represented an average of 70% volume in the winter diet, grasses were also frequently taken, representing around 28%V. These grasses tended




6: *Differences in beaver diet (faecal analysis %V) in winter at Trkmanka (n = 27) and Desná (n = 10), compared with the summer diet at Trkmanka and Litava combined (n = 5)*

to be grazed more on regularly mowed banks, where green shoots were available throughout the winter. In a number of cases, the grasses included *T. aestivum* sprouts, which remained available to the beaver during mild weather when snow was absent. If grain was being fed to game in the vicinity (up to 5 m from the bank), the beaver also fed on this throughout the winter (*H. distichon* kernels in T2), though they appeared not to actively search out such stations when they were more distant.

Faecal analysis confirmed the differences previously observed between the winter and summer diet, with woody plants accounting for 70%V of diet in winter but just 20%V in summer. In the Trkmanka river basin, where faecal samples were collected over three winters, the results indicated year-on-year variability in the consumption of woody species in winter. Similar variability was also evident between territories in the winter of 2017, with samples from Desná (D1) containing the most tree species (over 90%V) and samples from Trkmanka (T2) containing the fewest woody plants (Fig. 6). At T2, representation of the four main components (shrubs/trees, grasses, forbs, fruit and seeds) differed significantly between winter and summer ($\chi^2 = 6.33$, $df = 1$, $P < 0.05$). Likewise, the representation of woody plants and grasses was significantly different between D1 and T2 ($\chi^2 = 6.35$, $df = 1$, $P < 0.05$ and 19.87, $df = 1$, $P < 0.001$, respectively). In the Litava and Trkmanka river basins, consumption of grasses was significantly higher when using faecal analysis than analysis of damage ($\chi^2 = 4.13$; $df = 1$; $P < 0.05$), with no difference observed in the other components. The importance of agricultural crops indicated by analysis of damage was also confirmed by faecal analysis, with faecal samples at Trkmanka containing 82.5%V of *B. napus* in May ($n = 2$) and 60%V of *Z. mays* kernels in October ($n = 3$).

## DISCUSSION

In sparsely forested landscapes, where the beaver may not cause noticeable damage, it is often overlooked and, as such, little attention has been paid to beaver ecology in such areas. Research into beaver diet in such forest-free landscapes is important for our understanding of variability in beaver eating behaviour. Normally, one would rely on the evidence gained from an analysis of stomach contents; however, in our study, we were unable to obtain sufficient samples as a) beaver hunting is presently banned in the Czech Republic, and b) there were relatively few beavers in our study area, meaning that few carcasses were available. One way around this would be through the collection of fresh faeces, which are usually readily available from herbivores throughout the year (Putman, 1984). However, the beaver usually leaves its droppings in the water and only rarely on land and, despite considerable effort, it was not possible to obtain enough faecal samples for meaningful results over the entire year. For this reason, we used a combined methodology based on the analysis of both beaver droppings and direct evidence of grazing damage at the feeding site.

The beaver is highly adaptable in its choice of diet and the species utilised will vary according to diet availability (Fryxell and Doucet, 1993). In small streams, the beaver is capable of ensuring diet availability by constructing dams to retain water (Pollock, 2014), as was the case on all low-flow streams examined in the Trkmanka and Litava river basins. In some cases, particularly near temporary diet sources (e.g. ripening grain), the beaver built smaller, temporary dams; however, in flat terrain, the length of such reservoirs could be up to a kilometre long.

While beaver diet in the small agricultural streams in this study did not differ fundamentally from that in other areas of the temperate zone (Jackowiak *et al*., 2020; Vorel *et al*., 2015; Krojerová-Prokešová *et al*., 2010), it did show temporal and spatial variability, largely related to scattered or temporary food resources. Woody plant species, for example, tended to dominate in the winter diet, while herbs dominated in the summer diet. Furthermore, agricultural crops were a significant feature of beaver diet close to fields. This component is rarely consumed by the beaver elsewhere as it is usually not available within reach of its burrow; however, when they are available, they can form an important part of the diet (see also Mikulka *et al*., 2020).

Many factors affect a beaver's choice of tree species (Donkor and Fryxell, 1999; Jenkins 1980), such as changes in the nutrient content of bark over the year, distance from the bank and trunk diameter (Belovsky, 1984). For example, while *Salix* spp. are almost always the most consumed woody plant species in Europe (Haarberg and Rosell, 2006; Jenkins, 1975; Jenkins, 1980; Nolet *et al.,* 1994), the proportion of *Salix* spp. taken in our study fluctuated widely, depending on the diversity of woody plant species available. In summer, sites in the Litava river basin provided optimal feeding conditions, with a wide species range consumed and a high balance, while the opposite was true in the Desná river basin. In contrast, while the diversity of the riparian herbaceous layer was rather similar in all three areas, beavers at Desná consumed the lowest range of herbs but the balance was highest. This raises the question as to whether the high proportion of agricultural crops in the diet at Desná was the result of poor diet availability along the banks or the easy availability of such crops, the fields being separated from the river by just a narrow strip (3–5 m) of bank vegetation.

In general, agricultural landscapes do not provide suitable habitat for beavers due to the lack of woody plants (Halley and Rossell, 2002; Zwolicki *et al*., 2018). This also applies to the Morava river basin, where beavers mainly colonise larger streams with sufficiently developed woody plant stands along the banks (Mikulka, 2021 unpublished). On smaller streams, diet availability varies from territory to territory, though it may be of sufficient quality that the beaver can remain at a site for many years. Streams lacking enough woody plant material tend to remain uninhabited or are used only temporarily in the summer, when it is able to feed on herbaceous vegetation (e.g. site T1). Diet availability in the territories examined in this study was largely influenced by the width of bank vegetation, which was < 5 m wide in some places, and the area beyond the bank vegetation, which usually consisted of fields with crops that had already been harvested at the time of diet availability mapping in mid-summer (note the relatively small e1 cover in Fig. 3).

Overall, the composition of diet available along the banks tended to depend on bankside management rather than geographical location. For example, while territories L3 and L2 were both close by on the same stream, the diet availabile was only marginally similar. In this case, flow modifications last took place at L2 almost one hundred years previously, with no interventions in the development of bank vegetation since that time, while modifications at L3 took place just 40 years previously and the banks have been partially managed ever since. In some cases, streams in the agricultural landscape have been completely stripped of woody vegetation as a measure to protect the surrounding land from flooding, a clear case where bank maintenance has had a significant effect on the quality of diet available to beavers. As a further measure to reduce flood risk in agricultural areas, beaver dams are usually removed from small streams, further limiting the occurrence of beavers.

Beavers will generally choose diet items that are of sufficient quality and abundance and that occur as close to the banks of its home watercourse as possible. In accordance with optimal diet theory, the beaver's diet will consist of items that provide as much energy as possible for the lowest cost (Belovski, 1984). According to Vorel *et al*. (2015), beavers in the Czech Republic prefer *Salix* spp. and *Populus* spp., regardless of the locality or stand species composition, with other species being of little importance in the diet. Vorel's conclusions, however, were based on a study of 110 beaver territories from five different areas, with data from more than 20 territories (on average) included in each sample. This use of pooled data fails to capture variation in beaver feeding behaviour across territories. In our own family-based (territorial) study, diet composition and preference for woody plant species depended a great deal on local species availability, which could vary significantly within each territory year-to-year. Our results suggest that, on small streams, the beaver behaves more like an opportunist, utilising diet resources and grazing tree species that it might otherwise neglect at other localities, depending on the local situation. This adaptability in diet selection has also been noted in several other areas (e.g. Wazna *et al*., 2019). Furthermore, if diet availability or quality around the burrow deteriorates to such an extent that energy gained is disproportionate to the energy expended on searching and processing the diet, the beaver may gradually change its diet selection preference or move to another site. As an example, we observed a significant change in diet composition over the year at T2, with the beaver consuming all woody plants near its original burrow (mostly *A. negundo*) then moving to a new site 300 m away, following which *P. domestica* became more prominent in the diet as this was the dominant species in the new habitat.

An important outcome of this study has been the insights gained into the variability of beaver eating behaviour under different conditions, particularly as regards its potential conflict role with human activities. For example, we found no evidence of beaver damage/foraging on economically important woody plant species in the open countryside; instead, it mostly consumed unimportant species, with a high proportion of the diet consisting of woody plants from the shrub layer. In part, this was due to the relative scarcity of commercial species in the agricultural landscape, as well as the lower abundance of beavers than in more forested areas, where commercial tree species often dominate. One advantage of the low number of beavers is that felled trees in areas with well-developed vegetation were able to regenerate. On the other hand, in areas where beavers remained for some time, they were able to temporarily alter the local woody plant species composition. At T2, for example, the invasive, self-seeding tree, *A. negundo* was the dominant diet item in beaver diet for one winter. After just two months, all *A. negundo* growing along the stream bank had been felled up to 300 m from the burrow, allowing other native species to regenerate. Interestingly, agricultural crops formed a significant proportion of the diet during the growing season, and beavers were often recorded moving to sites/fields beyond the bankside zone with its 'preferred' species in order to make use of this resource (see also Mikulka *et al.*, 2019). Indeed, it is quite likely that such crops are an important factor allowing beavers to survive in agricultural landscapes in the absence of suitable woody species in riparian bank vegetation.

## CONCLUSION

Small streams in agricultural landscapes tend to be suboptimal for beavers in terms of diet availability as woody tree/shrub species are usually limited to narrow strips along the bankside and the number of species, particularly preferred species such as *Salix* and *Populus*, may be limited. As such, the beaver may be forced to adopt a more opportunistic foraging strategy, making use of seasonally abundant or less preferred species over the course of the year, particularly over the unfavourable winter period.

In winter, we found beaver diet to be dominated by woody plants, though green herbs also formed a significant proportion (30%V). Where *Salix* spp. and *Populus* spp. were rare or absent in the bank vegetation, other, less preferred woody plant species, such as *Prunus* sp. or *A. negundo*, became more dominant in the diet. In summer, however, beaver diet was dominated by herbs, with woody plants representing just a small proportion of the diet (10%V). Agricultural crops were an important dietary element on small streams in all territories examined, accounting for an average of 57%V of the summer diet.

Our results highlight the need for a greater understanding of variation in beaver diet and the need to monitor the specific conditions in each territory when evaluating the importance of individual woody plant species for beaver diet and when estimating the potential for damage to commercial tree species.

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## APPENDIXES

Appendix 1: *Food availability at individual study sites*

| | | Šumperk (D1) | Telnice (L1) | Újezd (L2) | Žatčany (L3) | Krumvíř (T1) | Terezín (T2) |
|---|---|---|---|---|---|---|---|
| Growing herbs (%) | *Poaceae* spp. | 17.3 | | 63.1 | 51.5 | 33.6 | 65.1 |
| | *Asteracea* spp. | 0.0 | | 26.2 | 37.4 | 11.0 | 13.3 |
| | *Urtica* spp. | 37.5 | | 8.2 | 4.6 | 8.9 | 1.8 |
| | *Ph. australis* | 0.0 | | 1.6 | 0.0 | 43.5 | 4.8 |
| | *Dicotyledoneae* spp. | 6.2 | | 0.9 | 6.5 | 3.0 | 15.0 |
| | *Impatiens* spp. | 19.8 | | 0.0 | 0.0 | 0.0 | 0.0 |
| | *Reynoutria* spp. | 19.2 | | 0.0 | 0.0 | 0.0 | 0.0 |
| Woody plants (%) | *Salix* spp. | 10.32 | 23.91 | 8.97 | 33.96 | | |
| | *Prunus spinosa* | 8.02 | 7.01 | 29.57 | 6.70 | | 36.76 |
| | *Sambucus nigra* | 15.94 | 0.78 | 14.97 | 22.95 | | 6.71 |
| | *Acer negundo* | 0.38 | 15.31 | 2.13 | 4.69 | | 36.18 |
| | *Alnus glutinosa* | 17.46 | | 3.41 | | | |
| | *Rosa canina* | 7.18 | 7.32 | 15.82 | 8.39 | | 5.41 |
| | *Populus* spp. | 3.97 | 9.17 | | 8.91 | | 12.06 |
| | *Fraxinus* spp. | 7.26 | 9.35 | 2.01 | | | |
| | *Crataegus* spp. | 6.73 | 0.37 | 12.07 | 0.47 | | |
| | *Cornus* sp. | 5.55 | 9.26 | 0.94 | | | 0.84 |
| | *Robinia pseudoacacia* | 0.94 | 8.55 | 2.31 | 0.41 | | |
| | *Aesculus hyppocastanus* | 0.14 | 0.66 | 8.51 | | | |
| | *Ligustrum vulgare* | 0.59 | 1.06 | 3.20 | | | 0.96 |
| | *Tilia* sp. | 5.51 | | | | | |
| | *Prunus avium* | 0.13 | 1.24 | 0.30 | 3.36 | | |
| | *Prunus padus* | 4.06 | | | | | |
| | Other | 5.96 | 6.54 | 3.64 | 1.65 | | 1.09 |
| Vegetation cover in summer (%) | e1 | 44.65 | 68.21 | 73.85 | 87.00 | 38.50 | 70.57 |
| | e2 | 30.75 | 34.10 | 33.08 | 20.17 | 1.00 | 7.63 |
| | e3 | 49.60 | 25.15 | 22.88 | 22.00 | 4.50 | 17.00 |

Appendix 2: *Relative frequency (%F) of items in the diet of Eurasian beavers during the growing season in three agricultural landscapes*

| | Relative frequency | | | |
|---|---|---|---|---|
| Items | Desná | Litava | Trkmanka | Mean |
| ***Echinops sphaerocephalus*** | 0.00 | 0.21 | 0.00 | 0.07 |
| ***Aegopodium*** | 0.10 | **2.94** | 0.00 | 1.01 |
| ***Lamium* spp.** | 0.00 | **3.77** | 0.22 | 1.33 |
| ***Asteracea* spp.** | 0.00 | **12.79** | **12.58** | **8.46** |
| ***Anthriscus sylvestris*** | 0.00 | 1.47 | 0.00 | 0.49 |
| ***Urtica dioica*** | **3.29** | 0.84 | 0.22 | 1.45 |
| ***Geum* spp.** | 0.00 | 1.68 | 0.00 | 0.56 |
| ***Amaranthus retroflexus*** | 0.00 | 0.42 | 0.00 | 0.14 |

| | Relative frequency | | | |
|---|---|---|---|---|
| Items | Desná | Litava | Trkmanka | Mean |
| *Cirsium* spp. | 0.00 | 0.21 | 0.00 | 0.07 |
| *Helianthus tuberosus* | 0.00 | 1.05 | 0.00 | 0.35 |
| Poaceae | **11.31** | **6.50** | **2.25** | **6.69** |
| *Rumex* spp. | 0.00 | 0.00 | 0.22 | 0.07 |
| *Ranunnculus* spp. | 0.00 | 0.00 | 0.45 | 0.15 |
| *Rubus fruticosus* | 0.00 | 0.00 | 1.80 | 0.60 |
| *Lactuca serriola* | 0.00 | 0.00 | **2.25** | 0.75 |
| *Papaver* spp. | 0.00 | 0.00 | 0.67 | 0.22 |
| *Chenopodium* spp. | 0.00 | 0.00 | **2.47** | 0.82 |
| *Galium* spp. | 0.86 | 1.89 | 0.89 | 1.21 |
| *Phragmites australis* | 0.65 | 0.00 | 0.45 | 0.37 |
| *Impatiens* sp | **10.09** | 0.00 | 0.00 | 3.36 |
| *Reynoutria* sp. | **12.34** | 0.00 | 0.00 | 4.11 |
| Free growing herbs (total) | **38.63** | **33.75** | **24.48** | **32.29** |
| *Crataegus* sp. | 0.00 | 0.21 | 0.00 | 0.07 |
| *Malus* sp. | 0.00 | 0.84 | 0.00 | 0.28 |
| *Acer negundo* | 0.00 | 0.84 | 0.45 | 0.43 |
| *Fraxinus* sp. | 0.00 | 0.21 | 0.00 | 0.07 |
| *Acer pseudoplatanus* | 0.00 | 0.42 | 0.00 | 0.14 |
| *Populus tremula* | 0.00 | 2.73 | 0.00 | 0.91 |
| *Prunus* sp. | 0.00 | 8.81 | 0.00 | 2.94 |
| *Rosa canina* | 0.00 | 0.42 | 0.00 | 0.14 |
| *Prunus avium* | 0.59 | 2.52 | 0.00 | 1.04 |
| *Salix* spp. | 4.16 | 6.29 | 0.45 | 3.63 |
| *Populus* sp. | 0.71 | 0.00 | 0.00 | 0.24 |
| *Prunus padus* | 0.12 | 0.00 | 0.00 | 0.04 |
| *Alnus* sp. | 1.43 | 0.00 | 0.00 | 0.48 |
| Woody plants (total) | **7.01** | **23.27** | **0.90** | **10.39** |
| *Hordeum distichon* | 0.00 | 6.71 | 1.35 | 2.69 |
| *Zea mays* | 10.10 | 3.77 | 6.52 | 6.80 |
| *Avena sativa* | 0.00 | 0.42 | 4.72 | 1.71 |
| *Triticum aestivum* | 44.26 | 16.35 | 30.11 | 30.24 |
| *Brassica napus* | 0.00 | 15.30 | 31.02 | 15.44 |
| *Helianthus annuus* | 0.00 | 0.42 | 0.90 | 0.44 |
| Crops (total) | **54.36** | **42.98** | **74.62** | **57.32** |
| Total | 100.00 | 100.00 | 100.00 | 100.00 |