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Vital rates and their multidecadal trends in the fir-beech old-growth forest of Badínsky prales

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Abstract: The study aimed to quantify annual mortality and recruitment rates on permanent research plots in the Badínsky prales old-growth forest. The data measured in four stands originate from six censuses, which together cover a 48-year period. The mean annual mortality rate reached 4.2% (*DBH* > 2 cm) or 2.3% (*DBH* > 8 cm). The mortality peaked in the first part of the observation period, probably indicating an intermediate disturbance activity, and the subsequent declining trend led to minimum annual mortality during the last 20 years. We found substantially higher fir mortality in comparison with beech, primarily during the first decades of the measurement period. Among three size categories, the stems with *DBH* 2–8 cm showed the highest mortality rate. We detected the minimum fir recruitment rate throughout the observation period; on the other hand, the beech recruitment rate was relatively high responding to the open canopy. Standing and lying deadwood volumes indicated similar trends like mortality did, and high values of fir standing deadwood observed during the first decades can signify that a relatively high proportion of mortality was related to the fir decline caused by air pollution.

Keywords: beech; deadwood; fir; mortality; old-growth forests; recruitment

The dynamics of beech or mixed-beech old-growth forests is generally viewed as continuous opening and closing of relatively small canopy gaps, which are typically created by the death of single or several trees (Kucbel et al. 2010; Feldmann et al. 2018). Besides the characteristic small-scale gap dynamics, the less common intermediate disturbances (Nagel et al. 2014; Frankovič et al. 2021) can affect the tree demography to a large extent. In temperate old-growth forests in Europe and North America, Woods et al. (2021) found considerable variation of mortality rate, which they attributed to larger disturbances and non-equilibrium dynamics of these forests. Impacts of higher mortality open larger gaps which create substantially different conditions (Muscolo et al. 2014) and release less shade-tolerant regeneration than smaller gaps (Nagel et al. 2014; Jaloviar et al. 2020).

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Even though the higher mortality rate has a considerable impact in the long run, this type of dynamics is rather infrequent in beech old-growth forests.

However, the climate change is expected to alter patterns of mortality and recruitment in forests worldwide (McDowell et al. 2020), whereas even minimum changes in mortality can have a significant impact on resulting forest dynamics (McMahon et al. 2019). To capture deviations from what has been taken as a standard we need the long-term data. The studies covering the long-term variability of vital rates are therefore essential (Nagel et al. 2021; Woods et al. 2021) and can shed light on the dynamics of beech old-growth forests in the changing environment.

We attempted to use the data covering 48 years to explore demography and its connection with changes in species composition in the National Nature Reserve (NNR) Badínsky prales (Šumichrast et al. 2020). Since the data needed to calculate vital rates were less robust, we also incorporated the volume of standing and lying deadwood measured on larger plots into this study. The main aim of our research was to analyse the annual mortality and recruitment rates on four permanent plots in the Badínsky prales reserve. We explored their changes through time and identified differences between two main species and diameter categories.

MATERIAL AND METHODS

The study was conducted in a fir-beech old-growth forest in the NNR Badínsky prales (Kremnické vrchy Mts., Slovakia, 48.6836°N, 19.0515°E), which covers 30.03 ha. The reserve is situated at the altitude between 700 m a.s.l. and 850 m a.s.l. on the NW to NE facing slopes. The mean annual air temperature is 5.3–5.8 °C, and annual precipitation ranges between 800 mm and 1 000 mm. The main soil types in the study area are Cambisols developed on andesite conglomerates covered by lava flows of pyroxenic andesite with breccias (Bublinec, Pichler 2001). Except the dominant beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.), there is an admixture of other tree species including sycamore (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.) and elm (*Ulmus montana* With.). Since 1970, the Department of Silviculture (Technical University in Zvolen) has been conducting research on four rectangular permanent research plots (0.5 ha each). We have included data from six measurements from the last 52 years (1970, 1977, 1986, 1996, 2007 and 2018) in this study.

Vital rates, i.e. the annual mortality rate (m_a) and annual recruitment rate (r_{af}), were quantified using data from four transects of various size (500–1 000 m^2), where coordinates of individual trees ($DBH \geq 2$ cm) were registered, and the history of individual trees could be identified. The annual mortality rate was calculated according to the following Equation (1) (Sheil et al. 1995):

$$m_a = 1 - \left(\frac{N_{ST}}{N_0} \right)^{\frac{1}{T}} \tag{1}$$

where:

N_0 – number of trees at time 0 (the initial census);

N_{ST} – number of trees at time T that were present in the initial census;

T – time of a census period.

and the Equation (2) of the annual recruitment rate was (Sheil 1998; Kohyama et al. 2018):

$$r_{af} = 1 - \left(\frac{N_{ST}}{N_T} \right)^{\frac{1}{T}} \tag{2}$$

where:

N_T – number of trees at time T (the final census).

Next, we considered biases resulting from varying census interval lengths and heterogeneous population, specifically the changing frequency bias and survivorship bias (Kohyama et al. 2018). We calculated the vital rates separately for beech and fir (frequencies of other tree species were not sufficient) and for three diameter classes (2–8 cm, 8–30 cm, > 30 cm). To calculate unbiased total and species-specific means of vital rates, we used the correction approach mentioned by Kohyama et al. (2018).

Since the data from transects might be insufficient to represent demographic processes at the whole-plot scale, we compared them with the deadwood dynamics. Deadwood volume was divided into four categories – standing deadwood (snags) and three decay stages of lying deadwood (logs) which were determined according to Korpeľ (1989). Snags and logs in the first decay stage can be a sign of recent mortality and the other two decay stages can roughly approximate former mortality rates. We expected that the changes in the deadwood volume of tree species and these four categories can indicate demography trends on a larger scale.

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RESULTS AND DISCUSSION

The analysis of vital rates confirmed their considerable temporal variability (Figure 1). Pooling all species and size classes, annual mortality and recruitment rates varied between 0.9–4.3% and 0.29–16.14%, respectively. In the case of trees with *DBH* > 8 cm, these rates varied between 0.41–4.73% and 1.23–3.93%. We also observed the decreasing trend in the annual mortality of trees with *DBH* > 8 cm and in the last two decades we recorded minimum values in this category (ca. 0.4%). The average of the total annual mortality rate was 3.0% (*DBH* > 2 cm) or 2.1% (*DBH* > 8 cm). In comparison with the study from Slovenian mixed-beech old-growth forests, where mean annual mortality ranged from 0.6% to 2.1% (*DBH* > 5 cm; Nagel et al. 2021), or the comprehensive study involving temperate old-growth forests in Europe and North America (Woods et al. 2021), mean annual mortality on permanent plots in the Badínsky prales Reserve reached relatively high values. The mean annual recruitment rate reaching in our study 4.2% (*DBH* > 2 cm) or 2.3% (*DBH* > 8 cm) was also in the upper quartile of the values found in Slovenian old-growth forests (Nagel et al. 2021). These results show that forest stands in Badínsky prales have undergone significant demographic changes in the last 48 years.

The elevated mortality rate during the first decades could indicate the occurrence of intermediate disturbance events. Depending on the diameter threshold (2 cm or 8 cm), the annual mortality rate prevailed over recruitment until 1986 or 1996, respectively (Figure 1). The pronounced mortality corresponds with the increased disturbance activity in the 1980s reported by Kucbel et al. (2010). A subsequent increase in the recruitment was probably a consequence of the mortality releasing a higher amount of regeneration. The significance of intermediate-severity disturbances in terms of long-term demographic processes was previously mentioned by other authors (Nagel et al. 2021; Woods et al. 2021), and this type of disturbances was also evident from studies on disturbance dynamics in mixed beech old-growth forests in Europe (Firm et al. 2009; Nagel et al. 2014; Frankovič et al. 2021). The lower frequency of these events generally hinders their detection in mortality studies with short observation period resulting in underestimated mortality rates (Woods et al. 2021). Although in our case the presence of intermediate disturbance event is probable [background mortality rate in mixed beech old-growth forests is approximately 1% (Nagel et al. 2021)], we cannot exactly disentangle it from the general mortality rate without recording the mortality mode (standing dead trees vs snapping/uprooting).

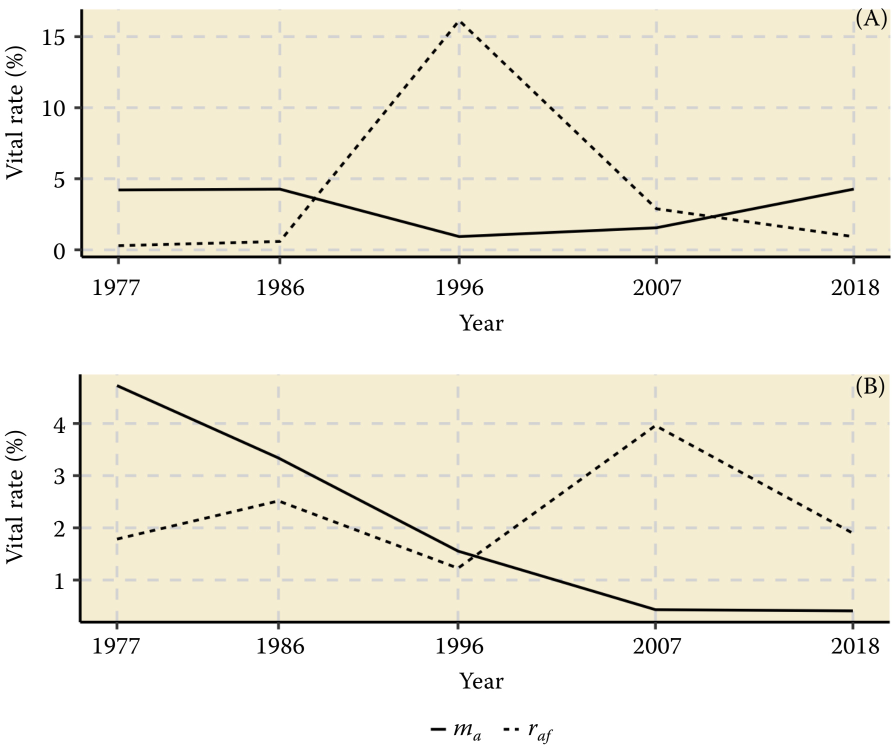

Figure 1. Mean vital rates calculated for diameter thresholds (A) *DBH* > 2 cm and (B) *DBH* > 8 cm

m_a – annual mortality rate; r_{af} – annual recruitment rate

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We registered substantial differences in the vital rates between beech and fir (Figure 2). Throughout the observation period, the annual mortality rate of beech did not exceed 5% or 3% depending on the diameter threshold. On the other hand, the annual mortality of fir reached significantly higher values in the first two decades (8.9–9.3% or 5.8–10.8%) and then it gradually decreased. The relatively high fir mortality in the 1970s and 1980s overlapped with the increased air pollution causing the fir decline in that period (Elling et al. 2009). A higher mortality rate of fir compared to beech was also detected in Slovenian old-growth forests (Nagel et al. 2021).

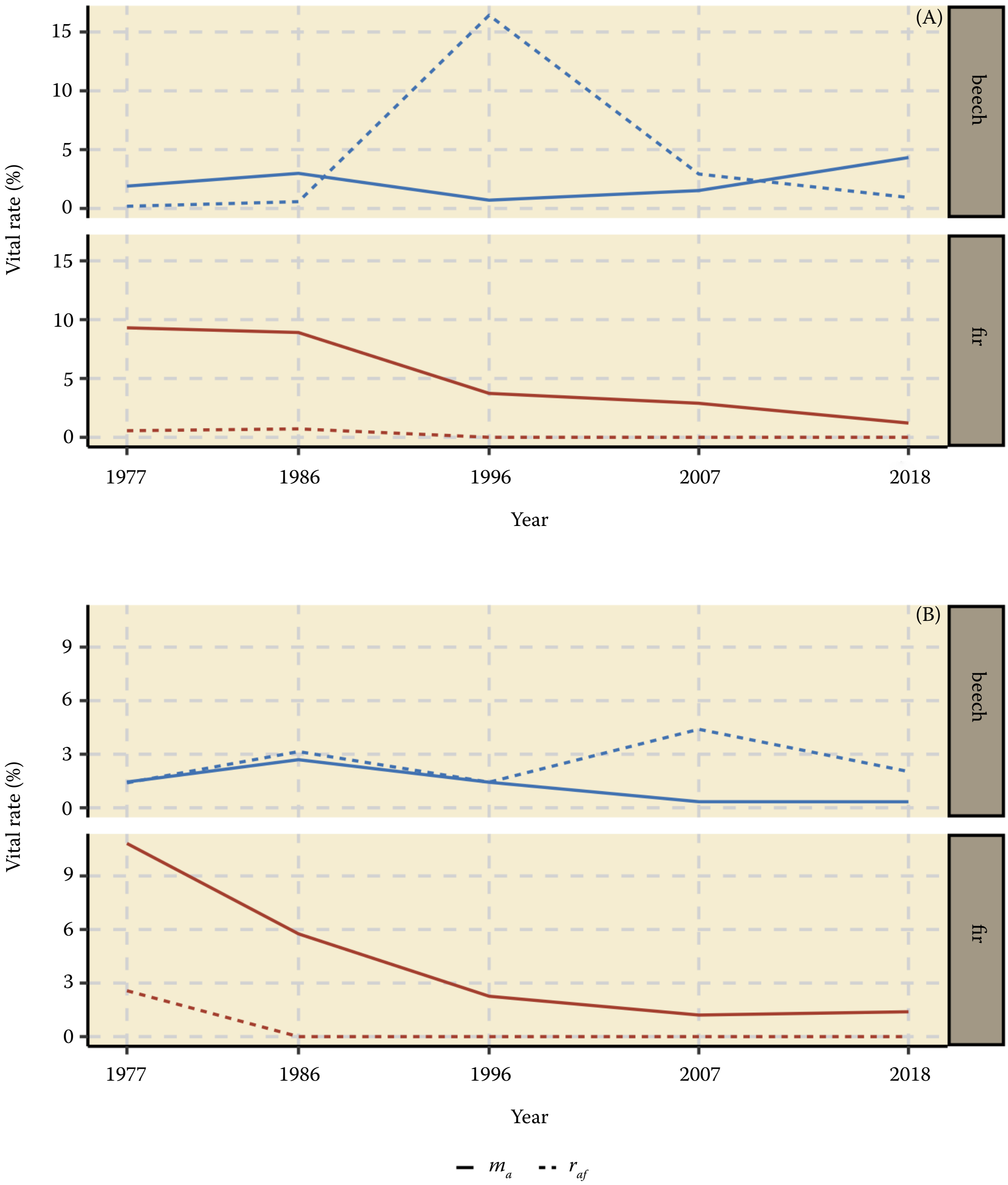

Figure 2. Vital rates of beech and fir calculated for diameter thresholds (A) *DBH* > 2 cm and (B) *DBH* > 8 cm

m_a – annual mortality rate; r_{af} –annual recruitment rate

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The annual recruitment rate of fir reached significantly lower values than that of beech (Figure 2). Unlike the fir, beech recruitment was able to flexibly respond to the higher mortality in preceding decades. In fact, we noticed virtually no recruitment of fir during the entire observation period. The fir regeneration was probably affected primarily by ungulates, whose artificially elevated populations in Badínsky prales have been reported since the beginning of the observation (Korpeľ 1958; Saniga et al. 2012). Ungulate populations inhibiting fir recruitment were reported from various parts of Europe (Vrška et al. 2009; Diaci et al. 2011; Nagel et al. 2021), and with other anthropogenic factors they led to considerable changes of the tree species composition in European old-growth forests (Diaci et al. 2011; Šumichrast et al. 2020; Diaci et al. 2022).

The annual mortality rate changed also depending on a tree dimension expressed by diameter classes (Figure 3), although these differences were not confirmed as significant. Within all three categories, fir mortality was evidently higher than that of beech during most of the observation period; however, the last decades were probably affected by a relatively small number of remaining fir trees (Table 1). Regardless of the tree species, the lowest layer (< 8 cm) mostly had the highest annual mortality throughout the entire observation period (beech 0.4–5.4%; fir 0–12.7%), and the canopy layer (> 30 cm) generally reached slightly higher values than the middle layer (8–30 cm). Higher values of mortality in the lowest category were presumably caused by stronger competitive conditions characteristic of this category, and also by overbrowsing. Nagel et al. (2021) also found the higher annual mortality for subcanopy trees in comparison with canopy trees (> 30 cm) in Slovenian old-growth forests. In temperate old-growth forests in Europe and North America, mor-

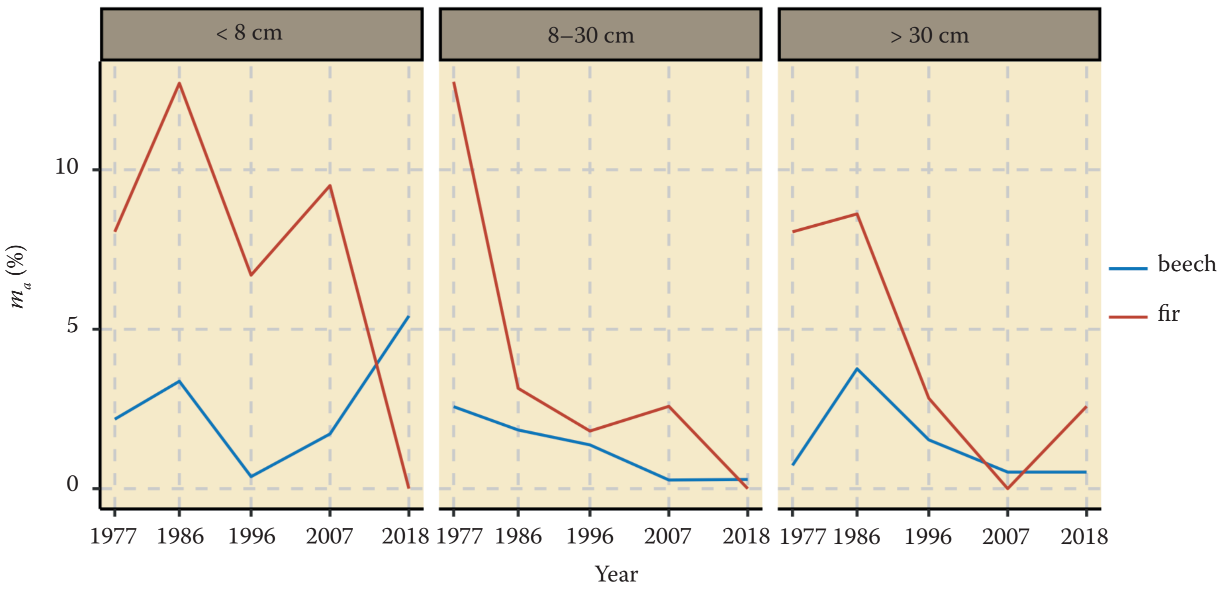

Figure 3. The annual mortality rate (m_a) of beech and fir divided into three diameter classes

Table 1. Number of fir and beech stems in 5 censuses (divided into three diameter classes)

Census	Beech			Fir			All		
	< 8 cm	8–30 cm	> 30 cm	< 8 cm	8–30 cm	> 30 cm	< 8 cm	8–30 cm	> 30 cm
1970–1977	56	12	20	27	13	9	83	25	29
1977–1986	49	26	24	17	8	9	66	34	33
1986–1996	27	31	21	6	6	4	33	37	25
1996–2007	375	34	18	3	4	4	378	38	22
2007–2018	417	64	18	1	3	4	418	67	22

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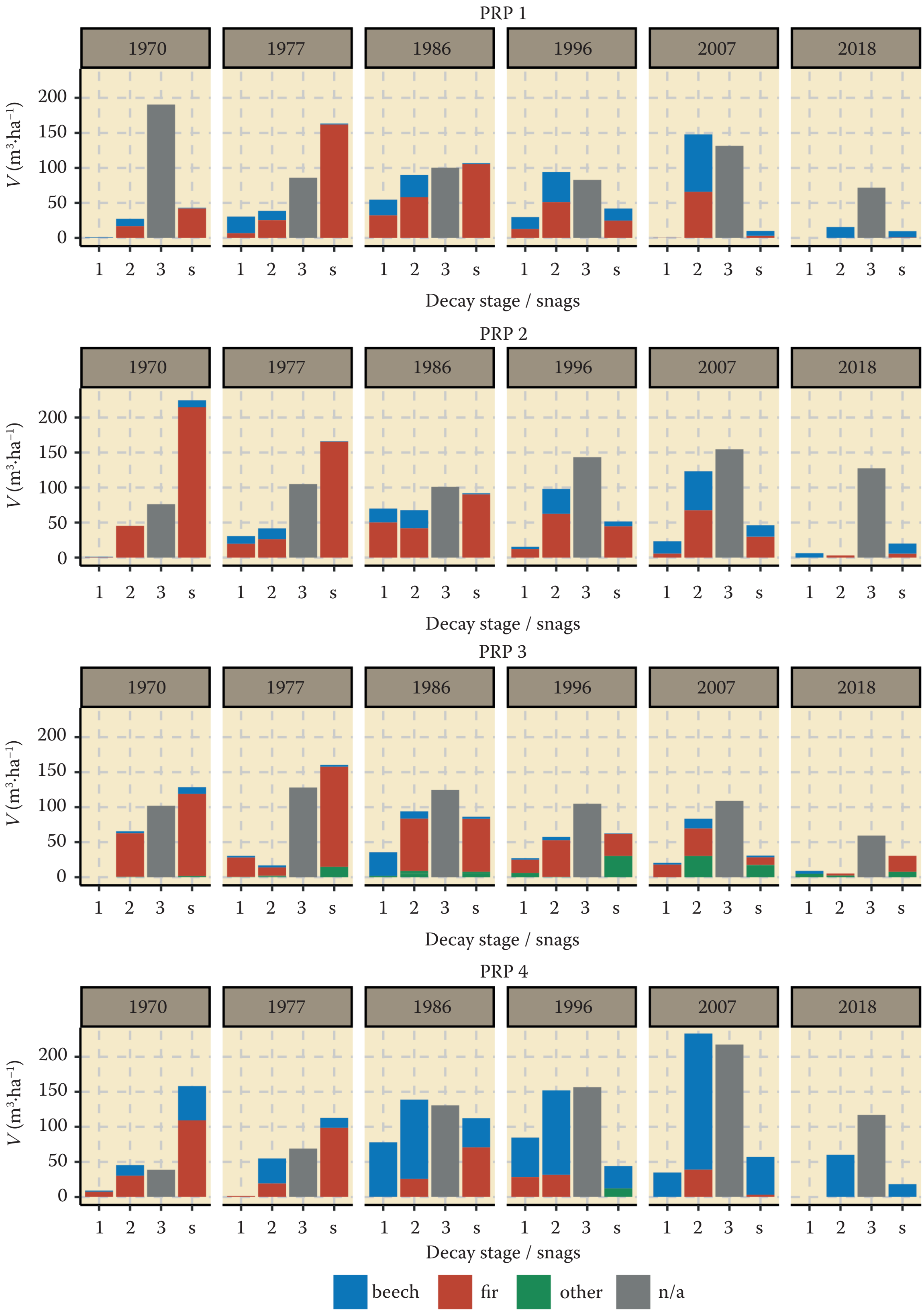

Figure 4. Volume (V) of standing and lying deadwood on four permanent research plots (PRP) between 1970–2018

1, 2, 3 – three decay stages; s – snags; n/a – not available

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tality was generally higher in the lowest layer and in the largest trees (Woods et al. 2021).

We attempted to employ the data on standing and lying deadwood from entire research plots (Figure 4) and compare them with the detected mortality rate, as deadwood can approximately indicate the history of mortality. From 1970 to 2018, the volume of total deadwood on individual research plots fluctuated between 97 $m^3 \cdot ha^{-1}$ and 543 $m^3 \cdot ha^{-1}$. The overall mean value calculated from four research plots reached the maximum in 1986 (370 $m^3 \cdot ha^{-1}$), whereas the minimum mean value was recorded in 2018 (138 $m^3 \cdot ha^{-1}$). The minimum total deadwood volume in 2018 was underlined by an extremely low volume of standing deadwood and logs in the first and second decay class. The volume of standing deadwood peaked between 1970 and 1977, and then it gradually decreased on each plot. We also found an apparent predominance of fir within standing deadwood in the first half of observation period and a subsequent decrease in the fir deadwood share.

The abovementioned trends of deadwood volume can be viewed as a rough confirmation of the investigated annual mortality rates. The maximum mean deadwood volume in 1986 could reflect the high annual mortality rate detected before that year. Next, the distinctively low deadwood volume in 2018 can be viewed as the result of the continually declining annual mortality rate and its relatively low values in the last two decades. A slightly delayed decrease in deadwood volume is a consequence of the decomposition time which can vary due to environmental conditions (Stokland et al. 2012), deadwood dimension (Herrman et al. 2015) or tree species (Weedon et al. 2009; Seibold et al. 2021). The dominant proportion of fir deadwood, primarily in the first part of the observation period, was caused by pronounced fir annual mortality recorded until 1986. This also overlapped with the most significant decrease of fir in the species composition in the Badínsky prales Reserve reported by Šumichrast et al. (2020). A relatively high proportion of fir deadwood in later measurements could be the result of longer decay times of coniferous deadwood (Weedon et al. 2009; Seibold et al. 2021). The high amount of fir standing deadwood in the 1970s and 1980s could corroborate the assumption that the air pollution was a key mortality factor which largely contributed to fir decline in the corresponding time (Elling et al. 2009; Dobrowolska et al. 2017). Thus, the dynamics of the deadwood volume provided an important insight into demography and made the results obtained from the transect data more relevant.

CONCLUSION

The analysis of the vital rates revealed their substantial changes during the last five decades. The deadwood volume dynamics showed trends similar to annual mortality and helped to understand the results better. High annual mortality in the first part of the observation period suggests the occurrence of an intermediate disturbance activity and was probably the result of increased natural and anthropogenic disturbances. Subsequently, the open canopy released considerable amounts of beech recruitment, but fir recruitment failed. The deficiency of fir recruitment was presumably caused by overbrowsing. The results suggest that the vital rates in the NNR Badínsky prales have been largely affected by anthropogenic factors.

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The factors limiting the venison market in the Czech Republic and options for limiting their impact on the forestry

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Abstract: This article focuses on the development possibilities of the venison market in the Czech Republic. The main factors affecting the primary game market were investigated, both production limitations on the side of the hunters and on the side of the game production purchase prices. These factors were analysed in the context of the consumer prices of general meat production and the purchase prices of common meat (beef, pork). Furthermore, the size of the total game market was estimated, taking into account the export and import of this commodity. The potential venison market size for the Czech Republic was also established in the study. The gap between the development of the market consumer prices and purchase prices of the venison was analysed. The conducted research further revealed that the respondents do not perceive a relationship between the production of venison and the protection of forest ecosystems. With few exceptions, they do not realise that by buying and consuming venison, they can contribute to the support of forestry. Furthermore, the perception of the role of the forest environment in relation to game meat by the public does not correspond to the need to regulate the game density to limit damage to forest stands. The results of this research are recommendations which mainly consist in expanding the offer of the primary production to products significantly closer to the consumer market (moving from a producer market to a consumer market), and the implementation of activation campaigns (tastings, presentations of opinion makers). At the same time, our work revealed the need for further development, and by increasing the value for the customer who, with the appropriate marketing strategy, can perceive this product as a premium organic food through which they contribute to sustainable forest management.

Keywords: Czech venison; game meat; game density regulation; non-timber forest production; venison marketing

In the Czech Republic (CR), forests are traditionally (Papánek 1972; Šišák et al. 2006) and legislatively by the Forest Act (Act 289/1995 Coll.) characterised according to their functions – production and

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non-production ones. It was only at the beginning of the new millennium when the term ecosystem service (ES) began to be used in Czech forestry, first as a synonym for functions, and later (with the development of ES classifications) specifically. The issue of non-production, especially non-wood production (NTFP) has been given a lot of attention in the CR (Šišák et al. 2016; Riedl et al. 2019b). However, these were mostly products related to gathering and harvesting (mushrooms and other forest fruits). Hunting is assessed in view of social importance (Krokowska-Paluszak et al. 2020; Frouz, Frouzová 2022) or in relation to forest protection (Stewart 2001; Apollonio et al. 2010), while a land's own game (as part of the NTFP) is given little attention. Game production can be classified as a supply activity within the framework of forest ecosystem services (MEA 2005), where the game production segment consists of the identification, commercialisation and reliable management of the related opportunities. Similarly, more recent classifications include game production among supply services, according to the TEEB (The Economics of Ecosystems and Biodiversity) in the subcategory of the food category, in the CICES (Common International Classification of Ecosystem Services) as a subcategory of the biomass production intended for nutrition (Maes et al. 2013).

More and more attention is also being paid to NTFPs due to the search for additional income from forestry and food resources (Olaussen, Mysterud 2012). The meaning and possibilities of using NTFPs differ significantly in individual countries. The importance of game within the NTFP is also evidenced by the fact that its value within the EU-28 amounts to 317 million EUR (UNECE 2018).

Venison is considered as a high-quality source of nutritional elements not only due to the beneficial high protein content and protein composition (Okuskhanova et al. 2017), but also for its antioxidant activity. This can be attributed to the specific peptides (APVPH I, APVPH II) detected in the enzymatic hydrolysates of venison protein, as suggested by the study of Kim et al. (2009). Deutz (2012) or Bureš et al. (2018) stipulate that venison is characteristic for its lower fat content compared to beef, pork, or lamb. Also, the nutritional value is considered high due to its high protein content, high amounts of minerals, vitamins, trace elements, and unsaturated fatty acids. In developed countries, venison is considered as meat of higher quality compared to red meats from farm animals by people who are conscious of healthy eating (Köttl et al. 2014). Another aspect comes from experience from South Africa, where McCrindle et al. (2013) provided evidence that harvesting edible venison by-products (liver, kidneys, lungs, heart) to lower-class consumers (rural areas) appears to be culturally acceptable, affordable, accessible and safe. Edible by-products from game could increase the food security in rural communities, as well as with low-income commuters. Game meat production creates local supply hubs (hunting areas) that generically generate edible by-products of lower market value. The local rural communities may have access to the source of high-quality proteins for an affordable/bargain price.

Based on the above, it can be assumed that, in the case of venison, it is usually a very high-quality food. Since the current era brings a number of uncertainties for the Czech forestry industry and forest owners (climate change and the related bark beetle outbreaks, large price fluctuations on the wood market, high growth rate of inflation, etc.), game production may become more important. In this context, it is necessary to find answers to two basic research questions:

(*i*) What are the main (economic) limits limiting the development of the game market?

(*ii*) Are there any ways to increase the forestry income from game production?

State of the game market in the Czech Republic. There is a total of 6 884 619 ha of hunting land in the Czech Republic. Of this, agricultural land accounts for 56.7%, forest land accounts for 37.6%, water areas account for 1.4% and other areas account for 4.3%. Of the total acreage, 49 041 ha are for game reserves and 91 069 ha are for pheasantries. Hunting is managed in 5 786 hunting grounds. Of these, there are 200 game reserves and 286 pheasantries. The average hunting area is 1 190 ha, the average game reserve is 245 ha and the average pheasantry is 318 ha (Ministry of Agriculture 2021).

Like any market, the game market is determined by supply and demand. A number of factors are important for further development of the market in terms of the supply and demand. The domestic supply is directly determined by the volume of the game hunted and the volume of the net trade balance with the game. The Czech Republic is a net exporter of game, i.e. the game exports exceed game

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imports (CZSO 2022b). The volume of the game hunted depends on the condition of the game, the planned hunting and the capacity of the hunters to effectively implement the hunting plan. Over 90% of all the harvested venison weight in the Czech Republic relates to the ungulate species (red deer, fallow deer, European mouflon, roe deer, wild boar) (CZSO 2021).

In the population of the Czech Republic, the level of game consumption is low in relation to other types of meat per person, amounting to approx. 1 kg per year (1.2% of the total annual meat consumption). This small value represents an obvious potential to increase domestic consumer demand (AKCR 2021).

In connection with the production and sale, i.e. the supply of game in the Czech Republic, it is necessary to emphasise the necessity of a significant reduction in the game density in connection with the restoration of Czech forests after the bark beetle outbreak (Stachova 2018; Ministry of Agriculture 2021). This is consistent with a general problem across the forestry sector across Europe, where the overpopulation of large herbivores poses a major risk to the main production function of the forest (Stewart 2001; Palmer, Truscott 2003).

MATERIAL AND METHODS

The works were methodically divided into two areas consisting of several steps, covering both official quantitative data and survey data. The synthesis of such diversified results then enables the research questions to be answered.

Acquisition and analysis of available official data. The data were obtained from the public databases of the Czech Statistical Office (CZSO), the Forest Inventory Office and the Forest Management Institute (UHUL) and the official Reports on the State of Forests issued annually by the Ministry of Agriculture (MAg). The analysis took place in the following steps:

(1) Analysis of the dynamics of development of domestic game production with a focus on the main species of ungulates: analysis of the data from the CZSO (CZSO 2022a). The data were put into the context of the dynamics of development of the selected species of ungulates in the Czech Republic and in the neighbouring countries (LDKČR 2021).

(2) Analysis of the development of the number of hunters and the related development of licences to hunters (hunting right holders): analysis of the data of the UHUL (2021) and the CZSO (2021, 2022a).

(3) Analysis of the dynamics of development of the trade balance (export − import) of game between the Czech Republic and other countries: analysis of MAg data (Ministry of Agriculture 2021), UHUL (2021) and Czech Statistical Office (2022b). Based on the analysis, the size and dynamics of development of the domestic game market were subsequently estimated using the relationship: market size = production – export + import.

(4) Comparison of the development of the game purchase prices compared to the development of the consumer price index in a comparable period: analysis of the CZSO data (CZSO 2022c) using the Laspeyres Index (Eurostat 2022).

Survey research. The survey was divided into two separate surveys. The first (step 5) was aimed at evaluating the public's opinion on game, the second (step 6) was aimed at analysing the consumer market.

(5) Poll survey investigating the attitude of the public and their perception of the function of the forest in relation to the wildlife: the research was carried out in 2018 through CAPI (Computer Assisted Personal Interviewing) by the STEM-MARK agency. The Internet population aged between 15 and 75 years, the general population of the Czech Republic, was included in the sample. The collection of the field data took place between May 24 and June 4, 2018. The data analysis was carried out on a sample of 1 519 respondents. Selection characteristics: gender, age, education.

(6) Poll survey on the consumer market analysis: the survey was conducted in 2021 through the Internet data collection CAWI (Computer Assisted Web Interwiewing) by the Nielsen agency. The collection of the field data took place between August 24 and August 30, 2021. The data analysis was carried out on a sample of 523 respondents. The sample included an Internet population of 20+ of age, people (jointly) responsible for purchases who, at a minimum, visit a restaurant twice a month and eat meat. Selection characteristics: gender, age, education, region and size of the place of residence.

Synthesis of results. The described methodology can be summarised in a brief diagram (Figure 1).

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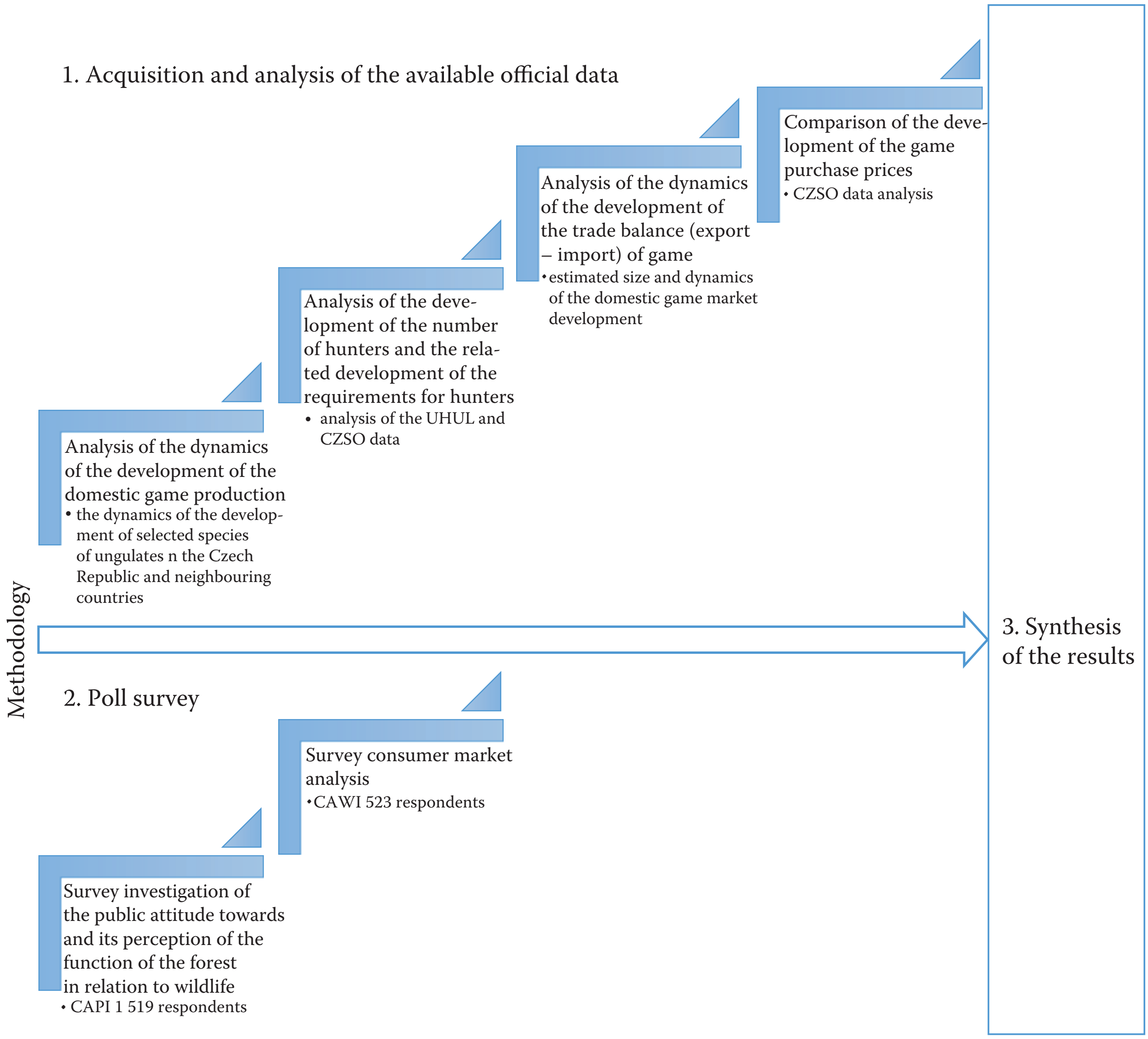

Figure 1. Methodology diagram

CAPI – Computer Assisted Personal Interviewing; CAWI – Computer Assisted Web Interwiewing

RESULTS

Venison market in the Czech Republic. As is clear from Table 1, the selected ungulates represent 92% of the total mass production of game in the Czech Republic. A comparison of the development of its production, the context of development in the surrounding countries and the volume and development of the market related to this production, thus, represent fundamental factors in the game production of the Czech Republic.

The total primary production and its development over time can be aggregated from the data obtained. From the graph (Figure 2) it is clear that the production is increasing with interannual fluctuations, especially in wild boar, when a record catch of black game was recorded in 2017, which was subsequently exceeded in 2019, and was influenced by the shooting fee per caught piece and secondly, by the increasing damage to agricultural production together with African swine fever. This record was exceeded in 2019 for similar reasons. Every year following a record hunt, a decrease is recorded reflecting the reduced initial conditions.

The supply side of the venison market in the Czech Republic belongs to the broader context of the venison market of the neighbouring countries. To compare the status and development dynamics, the basic development in the available time

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Table 1. Ungulate species harvested in the Czech Republic (CZSO 2021)

Harvest of ungulates (in pieces)	Year											
	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Red deer (*Cervus elaphus*)	21 511	20 958	23 092	23 578	23 361	23 978	26 152	27 878	28 287	29 017	29 842	30 792
Fallow deer (*Dama dama*)	1 393	13 131	14 591	16 404	16 761	18 968	20 402	23 069	23 800	28 978	30 982	33 250
European mouflon (*Ovis musimon*)	8 764	8 146	9 112	9 222	9 059	9 495	9 506	9 400	9 531	10 105	10 580	10 019
Roe deer (*Capreolus capreolus*)	131 873	113 913	108 591	105 680	100 348	99 828	100 834	103 455	102 229	103 018	105 570	107 433
Wild boar (*Sus scrofa*)	121 690	109 383	185 176	152 250	168 974	185 496	160 139	229 182	137 823	239 818	160 811	230 905
Game weight (in tonnes)	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Red deer (*Cervus elaphus*)	1 613.3	1 571.9	1 731.9	1 768.4	1 752.1	1 798.4	1 961.4	2 090.9	2 121.5	2 176.3	2 238.2	2 309.4
Fallow deer (*Dama dama*)	392.8	393.9	437.7	492.1	502.8	569.0	612.1	692.1	714.0	869.3	929.5	997.5
European mouflon (*Ovis musimon*)	219.1	203.7	227.8	230.6	226.5	237.4	237.7	235.0	238.3	252.6	264.5	250.5
Roe deer (*Capreolus capreolus*)	1 978.1	1 708.7	1 628.9	1 585.2	1 505.2	1 497.4	1 512.5	1 551.8	1 533.4	1 545.3	1 583.5	1 611.5
Wild boar (*Sus scrofa*)	6 084.5	5 469.2	9 258.8	7 612.5	8 448.7	9 274.8	8 007.0	11 459.1	6 891.2	11 990.9	8 040.6	11 545.3

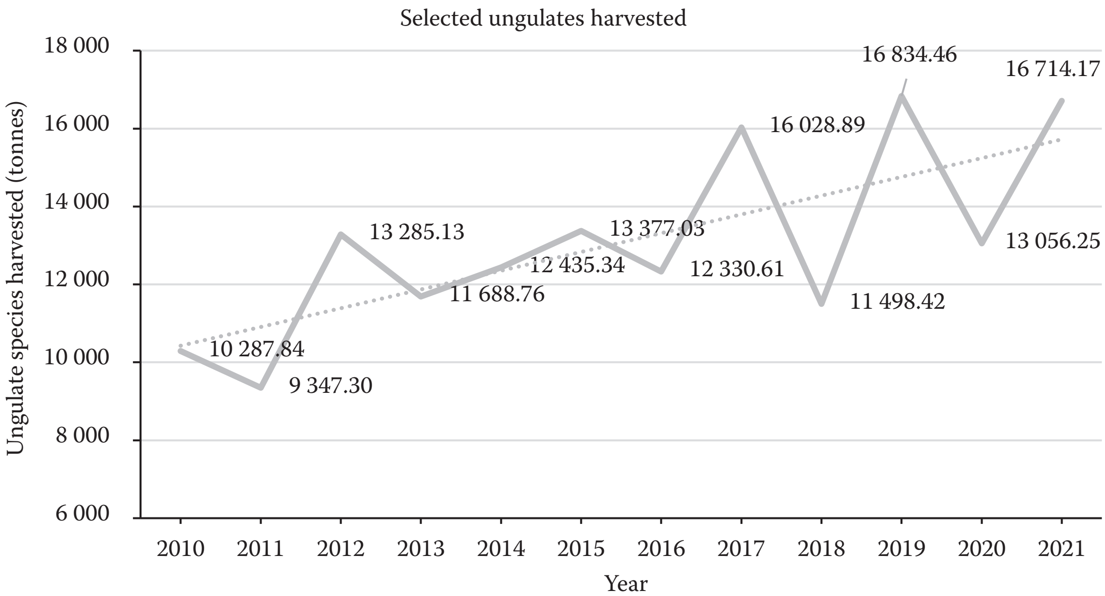

Figure 2. Ungulate species harvested in the Czech Republic in tonnes, adjusted dynamics (CZSO 2021)

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series in the Czech Republic, Germany, Poland, Austria and Slovakia was used.

Primary production, compared in 1995 and 2019, is the basic supply factor as shown in Table 2.

The size of the offer is derived from the volume of hunting the most important species. Here, you can see a strong increase in the supply in the surrounding countries, which recorded a 77% increase in the total number of selected species of ungulates between 1995 and 2019. It is also clear that the dynamics of development of the primary production volume differs fundamentally in the individual countries from a relatively lower increase in the order of tens of percent 38–66% (Austria, Germany) through 102–130% (Czech Republic, Poland) to 316% (Slovakia). In both the absolute and relative increases, the influence of the increase in black game catches prevails.

Analysis of development of the number of hunters. The growing number of catches places pressure on the available hunting capacity. According to the obtained data, the number of hunting licence holders (hunters) is decreasing. Figure 3 shows the details.

When comparing the number of shot individuals of selected ungulates, the need for shot individuals per hunting licence holder increased by 47% during the observed period (2010–2021) (Table 3). Due to the long-term decreasing number of hunting licence holders, the increasing burden in this part of the primary production is, thus, obvious.

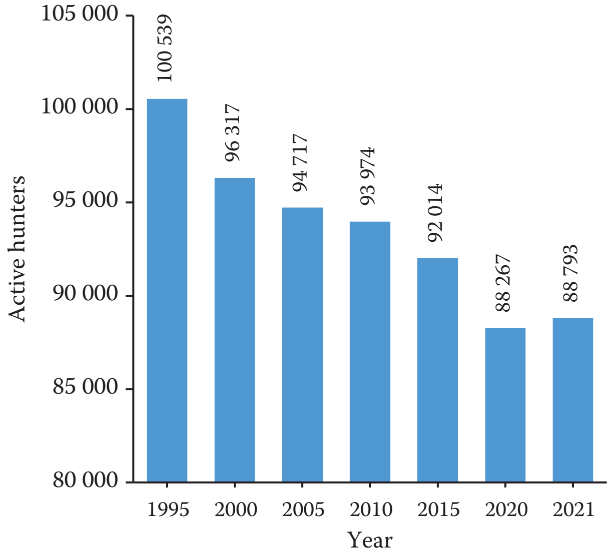

Figure 3. Number of hunters (UHUL 2021)

The decrease in hunter's status is all the more serious as the rate of shooting requirements per hunter increases along with it.

Analysis of the dynamics of development of the trade balance and the dynamics of the domestic market. The increase in the number of shot animals is also reflected in the trade balance statistics (export minus import) between the Czech Repub-

Table 2. Selected ungulates harvested, dynamics in pcs. (LDKČR 2021)

Species	Year	Czech Republic	Germany	Poland*	Austria	Slovakia	Total
Red deer (*Cervus elaphus*)	1995	16 873	52 813	35 400	35 402	2 909	153 397
	2019	29 863	76 897	83 200	57 524	45 320	292 804
	change (%)	77	46	135	62	251	91
Fallow deer (*Dama dama*)	1995	6 643	35 314	4 700	–	974	47 631
	2019	31 057	65 427	6 600	1 034	16 597	120 715
	change (%)	368	85	40	–	1 604	153
Roe deer (*Capreolus capreolus*)	1995	101 353	1 016 200	129 800	230 895	14 792	1 493 040
	2019	105 665	1 226 169	200 000	278 312	25 689	1 835 835
	change (%)	4	21	54	21	74	23
Wild boar (*Sus scrofa*)	1995	37 775	253 788	61 300	11 451	10 376	374 690
	2019	161 699	882 231	242 200	47 251	74 947	1 408 328
	change (%)	328	248	295	313	622	276
Total	1995	162 644	1 358 115	231 200	277 748	39 051	2 068 758
	2019	328 284	2 250 724	532 000	384 121	162 553	3 657 682
	change (%)	102	66	130	38	316	77

*data from 2018

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Table 3. Hunters' workload ratio, dynamics

Ratio parameters	2010	2015	2021	Change 2010–2021 (%)
Hunters	93 974	92 014	88 793	–5.51
Selected ungulates (pcs)	296 931	337 765	412 399	38.89
Ratio	3.16	3.67	4.64	46.99

lic and other countries. Table 4 shows a comparison of the years 2008 and 2021. Here, the relative dependence of the development of the expansion of the number of game caught on the trade balance with the above-mentioned neighbouring countries and vice versa is evident.

A relatively higher increase in the catches in the CR is recorded compared to the development in Germany, and, at the same time, a significant increase in the exports to Germany was recorded, similarly like in the case of Austria. On the contrary, in the case of Slovakia and Poland, where a relatively slower increase in primary production was recorded, a significant increase in the import of game from these countries was also recorded.

The size of the domestic market is determined by the difference between the production and the trade balance, i.e. the relationship market size = production – export + import.

Table 5 shows that between 2008 and 2021, the potential market increased by 5 352 tonnes of game, which is an increase of 43% while the net export increased by 90% (182 tonnes). The total volume of the game, and, thus, the potential market, is estimated at 17 794 tonnes of game in the Czech Republic in total. From the primary production, at the end of the period (2021), the selected ungulates presented in the previous points represent 92% of total venison harvest in the Czech Republic.

Comparison of the game purchase prices and consumer price index (*CPI*) of meat production. During the analysis of development of the purchase prices of cloven-hoofed game, it was found that the prices were stagnant for a long time. Table 6 shows the details.

For the purpose of comparing the dynamics of the consumer market with the market of primary production, the development of the game purchase prices was compared with the development of the meat *CPI* (consumer price index), when the available data of the period 2003 to 2021 were compared.

When adjusting the data in Table 6 and using the comparable available periods, it follows that although the meat consumer price index increased by 42.1%, no such a similar increase in the purchase prices, as shown in Table 7, was recorded. To compare the dynamics of the production prices of the assumed substitute, the development of the prices for common meat (pork, beef) was used. The increase in consumer prices of meat, which can be considered as a general substitute for game production, thus results in a fundamental gap between the development of the market consumer prices and purchase prices of game. Furthermore, the dynamics of the purchase prices of pork and beef for the given period were verified. From this verification, it is clear that producer prices of pork and beef do not have the same dynamics as consumer prices (their growth is lower), although the gap in the growth dynamics between the production prices of pork and beef and the dynamics of the consumer prices is significantly lower than for game.

Consumer market analysis. CAWI research revealed that the main source of game for the end

Table 4. Venison trade balance of the Czech Republic (CZSO 2021, 2022b)

Trade counterpart (tonnes)	2008			2021			2008–2021	
	export	import	balance	export	import	balance	balance change	(%)
Germany	1	98	–97	819	256	564	661	n/a
Poland	0	3	–3	0	295	–295	–292	11 378
Austria	41	28	13	125	–	125	112	863
Slovakia	37	2	35	46	45	2	–33	n/a
Subtotal	79	130	–51	991	595	396	448	n/a
Other	272	18	253	281	293	–12	–266	n/a
Grand total	351	149	202	1 272	888	384	182	90

n/a – not available

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Table 5. Venison market estimate in the Czech Republic (in tonnes) (CZSO 2021, 2022b, c)

Trade balance market impact (tonnes)	2008	2021	Change 2008–2021
Germany	97	–564	–661
Poland	3	295	292
Austria	–13	–125	–112
Slovakia	–35	–2	33
Sub total	51	–396	–448
Other	–253	12	266
Grand total	–202	–384	–182
Primary production (tonnes)	**2008**	**2021**	**Change 2008–2021**
Selected ungulates	11 067	16 714	5 648
Other focus species*	1 577	1 463	–114
Total primary production	12 643	18 177	5 534
Total CZ venison market estimate	12 441	17 794	5 352

*hares *(Lepus europaeus)*, ducks (*Anas* sp.), pheasants *(Phasianus colchicus*), sika deer (*Cervus nippon*)

Table 6. Primary purchase prices of the selected ungulates, dynamics (LDKČR 2021; GoodVenison 2022; MSVK 2022; OMSČB 2022); 1 EUR = 24.055 CZK

Species	Purchase prices (kg) in EUR		
	2003	2021	2022
Deer	1.66–2.91	1.04–1.87	1.25–2.08
Fallow Deer	1.66–2.08	0.83–1.25	1.04–2.00
Roe deer	3.33–4.16	1.45–3.33	1.45–3.74
Wild boar	1.25–1.66	0.62–1.25	0.62–1.45

Table 7. Meat *CPI* vs. venison purchase prices (in EUR per kg; 1 EUR = 24.055 CZK)

Item	2003	2021	Change 2003–2021 (%)	Gap to meat *CPI* (%)
CPI Czech Republic	100.0	150.2	50.2	–
Meat (*CPI*)	100.0	142.1	42.1	–
Beef without bones (price) PP*	6.13	6.54	6.6	35.5
Pork with bones (price) PP*	3.39	3.14	–7.4	49.5
Red deer (mid)	2.29	1.45	–36.4	78.5
Fallow deer (mid)	1.87	1.04	–44.4	86.5
Roe deer (mid)	3.74	2.39	–36.1	78.2
Wild boar (mid)	1.45	1.87	28.6	13.5

*Producer prices (kg) year average; *CPI* – consumer price index

customer is the local hunter. This represents 38.8% of the deliveries to the consumers (N = 472); see Table 8.

Regarding the consumer demand, the research further identified that the game most often prepared in households is wild boar (52%) and roe deer (20%). Only 9.9% of the respondents (N = 523) perceive the fact that the regulation of the game status and income from game are connected with forestry and its support. 41.9% of the respondents rather or completely disagree with the concept of game consumption as an activity that supports forest management (Figure 4).

In this case, a significant mismatch between the needs to support the main production function of the forest, which consists in the regulation of game, and at the same time, in the development of non-timber forest products (game) as an additional source of income, is evident. Furthermore, only 24% of the respondents (N = 523) fully agree with the statement that venison is a healthy product of organic quality. 16.1% of the respondents rather or completely disagree with this statement. In this case, the shift in public opinion is less significant from the state that allows game production to be presented as a premium product on the consumer market, forming either a substitute for the highest quality meat production, or a premium product *sui generis.*

Perception of venison and forestry. The research performed by STEMMARK Agency in 2018 showed that the public (73% of the respondents, N = 1 519) perceives the role of a shelter for animals as a very important role of the forest environment. This perception is contrary to the needs of effective forest production management.

As can be seen from Table 9, a significant and strong expectation of the public from the function of the forest is to provide a refuge for wildlife. We further

Table 8. Venison point of purchase for the final consumer (LDKČR 2021)

Venison source	N	Relative share (%)
Local hunter	183	38.8
Supermarket	110	23.3
Local store/butchery	103	21.8
Specialised e-shop	22	4.7
General e-shop	12	2.5
Other	42	8.9
Total	472	100

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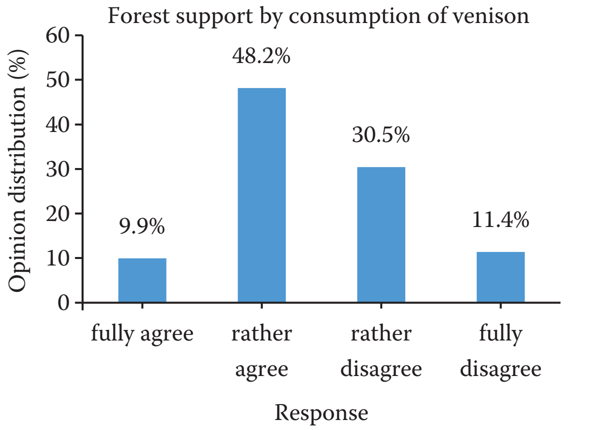

Figure 4. Public opinion on venison consumption as a part of forest support (LDKČR 2021)

put this fact into context with the needs of the forest management in the summary of the results.

Synthesis of the results. By comparing the development of the production of the selected species of ungulates, which represents 92%, by weight, of the primary production of game in the Czech Republic (2021), it is clear that there is a long-term permanent increase in the production, which records fluctuations in connection with high hunting of wild boar and a subsequent decrease in the subsequent year.

An increase in the production of the selected species of ungulates is also recorded in the surrounding countries, although the dynamics is not the same.

There is an obvious increase in the trade exchange of game production between the Czech Republic and other countries, where an increase in net exports by 90% was recorded in the period 2008–2021.

As stated in the results (also see Table 2), in some selected neighbouring countries (Slovakia, Poland), the dynamics of the game production is stronger than in the Czech Republic, which is reflected in the game trade balance with the given countries. On the contrary, countries with a slower growth rate of game production are net importers of game from the Czech Republic (Germany, Austria). The targeted development of venison production and maintenance of a comparable growth rate by the leaders of the neighbouring countries (especially Poland according to our research) can, thus, ensure a significant competitive position in the Central European venison market. This starting point will be further developed by a detailed comparative analysis taking into account the specifics of the individual neighbouring countries.

The size of the potential venison market in the Czech Republic can be estimated at 17 794 tonnes. The dynamics of the market shows growth, with an increase of 43% between 2008 and 2021. While

Table 9. Perception of the forest and forest management role by the public – adjusted; N = 1 519

Domain	Very important	Partially important	Indifferent	Mostly unimportant	Unimportant
	(%)				
Shelter for wild animals	73	21	6	0	0
Water resources protection	73	20	6	1	0
Rare plants protection	64	27	7	2	0
Forest fire protection	66	25	8	1	0
Protection from pests and diseases	63	27	8	1	0
Rainwater retention	69	21	8	1	0
Climate stabilisation	66	24	9	1	0
Increasing the area of the forest by new planting	60	29	9	1	1
Flood protection	62	27	9	1	0
Capture of dust and disposal of some pollutants in the air	62	26	10	1	0
Maintaining the diversity and traditional character of Czech forests	55	33	12	1	0
Prevents soil and landscape erosion	64	23	11	1	1

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the primary production is increasing, the hunting capacity is decreasing, where the burden on the hunters calculated for the shooting of the selected ungulates increased by 47% between 2010 and 2021. The consumer market research showed that hunters are a significant part of the distribution chain, representing 39% of the game supplies to the final consumer. As expected from the statistical data, the consumer market survey showed that the most frequently prepared game in the household is wild boar (52%), followed by roe deer. The comparison of the growth of game purchase prices (primary production) is stagnant, while the CPI (consumer price index) of the meat increased by 42% in the monitored period 2003–2021. The perception of the role of the forest environment in relation to game by the public who perceives it as a shelter for game (73% of the respondents marked this point as very important) does not correspond to the need to develop this non-wood production function. At the same time, this perception does not correspond to the needs of regulating the game density to limit damage to forest stands.

DISCUSSION

As is clear from the research, the overall supply side is growing in the Czech Republic and in the surrounding countries, and regardless of the development or possible stagnation of the production in the Czech Republic, venison appears to be a product whose importance is growing in the EU-28 and especially in the surrounding countries. Further research would be appropriate to determine the critical factors of the demand side and the possibilities of its stimulation to increase the value of venison for consumers as a product.

A comparison of the development of the purchase prices of meat from farm animals (pork, beef) with the development of the purchase prices of venison deserves deeper attention. Comparison of these commodities, an estimation of the degree of correlation and then an analysis of the increased added value within the value chain from the primary production to the final consumer is necessary. The tasks of further research would be appropriate to concentrate on determining the optimal density of game with regard to sustainable forest management and the related increase in shooting.

At the same time, an evaluation of the possibilities of an increase in active hunters' capacity is necessary. Support on the side of communication, promotion and incentives for hunters may be the solution.

Such measures are even more important with the increasing average age of the hunters, which was around 60 years old in 2013 and currently (2022) has risen to 65 years a further reduction can be assumed in the hunting capacity in the foreseeable future.

With regard to the consumer, the factors of specific taste, smell, preparation, concerns about possible risks associated with the consumption of game, as well as the ethical issues related to hunting as such must be taken into account. This follows from previous studies; a study of Proskina et al. (2013) in Latvia shows that consumers regard the quality and taste aspects of venison as the most important criteria for purchasing venison. Nevertheless, most of the consumers highlighted that price incentives to purchase quality venison at a lower price are important factors for them (such as avoiding retailers). This was confirmed by a previous study (Radder, Le Roux 2005), from which it follows that the choice of venison for consumption tends to be influenced by the specific taste and associated concerns that it will not correspond to any other types of red meat in a sensory way. Currently, according to the study by Leroy and Degreef (2015) on the relevant markets of Western Europe, the eating of meat does not always go unquestioned, leading to a moral crisis in specific consumer segments. The need for consumer education for venison consumption was raised, for example, in the study by Mesinger and Ocieczek (2021), which concludes that game meat in Poland is beginning to very slowly enter the next product life cycle and through the gradual promotion of meat products. Should the promotion continue at a sufficient level, consumer acceptance of this type of meat could increase.

With regard to the above, it is possible to recommend a marketing approach to consumers on two levels. In one line, build brand differentiation (e.g. CzechVenison) for exclusive quality with a certificate of origin with the subsequent processing. In this part of addressing consumers, it is advisable to use opinion makers, television/internet cookery programmes, etc. In the second line (game as a substitute for affordable meat), it is advisable to standardise the processing process, the labelling of different quality levels and offer folk recipes for preparation. Here, due to some specific preparation procedures, the offer should be extended to pre-processed semi-finished products.

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Based on the results of the analysis, the possible potential in the final prices for the customer was quantified, which could not be realised annually at the level of primary production through the purchase prices of the game. It should be noted that common meat (pork, beef) also suffers from an insufficient rate of increase in the purchase price of producers, however, the primary production of game is significantly disadvantaged in this respect. Here, the increase in the consumer prices of meat was either reflected in other links of the game production value chain, or it was not realised on the market at all. It is, therefore, clear that the final consumer is ready and able to pay a significantly higher price for meat in the period under review than what results from the stagnation or decline in the prices of the primary production. Part of the solution is to expand and move the offer of the primary production to the processing phase, or to offer semi-finished products and, thus, move closer to the consumer in the distribution chain.

Subsequently, an existing gap (Table 10) in the estimated annual production was identified. For the volume of the estimated annual production, we used the latest published data from 2021, which we consider sufficient for the volume extrapolation, where the volume of the production is further reduced by 35% (qualified estimate) of the estimated difference in the volume of the primary production of unprocessed venison versus the product for the end customer. For the difference in the purchase price, the value assumed from the theoretical growth dynamics of the purchase prices was used, so that it follows the growth dynamics of the meat prices for the final consumer. The production volume of the last statistically known period was used to estimate the volume. This was recalculated based on the selected species of ungulates, which have a dominant mass representation in the total game production in the Czech Republic.

We thus estimate the unrealised income from the inability to reflect the development of the consumer price market for the main selected types of production in the order of hundreds of millions of CZK. Using our assumptions, it comes to 11.5 million EUR per year for the four selected species of ungulates which represent the core of the game production in the Czech Republic.

On the basis of the conducted research, it is so obvious that an important factor limiting the development of the venison market is the inability to realise an adequate income corresponding to the growth of the consumer prices for the primary production. This can be achieved if an additional value is added to the basic offer in the form of processing or the production of semi-finished products. The impact of the inability to realise an adequate income is also related to the low motivation of hunters, when the growing demand derived from the import of game indicates the market potential. However, this is partly lost due to the more dynamic development of the industry in the selected neighbouring countries (especially Poland), as it is evident from the increase in imports in the monitored period 2008–2021 by 356.6%.

In the context mentioned above, there is a public perception that one of the main tasks of forest management is to provide shelter in forests for forest animals, which is a challenge that should be solved by an adequate communication strategy from the forestry sector (Dembner, Anderson 1996; Riedl et al. 2019a). It is likely that the public does not associate game production, forest timber production and forest management with an adequate level of wildlife management and the extraction of sustainable maximum benefits from this NWFP (non-wood forest products) resource. The recommendation resulting from our research is to communicate to the public the need for the adequate regulation of game as a possible

Table 10. Meat *CPI* to venison purchase price gap

CPI	Unit	2003	2021	Change (%)	Gap to *CPI* (%)	Implied prices to *M-CPI*	Reality 2022	Price gap (EUR·kg^{-1})
Meat (*CPI*)	–	100.0	142.1	42.1	–	–	–	–
Red deer	midprice per kg	2.3	1.5	–36.4	78.5	2.6	1.7	–0.9
Fallow deer		1.9	1.0	–44.4	86.5	1.9	1.5	–0.4
Roe deer		3.7	2.4	–36.1	78.2	4.3	2.6	–1.7
Wild boar		1.5	1.9	28.6	13.5	2.1	1.0	–1.1

CPI – Consumer price index; *M-CPI* – meat (*CPI*)

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factor of damage to the forest as an ecosystem and as a source of the main wood production.

CONCLUSION

Based on the results and the above discussion, it is possible to answer the research questions.

What are the main (economic) limits limiting the development of the game market? The most significant economic limits to the development of the game market are the low game purchase prices, the inability to translate the rising costs (of the *CPI*) of hunters into primary production prices, and an underdeveloped processing and distribution chain, with hunters playing a significant role in the sale of unprocessed game with a low added value directly to the end consumer.

Although low purchase prices (primary production) can support the game market growth in general theory, the current situation is critical for the primary producers. At current primary production price levels, there is no economic incentive for the expansion of game meat production. For the primary producers, this situation represents the burden of necessary game regulation (to minimize forest and agricultural damage) with minimum or negative fiscal impact. Game meat is a close substitute for existing industrial meat products at higher levels of the value chain. This study focuses on the possibilities of bringing fair value down through the value chain to the primary producers.

Are there any ways to increase the forestry income from game production? A significant opportunity is the expansion of the range of primary production into products significantly closer to the consumer market (i.e. advanced processing of game at the level of primary producers, e.g. cutting plants, preparation of semi-finished products, etc.).

Another important factor is the creation of the consumer demand for venison as a *sui generis* product through active campaigns and through opinion makers, including TV coverage in cookery programmes. Due to the high costs of communication on the consumer market, it should be the collective advertising of all the interested entities in the forestry sector with possible state support.

It is therefore possible to increase the forestry industry income from venison through further development and an increase in the value for the customer, who, with an appropriate marketing strategy, can perceive this product as a premium organic food, through which it contributes to sustainable forest management. For a more detailed segmentation of the consumer market, which is a prerequisite for the effective use of marketing tools and targeting of communication, it will be necessary to analyse the demographic and geographic characteristics of the end consumers in more detail.

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Are they both the same shit? Winter faeces of roe and red deer show no difference in nutritional components

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Abstract: Herbivorous ungulate diets affect population performance and overall forest health through balanced interactions on plant-herbivore relations; therefore, understanding them is critical. Faeces are frequently used in ungulate nutritional ecology because they can provide information about animals' digestive efficiency. Roe deer (*Capreolus capreolus*) and red deer (C*ervus elaphus*) have different morpho-physiological and ecological constraints, and these differences should be reflected in their faeces. On the other hand, the lack of information about the animal (sex, age, reproductive status, diet selection, etc.) may be challenging for such studies. This study aimed to detect species' different susceptibility to these factors reflected in animals' faeces. Thus, we hypothesised that near-infrared reflectance spectrometry (NIRS) could distinguish between the faecal nutrients of two cervids. We collected 94 usable faeces from both species along the forest transect in Bohemian forests in the Czech Republic, covering 2 500 ha. Roe and red deer overlap was determined using the four faecal nutritional components on two axes. No discrimination occurred, refuting our hypothesis and highlighting that out-of-control variables are critical for faecal studies in uncontrolled settings. Fibrous parts explained the most variance (48%), indicating animals' strong reliance on nutrition quality. Apparently, uncontrolled supplementary feeding produced similar faecal nutrient outcomes during the nutrition-limiting winter, which was theoretically supported by the animal's response to predation and hunting pressure. The inability of NIRS to identify the source of N in faeces may also explain the lack of discrimination.

Keywords: *Capreolus capreolus*; *Cervus elaphus*; diet overlap; faecal nutrients; fibre; nitrogen; nutritional ecology

The nutritional quality of the feed ingested determines wild ungulate populations' performance and well-being, which is, at the same time, essential for maintaining healthy forest habitats (Parker et al. 1999, 2009; Christianson, Creel 2007; Felton et al. 2017). Understanding the ungulates' feeding behaviour and the drivers of diet selection regarding nutritional quality, chemical defence, and availability has been of high interest to scientists (Naiman 1988; Hodgman et al. 1996; Barboza et al. 2009; Lambert, Rothman 2015; Corlatti 2020) but is often overlooked during management and conservation decision-making (Morgan et al. 2021). After Raymond (1948) and Lancester (1949) described how the or-

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ganic matter digestibility of pasture could be calculated from the nitrogen content of the faeces, the use of faecal nitrogen (fN) as a research proxy has been extensively applied in ecological research, and especially in studies related to the nutrition of wild ruminants (Putman 1984; Leslie Jr, Starkey 1987; Osborn, Jenks 1998; Dryden 2003; Leslie Jr et al. 2008). Certainly, there are circumstances in which fN is limited as a nutritional quality indicator for wildlife ungulates in natural settings due to numerous interacting factors that directly or indirectly affect animal nutrition. For instance, high parasite load alters N metabolism and increases fN output (Gálvez-Cerón et al. 2013), or tannins can directly or indirectly affect food intake, digestive efficiency, or protein digestibility through binding to digestive enzymes (Robbins et al. 1987). Furthermore, recent studies have shown that faecal nutritional components can also be influenced by individual factors at the intra-specific level [factors that cannot be controlled for in studies in the wild (Čupić et al. 2021)] and by species-specific differences in digestive capability (Mould, Robbins 1982; Redjadj et al. 2014). Nevertheless, a simultaneous study of other faecal nutritional fractions like lignin (fLig) and acid (fADF) and neutral detergent fibre (fNDF) may help to draw a better picture of the diet quality. Nowadays, this can be achieved through a fast and cheap technique like near-infrared reflectance spectrometry (NIRS) (Putman 1984; Leite, Stuth 1995; Foley et al. 1998; Dryden 2003; Tolleson et al. 2005; Landau et al. 2006; Showers et al. 2006; Gálvez-Cerón et al. 2013; Villamuelas et al. 2017). Indeed, the technique has already been successfully used for estimating the diet quality of roe and red deer in the Czech Republic (Kamler et al. 2004).

These large ungulates are commonly classified along the browser-intermediate-grazer continuum in the context of botanical diet composition (Clauss et al. 2008, 2010; Codron et al. 2019). Roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are the two most widely distributed cervid species in Europe (Tixier, Duncan 1996; Burbaitė, Csányi 2009, 2010). The roe deer is a small-bodied concentrate selector (browser) that selectively ingests the vegetative parts of herbaceous and woody plants (leaves, buds, and twigs), fruits, and forbs (Hofmann 1988; Tixier, Duncan 1996). As predicted from the digestive morphology and body size of this concentrate selector, they tend to depend on high-quality low-fibre food items (Illius, Gordon 1992) and consume plants with low cell wall contents (Jung, Allen 1995). Grasses usually do not form a large part of the roe deer diet due to the large volume of poorly digestible fibre (Danell et al. 1994). On the contrary, the red deer is classified as an intermediate feeder (generalist). They can adapt to either browsing or grazing, shifting according to plant availability (Hofmann 1989; Langvatn, Hanley 1993). Their general patterns of diet selection focus on maximising the energy intake rate and minimising the intake of antinutritional or toxic compounds (Hanley 1997). Red deer select concentrate food items when the overall browse quality and availability are high (during the vegetation season) and switch to a grass-based diet in response to the decline of concentrate food availability which usually occurs during winter (Dumont et al. 2005; Verheyden-Tixier et al. 2008). In the Bohemian Forest (Central Europe), both deer species display their typical feeding strategies (Barančeková et al. 2010; Krojerová-Prokešová et al. 2010). Meadows are the favourite sites providing a diversity of protein-rich plants significant for the winter diets of both species (Zweifel-Schielly 2005; Hewison et al. 2009; Bonnot et al. 2013), but spruce (*Picea abies*) also constitutes an important portion of their diets (Homolka 1995; Mysterud et al. 1997, 2002; Barančeková et al. 2010; Krojerová-Prokešová et al. 2010). Furthermore, meadows, as a part of the contemporarily frequent fragmented mosaic natural habitats across Europe, are particularly favourable sites for roe deer (Hewison et al. 2001; Jepsen, Topping 2004), which often visit them in search of plants or plant parts that are indispensable for their more selective diet when compared to the one of red deer.

Despite the certain similarities in the winter diets of roe and red deer (Spitzer et al. 2020), partly due to the low food quality and availability, species-specific factors like differences in their digestive tract allow to predict the existence of differences in the faecal nutrients: in fibres due to the different quality of the selected diet, and in nitrogen because of the species-specific digestive efficiency (Hofmann et al. 1988; Hofmann 1989; Clauss, Rössner 2014). Furthermore, distinct life-history traits of these two species should be the source of variety regarding nutritional needs and the capability to fulfil them. Therefore, we hypothesise that the set of overall influencing factors will be clearly reflected in species' faecal samples – roe and red deer will excrete distinguishable faeces in their composition of fN, fADF,

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fNDF, and fLig. Consequently, we will test the NIRS and provide an insight into its applicability level for wildlife, game, and forest management and whether it can depict these fluctuations that reflect the ungulate-feed interaction and the difference in their morphophysiological-induced differences. The potential differences in faecal nutrients between samples collected in meadows and forests would also be tested (Ossi et al. 2017). However, considering the size-scale of the area in this experiment, its associated mosaic landscape structure, the large home range of these species, and their long food retention time, we did not set our hypothesis based on previous arguments, but rather include this analysis as support to the main research hypothesis.

MATERIAL AND METHODS

The study area is situated in the Bohemian Forest, outside the Šumava National Park in the Czech Republic. This is a forested mountain area and the most continuous mountain range in Central Europe, approximately 130 km long and 60 km wide. Elevation ranges from 370 m a.s.l. to 1 456 m a.s.l., and the climate is continental with a light maritime influence. The mean annual temperature is 6.5 °C in the valleys and 2 °C at higher elevations. Annual precipitation ranges from 400 mm to 2 500 mm without a dry period, but a considerable amount of precipitation occurs as snowfall. Snow cover persists for 7–8 months at higher elevations and 5–6 months in the valleys (this might have undergone certain changes due to the global climate conditions changes in the last years). Cold air pockets are often present in the valley bottoms, leading to an inversion of the thermal gradient, especially in winter. The coldest period is December and January, when temperatures could drop below –15 °C (Heurich et al. 2015).

The area is dominated by Norway spruce (*Picea abies*) with European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and larch (*Larix* sp.). There are some other tree species, such as white birch (*Betula pendula*), sycamore maple (*Acer pseudoplatanus*), and common rowan (*Sorbus aucuparia*) (Wild et al. 2004). We also noticed the presence of aspen (*Salix* sp.) and poplar (*Populus* sp.) in the area. The understorey is dominated by brambles (*Rubus* sp.), which were found to be an important food resource for roe deer (Moser et al. 2006), common honeysuckle (*Lonicera eryclimenum*), ivy (*Hedera helix*) and butcher's broom (*Ruscus aculeatus*). Forest covered most of the study area (Figure 1), while the proportion of meadows was around one-third (Mašková et al. 2009; Voženílková et al. 2010).

The roe and red deer co-occur in the area, 0.6 and 2.9 individuals per km^2, respectively (Košnář, Rajnyšová 2012). Wild boar (*Sus scrofa*) is also widely distributed in the area, while moose (*Alces alces*) is found only in small numbers in the southern part. The main large predator is the Eurasian

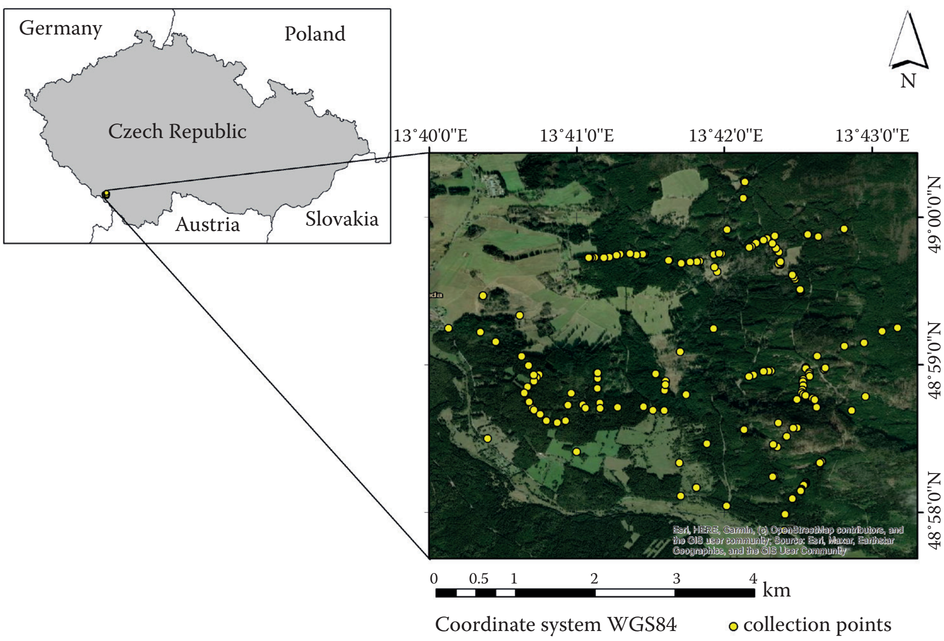

Figure 1. Study area, situated outside the protected zone in the Czech part of Bohemian forests, encompassing approximately 2 500 ha, with meadows comprising around one-third of the area (yellow dots represent sampling spots)

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lynx (*Lynx lynx*) which preys mainly on roe deer and, to a much lesser extent, on red deer calves (Heurich et al. 2012). Nevertheless, a wolf appearance has been reported in the area recently (Dvořák 2018; Janík 2020), although that happened after the samples for this study were collected. There is no significant agricultural activity nearby; crop feeding is therefore not common in the area.

We collected 156 faecal pellet groups from roe and red deer along 51.97 km of transects which covered an area of approximately 2 500 ha (Figure 1) at elevations between 782 m a.s.l. and 1 079 m a.s.l. The collection of the samples was conducted in December 2016 and the following January. Snow cover was present during the days of sampling, which facilitated the collection of fresh (recently exposed) faecal samples and avoided soil contamination. Samples in the close surroundings of previously collected samples were discarded to avoid repeated sampling of the same individuals. Discrimination between roe and red deer samples was done by *in situ* visual identification of morphological features (shape and size), further supported by animal tracks in the snow in the approximate vicinity of the sample group. Once in the lab, we calculated the length/width ratio to classify the samples according to their shape [following Chame (2003)] and discarded samples with outlier values (probably calves/fawns). The remaining samples were further confirmed by a senior expert researcher (Prof. Jaroslav Červený). All samples that were unclear to determine or did not pass the previous methodological criteria were discarded. Thus, we finally analysed 94 confirmed samples, 59 for red deer and 35 for roe deer.

The fresh faecal pellet groups were stored in plastic bags and labelled. Afterwards, we air-dried the samples at 50 °C for 48 h, ground them to pass a 1-mm sieve, and mixed them until being homogeneously distributed. We used NIRS™ DS 2500 FOSS analyser under the ISIscan™ Routine Analysis Software (Foss, Denmark) for scanning the samples and obtaining their near-infrared spectra, following Čupić et al. (2021). The contents of *fN*, *fNDF*, *fADF* and *fLig* were calculated with WinISI 4 Calibration Software (Foss, Denmark), according to a calibration set previously developed for red deer faecal samples (Holá et al. 2016) based on 100 samples, which showed a very high predictive power ($R^2 > 0.98$). To increase the robustness of the results, 21 samples with at least one faecal nutrient showing high global and neighbourhood distances (GH1 and NH1) were discarded. Thus, the final dataset consisted of 45 red deer and 28 roe deer samples.

Statistical analyses. The independent samples *t*-test was used to detect differences in faecal nutrients between the studied species and, within each species, between forest and meadow locations. Levene's test for equality of variances was applied in this procedure. Pearson correlations showed the relationships among the four faecal nutrients analysed (*fN*, *fADF*, *fNDF*, *fLig*). Since these were highly correlated, principal component analysis (PCA) was conducted based on these four faecal nutrients to obtain two axes. Varimax rotation with Kaiser normalisation was used as an extraction method to minimise the number of components extracted. Only those components with eigenvalues above 1 were selected. These axes were used to determine the overlap or discrimination between red and roe deer samples and between forest and meadow samples. For the interpretation of the selected axes, only the variables correlating > 0.7 were considered.

RESULTS

The *t*-test analyses failed to detect differences in the winter faecal nutrients between red and roe deer: *fN* (2.54% vs 2.50% respectively for red and roe deer; $t = -0.637$, $P = 0.526$), *fNDF* (56.4% vs. 56.3%; $t = 0.043$, $P = 0.965$), *fADF* (38.3% vs. 38.7%; $t = -0.315$, $P = 0.754$), *fLig* (29.3% vs 30.2%; $t = -1.243$, $P = 0.218$). Similarly, no differences were detected in the winter faecal nutrients of red and roe deer collected in meadow and forest habitats, with just a marginally significant difference in *fN* content in roe deer (2.48% in forest vs. 2.67% in meadow; $t = 1.941$, $P = 0.064$).

The four faecal nutrients analysed were significantly correlated in the 69 samples analysed, ex-

Table 1. Pearson correlations of the studied faecal nutritional components ($N = 94$)

Faecal nutritional components	*fN*	*fADF*	*fNDF*
fADF	-0.368^{**}	–	–
fNDF	-0.658^{***}	0.831^{***}	–
fLig	0.577^{***}	-0.083^{ns}	-0.328^{**}

$^{**}P < 0.01$, $^{***}P < 0.001$; ^{ns}non significant; *fN* – faecal nitrogen; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

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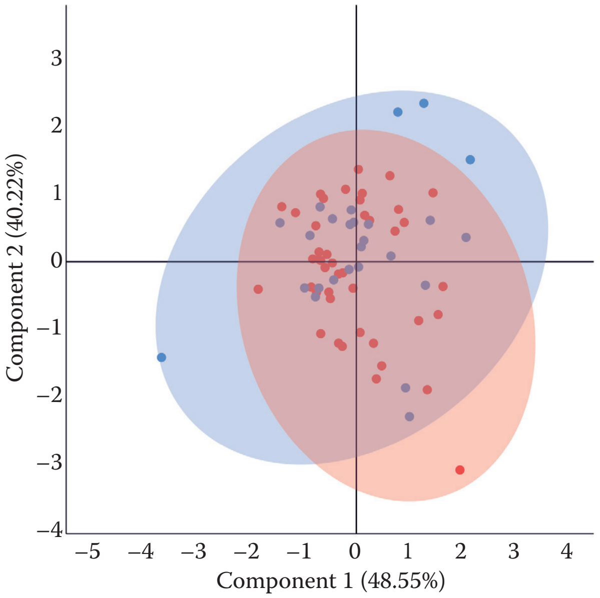

Figure 2. Graphical representation of the samples studied for red deer and roe deer along two axes based on faecal nutrients; component 1 is linked to the fibrous components *fADF* and *fNDF*, while faecal lignin and nitrogen are linked to component 2

Red – red deer; blue – roe deer; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

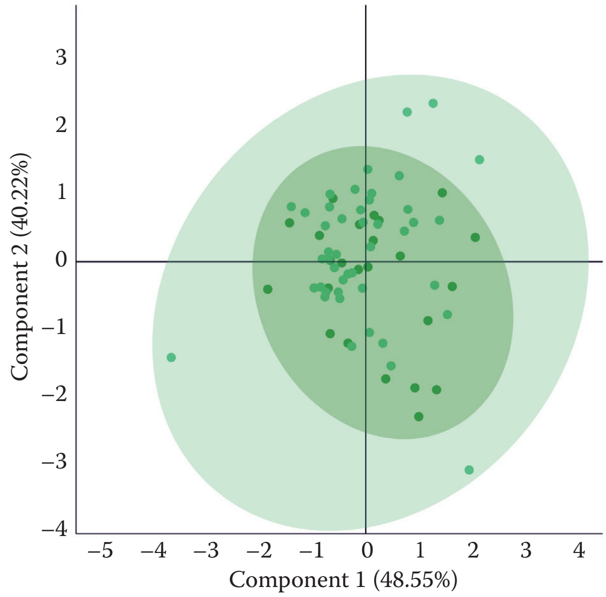

Figure 3. Graphical representation of the samples studied based on the collection habitat along two axes based on faecal nutrients; component 1 is linked to the fibrous components *fADF* and *fNDF*, while faecal lignin and nitrogen are linked to component 2

Dark green – forest; light green – meadows; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

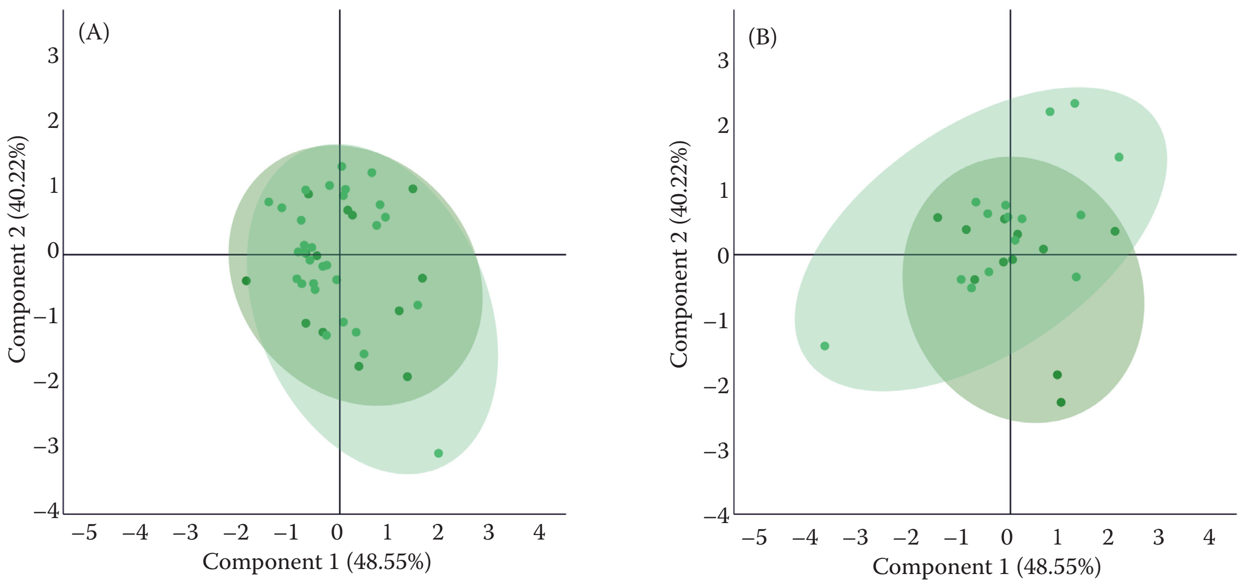

Figure 4. Graphical representation of the samples studied for (A) red deer and (B) roe deer along two axes based on faecal nutrients; component 1 is linked to the fibrous components *fADF* and *fNDF*, while faecal lignin and nitrogen are linked to component 2

Light green – samples collected in meadow habitats; dark green – samples collected in forest habitats; *fADF* – faecal acid detergent fibre; *fNDF* – faecal neutral detergent fibre

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cept *fLig* and *fADF* (Table 1). The PCA selected two components (axes) with eigenvalues above 1, well representing the original dataset of faecal nutrients. The first component (eigenvalue = 1.942) explained 48.55% of the variance and correlated with *fADF* (r = 0.963) and *fNDF* (r = 0.904). The second component (eigenvalue = 1.609) explained 40.22% of the variance and correlated with *fLig* (r = 0.934) and *fN* (r = 0.781). The plots of the samples studied on these two axes do not allow for discrimination between red and roe deer samples (Figure 2), and neither between samples collected from the forest and meadow habitats (Figure 3). When analysed separately for each species, it was not possible to discriminate between samples from the forest and meadow habitats neither in red (Figure 4A) nor roe deer (Figure 4B).

DISCUSSION

Even under the numerous environmental, species-specific, and animal-specific factors (susceptible to continuous spatiotemporal changes) directly or indirectly connected to the diet selection of red and roe deer, our hypothesis of different winter faecal nutrients between both species was not supported. The four faecal nutritional components grouped in two axes were used for determining the overlap between roe and red deer, but no discrimination was observed. The component that explained the highest portion of variance (48%) correlated with fibrous components, indicating animals' strong reliance on the quality of ingested nutrition.

In this research, the wide variety of environmental, morphophysiological (species-specific), and animal-specific factors and the complexity of their interrelatedness are unknown, which is indeed a general characteristic of most research conducted in natural settings. According to our previous study (Čupić et al. 2021), factors such as pregnancy, pasture availability, and even physical condition or body weight can induce significant variations in faecal output, even when animals consume a similar diet. Thus, under controlled or captive environments, intra- and inter-specific differences in faecal nutrients are indeed observed. However, in nature, where all these factors are unknown, and animals have free access to a greater diversity of plant species, it is extremely improbable that their diet similarity will be even close to that of populations in a controlled environment. Different rations of even the few sources available during the nutritionally-limiting winter season and the attendant specific morphophysiological response during the processes of ingestion, retention, digestion, and excretion should shape their final output. Tannins, already mentioned, could further support this interspecific diet dissociability. Simultaneously, in such a context, it is even more difficult to predict animals' energy expenditure, as well as inter- or intra-specific variation in required energy and, consequently, intraspecific dietary preference. Winter supplementary feeding of large mammalian herbivores is a common management tool in the Czech Republic (Conover 2001; Hothorn, Müller 2010; Möst et al. 2015) and elsewhere, mainly aiming at promoting healthy populations and increasing productivity and trophy sizes. Hunters in our research area provided that, but in low amounts considering the density of cervids. We were unable to obtain exact information either about the amount or about the ratio of supplementary feeding provided since it is a non-protected area. The decision-making process is in the hands of local hunters who do not have strict protocols to follow regarding supplementary feed or a defined law to comply with. Indeed, none of the previous research in this area provided information about this procedure. However, we did not expect a strong impact of supplementary feed, taking into consideration the entire set of previously mentioned potential influencing factors and experience from our previous research with captive animals. Given the almost total overlap observed in the nutritional outputs of both species, predominantly explained by the food quality ingested, the role of the supplementary feed should be further discussed.

The long retention times should be advantageous for ungulate species during harsh winter conditions. Ruminants with higher body mass are prone to having a larger relative gut fill, which leads to increased mean retention time (Demment, Van Soest 1985; Illius, Gordon 1992; Robbins 1993; McNab 2002). Moreover, browsers like roe deer have smaller digestive tracts and shorter retention times than grazers or intermediate feeders [three times larger rumen as a percentage of body weight in red deer compared to roe deer (Prins, Geelen 1971)]. Higher tolerance to fibrous forage has also been attributed to the same interspecific differences (Hofmann, Stewart 1972; Hofmann 1989; Clauss, Lechner-Doll 2001; Clauss et al. 2003). In habitats where un-

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gulates must account for expensive activities such as avoiding hunting and predation, this benefit is increased as energy expenditures are higher. The maintenance requirements may increase with movement and stress by as much as 200–300% (Weiner 1977). Therefore, large ungulates often find themselves in a trade-off between shelter and food search. According to this, that trade-off should be easier to solve by red deer compared to roe deer, given its body size and previously discussed morpho-physiological characteristics. In a scenario where animals must rely exclusively on natural feed sources, roe deer acts as a typical browser, selecting diets with a higher nutritional value in terms of high protein content and avoiding high-fibre diets (Drescher-Kaden, Seifelnasr 1977; Hofmann 1989; Duncan et al. 1998). Given the morpho-physiology of the species, in times of increased energy demands (e.g. heat production during winter), this means reduced locomotor activity and higher exposure to hunting and predation. However, when increased amounts of carbohydrates are available in the form of supplementary feed, these may be mainly consumed by roe deer since that may be of higher vital importance for them than for red deer. The supplementary feed may thus help both species, but especially roe deer, to survive the winter while feeding on natural plant species with low nutritional value (Miranda et al. 2015), leading to more similar diets than initially expected and thus to similar faecal nutrients.

The above explanations can be supported by further incorporating the impact of predators and hunting pressure on the distribution, habitat preference, and nutritional ecology of roe and red deer in the study area. The Eurasian lynx (*Lynx lynx*) is the main predator in the area, predominantly preying on roe deer but also on young red deer individuals. As already commented, hunting pressure is relatively high in the area for both species, with greater exploitation of red deer due to their attractive trophies. That may induce stress in both species, and the consequence may be lower time searching for food, lower feed quality and increased compensation through the supplementary feed. In the study area, supplementary feeders are usually situated on the edges of forests and meadows, the habitat preferred by roe deer (Heurich et al. 2015). Indeed, this same study showed that roe deer in Bohemian forests prefer unprotected areas, despite the high impact of hunting, over protected areas of the park due to the supplementary feeding provided by hunters out of the national park. In contrast, red deer prefer vegetation-dense forest habitats of around 70% of cover (Heurich et al. 2015). In these areas, the shrub vegetation layer, which red deer can use, stands during winter. Red deer probably keep feeding on this resource more extensively than roe deer due to the necessity to reach a certain threshold of fibres for supporting the proper functioning of their large rumens (Bauchop 1979; Gebert, Verheyden-Tixier 2001), thus showing less dependence on supplementary feed.

CONCLUSION

The inability of NIRS to identify the source of N in faeces may be another reason behind the lack of discrimination between free-ranging roe and red deer faecal samples. The difficult interpretation of *fN* has been mentioned in previous research (Čupić et al. 2021). This problem might be solved in future studies by analysing the amount of N bound to ADF (Van Soest 2018), which would allow the calculation of metabolic faecal nitrogen (MFN). That would inform about the proportion of N being used by the animal cell function and not only excreted by it. Such analysis would confirm if there was an actual lack of differences in the diet consumed by both species or if our hypothesis was rejected just because of the inability of NIRS to detect the source of protein excreted. Even if the second reason was correct, certain discrimination at the axis explained by fibres could still have been found.

Altogether, the results thus suggest that NIRS and the analysis of faecal nutrients should not be employed for this type of research during periods when dietary overlaps across species can be expected, but especially when we have neither other sources of information about what the animals could have consumed (e.g. camera traps, direct observation, or GPS collars), nor information about each individual. The sum of uncontrolled factors may easily lead to non-significant results, which, theoretically, should have been expected. That may subsequently lead to making incorrect management decisions.

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Use of bioreactors RITA® in the propagation of *Pinus patula* Schiede ex Schltdl. & Cham.

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Abstract: The objective of the present work was to evaluate the efficacy of use of the RITA® temporary immersion system in the large-scale propagation of *P. patula*. The effects of four concentrations (0.00 µM, 4.50 µM, 9.00 µM, and 13.51 µM) of 6-benzylaminopurine (BAP) on 10 hypocotyl explants were studied using a completely randomised design with three replicates per treatment. Five hypocotyl explants were grown in 250 mL RITA® containers of Woody Plant Culture Medium (WPM) supplemented with 20 $g \cdot L^{-1}$ sucrose and 10 $mg \cdot L^{-1}$ vitamins from Murashige and Skoog (MS) culture medium. The frequency of immersion of the explants into the culture medium was 2 min every 8 hours. The number of adventitious buds and calli formed, as well as shoot growth, were evaluated after 6 weeks of *in vitro* culture. The 4.50 µM concentration of BAP was the best treatment for shoot production (5 shoots per plant) and shoot length (1.32 cm). These results could help the widespread vegetative propagation of this important forest species.

Keywords: conifers; *in vitro*; micropropagation; temporary immersion system; recipient for automated temporary immersion

Pinus patula Schiede ex Schltdl. is an endemic species with significant value for Mexican forestry (Farjon, Styles 1997). It is characterised by its straight, knotless stem and its adaptation to a wide range of soil and climatic conditions (Leibing et al. 2009). Due to the high quality of its wood, this species is in great demand in the global forestry industry, so it is necessary to have enough plants of this species to contribute to the development of reforestation programs and the restoration of degraded soils (Orwa et al. 2009).

The micropropagation techniques are potentially useful for rapidly multiplying high-value forest genotypes. Currently, most of the micropropagation protocols established in *Pinus* have been developed using semisolid media (De Diego et al. 2010). Although micropropagation protocols have been successfully established for *in vitro* regeneration of *P. patula* through the two main morphogenetic routes of somatic embryogenesis and organogenesis (Sarmast 2018; Ramírez-Mosqueda et al. 2019), there is no information on the use of Temporary Immersion Systems (TIS) in *P. patula* micropropagation.

TIS systems are characteristic due to the explants being immersed in the growing medium for brief periods of time, allowing for more effective nutrient and growth regulator absorption. These systems

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Table 1. Organogenesis response of *P. patula* explants (means + SE)

BAP concentration (μM)	Response type	Shoot length (cm)	Number of shoots	Number of calli
0.00	BA	0.49 ± 0.03[b]	0.20 ± 0.07[b]	0.00 ± 0.00[b]
4.50	BA	1.32 ± 0.09[a]	5.00 ± 0.29[a]	0.00 ± 0.00[b]
9.00	BA	0.60 ± 0.04[b]	0.73 ± 0.15[b]	0.00 ± 0.00[b]
13.51	BA + CO	0.59 ± 0.05[b]	0.93 ± 0.21[b]	1.49 ± 0.27[a]

[a,b]statistically equal means with the Tukey test ($P \leq 0.05$); BAP – 6-benzylaminopurine; BA – adventitious shoot, CO – callus

have been particularly popular because they reduce crop manipulation and, as a result, production costs (Etienne, Berthouly 2002; Gomes et al. 2016; Vidal, Sánchez 2019). There are various types of bioreactors, such as the Automatic Temporary Immersion Vessel (RITA®). Propagation in RITA® bioreactors is an appealing option for the mass micropropagation of various forest species. Furthermore, it has been demonstrated that the use of these systems increases plant growth rates when compared to those based on the use of semisolids (Arencibia et al. 2017).

Three-month-old plants from *in vitro* germination of *P. patula* were used in this study, following the protocol of Ramírez-Mosqueda et al. (2019). Five hypocotyl explants (0.5 cm in length) were obtained from each plant as an initial source of explants. For propagation, a 1 000 mL RITA® temporary immersion system (150 mm × 133 mm; VITROPIC, France) was used. Explants were grown in RITA® vessels containing 250 mL of WPM (Woody Plant Medium; Sigma, USA) Culture Medium (Lloyd, McCown 1981), supplemented with 20 $g \cdot L^{-1}$ sucrose and 10 $mg \cdot L^{-1}$ vitamins from MS Culture Medium (Murashige, Skoog 1962), as well as various concentrations of 6-benzylaminopurine (BAP: 0.00 μM, 4.50 μM, 9.00 μM, and 13.51 μM).

The pH of the medium was adjusted to 5.7, and the medium was sterilised at 1.5 $kg \cdot m^{-2}$ at 121 °C for 15 min. All cultures were incubated at 22 °C ± 2 °C with a photon flux density of 30–50 $\mu E \cdot m^{-2} \cdot s^{-1}$ using fluorescent light lamps under a photoperiodic regime of 16 : 8 h (light: dark). The frequency of immersion of the explants into the culture medium was 2 min every 8 h. After 6 weeks of culture, the growth of the explants, the number of adventitious shoots, and/or calli formed were evaluated. In all experiments, a completely randomised design with 120 explants (10 explants per treatment, with 3 repetitions each) was used. Each treatment was repeated twice. After 6 weeks of culture, the effect on the number of adventitious shoots and/or calli formed was evaluated, as well as the length (cm) of the shoots. The data were statistically processed with the IBM SPSS Statistics software (Version 24, 2016). An analysis of variance (ANOVA) was performed, followed by the Tukey test ($P \leq 0.05$).

There were statistically significant differences in the morphological characteristics of shoots formed after 6 weeks of cultivation under different BAP concentrations. The 4.50 μM BAP treatment produced the largest number and size of shoots. This treatment tripled the initial shoot length (1.32 cm). The other treatments (0.00 μM, 9.00 μM, and 13.51 μM BAP) produced statistically comparable results (Table 1).

Figure 1 depicts the effect of different BAP concentrations on the size of the shoots formed. The effect of higher concentrations of cytokinin on callus formation was observed. It is noteworthy that callus formation only occurred in the WPM medium containing 13.51 μM BAP (Figure 2). These results show the effect of using higher concentrations of this cytokinin on callus formation compared to the rest of the treatments evaluated. The response of plants to various stress factors, in this case, the different concentrations of cytokinins with the capacity to stimulate a biphasic response ("hormetic effect") depending on the concentration of the stressor, has been demonstrated in numerous studies. Low doses stimulate a favourable response, while high doses of the same reagent have a negative effect on the same plant. BAP as a cytokinin has been widely used to induce adven-

Figure 1. Growth of explants exposed to different concentrations of BAP: (A) 0.00 μM; (B) 4.50 μM; (C) 9.00 μM; and (D) 13.51 μM

BAP – 6-benzylaminopurine

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Figure 2. Organogenetic response exposed to different concentrations of BAP: (A) 0.00 μM; (B) 4.50 μM; (C) 9.00 μM; and (D) 13.51 μM; arrows indicate the formation of the cell callus

BAP – 6-benzylaminopurine

titious shoot development in the propagation of conifers (Humánez et al. 2011). It was interesting to note that relatively low doses of BAP were needed to induce shoot multiplication and elongation processes.

Several authors have found the presence of direct (Sul, Korban 2004) and indirect (Bello-Bello et al. 2012) organogenesis responses in *Pinus* species, using various concentrations of cytokinins such as BAP, Thidiazuron (TDZ), Zeatin (Z), and 2,4-dichloro-phenoxy-acetic acid (2,4-D). Although the use of BAP (4.50 μM), in combination with the use of temporary immersion systems (RITA®), allows the formation of adventitious shoots by direct organogenesis in *P. patula*, future research will evaluate the efficacy of other temporary immersion systems in the propagation of this valuable forest species. Future research will allow us to evaluate the effectiveness of other temporary immersion systems in the propagation of this valuable forest species, such as temporary immersion bioreactors (BIT®) and gravity immersion bioreactors (BIG).

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