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Are reintroduced wisents a threat to mountain forests?

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The diet of wisents (*Bison bonasus*) inhabiting the Carpathians, studied during a snow-cover period, consisted of 46.8% of woody species consumed in the following manners: debarking (86.3% of dry mass), gnawing (12.6%) and browsing (1.1%). The top two species consumed were the common ash (39.5%) and fir (22.9%). Of the 23 consumed tree and shrub species, 19 species were debarked and 10 were browsed. Fallen trees, cut tree branches and logs of seven woody species were gnawed. The proportion of consumed woody species was positively correlated with snow depth. When ground flora were available, the percentage of twigs and tree bark in the wisent diet decreased, and brambles provided 99.1% of the consumed ground flora dry mass. Access to timber remnants at logging sites and non-valuable species like the willow or aspen may significantly reduce debarking of economically important tree species.

Introduction

Wisents (*Bison bonasus*), also known as European bison, were almost totally extirpated in the 1920s. The last free-ranging population of the subspecies *Bison bonasus bonasus*, occurred in the Białowieża Forest (Poland) in 1919, and of the second subspecies *Bison bonasus caucasicus*, occurred in the Caucasus Mountains in 1927 (Pucek *et al*. 2004). Only several dozens of animals survived in private and public zoological gardens. They were used to initiate the restoration of the species, at first in captivity and later in the wild. Restoration in the wild started in 1952 in the Polish part and in 1953 in the Belarussian part of the Białowieża Forest (Krasińska & Krasiński 2007). Gradually the species was restored at many sites in several countries (Belarussia, Germany, Lithuania, Poland, Romania, Russia, Slovakia, and Ukraine), and there are further plans for the Czech Republic, Denmark and Sweden (Krasińska *et al*. 2014).

Initiatives for the wisent introduction are not supported by foresters due to fear of possible damage to forests (Perzanowski & Marszałek 2012). However, foraging patterns of this species were thoroughly studied only in the Białowieża Forest (Wróblewski 1927, Borowski & Kossak 1972, Gębczyńska *et al*. 1991, Krasińska & Krasiński 2007, Kamiński *et al*. 2010, Kowalczyk *et al*. 2011). There are also some data on its foraging habits from Belarussia, Russia, Lithuania and Slovakia (Korochkina 1969, 1972, Kaz'min & Smirnov 1992, Balčiauskas 1999, Pčola & Gurecka 2008, Gusarov 2011, Kozla *et al*. 2013, Treboganova 2014), but that knowl-

edge concerns populations in lowland forests where the plant composition is different from that in mountain ecosystems.

Large herbivores, including various deer species and moose, are known to cause significant damage to tree stands by browsing and debarking. This problem becomes more intense in winter when access to ground flora is limited by snow cover (Tefler & Kelsall 1984, Bobek *et al*. 1992, Shipley *et al*. 1998).

However, as forest dwellers, wisents are generally classified as grazers or intermediate feeders. The findings by Kowalczyk (2010) and Kerley *et al*. (2012) further support this classification. They indicated that this species had originally been found in open grasslands, but it was forced to inhabit forests solely due to anthropogenic pressures. Nevertheless, even typical grazers like cattle or horses tend to consume a certain proportion of leaves, twigs, or bark of woody species (Hofmann 1989, Vera 2000). Therefore, at every planned introduction site, negative effects of wisents on woody species, especially in commercial forest stands, are considered.

The question of which plant species and which plant parts are mostly selected by wisents is especially important for the evaluation of their potential impact upon woody species that are considered valuable for forest management. The answer to this frequently raised question may be crucial for the acceptance of further reintroductions of this species to various European regions.

Within the framework of the wisent restitution to the Carpathians, sites identified as suitable for its reintroduction occur in a number of countries (from Romania through Ukraine, Poland, Slovakia, and Hungary to the Czech Republic). Those sites are essentially dominated by forest ecosystems, which in most cases are managed for commercial purposes (Kuemmerle *et al*. 2011, Perzanowski *et al*. 2011). Hence, it is important to gain knowledge of the feeding habits of this species in typical Carpathian ecoregion conditions, which could help predict and mitigate potential conflicts between reintroduced wisents and the forest industry. Data for this study, collected during typical Carpathian snowy winters in forest stands of the Bieszczady Mountains, provide information regarding which tree species and which parts of trees are mostly consumed by wisents during periods of snow cover. Furthermore, this study also addresses questions regarding the importance of woody species in the winter diet of these animals, and possible effects of wisent foraging on forest stands.

Material and methods

We carried out this study in the Bieszczady Mountains, a range in the central-eastern part of the Carpathians, situated in southeastern Poland. We collected field data from the winter home range of a western sub-population of wisents (comprising about 250 animals at the time of the study) belonging to a Lowland-Caucasian line. The following three neighbouring forest districts were within the study area: Lesko (600 km^2, 44% forested), Baligród (193 km^2, 98.5% forested), and Komańcza (285 km^2, 77% forested). The forest stands in those districts are dominated by the beech (*Fagus sylvatica*), fir (*Abies alba*) and Scots pine (*Pinus sylvestris*) together accounting for 70%–80% of the stands (Perzanowski 2013) (Table 1).

Snowy winters are typical for this area. Below 500 m a.s.l., snow cover lasts on average for about 90–100 days, but at altitudes above 800 m a.s.l. it can last for up to 140 days. The depth of snow above 800 m a.s.l. may reach 150 cm (Zarzycki & Głowaciński 1970, Michna & Paczos 1972, Nowosad 1975).

Table 1. Proportions (percentage of forested area) of main tree species in forest districts within the study area in the Bieszczady Mountains (source www.krosno.lasy.gov.pl).

Forest district	Beech	Fir	Scots pine	Common ash	Alder
Baligród	38	29	8	1	10
Komańcza	44	18	21	< 1	5
Lesko	29	27	31	< 1	2

Gradual reintroduction of wisents to the area began in 1980, and during the last 3 years (2010–2013), their number was estimated to be approximately 270. The annual home range of this sub-population slightly exceeds 470 km^2, but the truly penetrated area (estimated as 90% kernel) ranges between 150 km^2 in the vegetative season and about 220 km^2 in winter. However, areas of concentration (50% kernel) are only about 11 km^2 in the vegetative season and 30 km^2 in winter (Perzanowski 2013).

We estimated the composition of the wisent diet during the period of snow cover between 1 December and 31 March, during the winters of 2011–2012 and 2012–2013, from all fresh signs of wisent foraging along transects, the method similar to the one used in earlier studies on red deer by Dzięciołowski (1967) and Jamrozy (1980). Along each transect, we measured snow depth several times at randomly selected sites. We performed tracking only on days with continuous snow cover and when snow was sufficiently deep to cover ground flora, which was necessary to determine the area of a single foraging bout. Tracking was undertaken only if tracks were fresh and highly visible, and if the number of animals in a group was sufficiently low to allow for individual identification and measurements of all foraging signs.

We studied a total of 27 transects, and the data from 26 transects (total length of 29.5 km) were used in all calculations. The tracks of about 200 animals were identified along those transects. One additional transect of 2.4 km was treated separately because supplemental food was available there, and also snow cover was exceptionally deep. We recorded every tracking session with GPS and plotted it on a numerical forest map. We processed all thematic layers with ArcMap 10.

We distinguished the following five basic foraging types: (1) debarking which is consumption of bark from living trees or bushes, (2) gnawing which is consumption of bark from fallen or cut trees and their branches, (3) browsing which is consumption of woody plant twigs, (4) foraging on brambles (*Rubus hirtus*), and (5) grazing on other species of ground flora.

To evaluate bark consumption by debarking or gnawing we collected the following data:

- tree or bush species,
- length of the debarked or gnawed area (L_d or L_g, respectively, accuracy 1 cm),
- width of the debarked or gnawed area (W_d or W_g, respectively, accuracy 1 cm),
- percentage of overlap between the debarked or gnawed area and a rectangle of the same length and width (P_d or P_g, respectively),
- thickness of the bark in the central part of the debarked area (G_d, accuracy 0.5 mm),
- diameter of a branch in the gnawed/debarked area (accuracy 0.5 mm).
- tree diameter at 1.3 m above ground (dbh) ($d_{1.3}$, accuracy 1 cm).

We calculated the volume of consumed fresh bark by debarking (V_d) or gnawing (V_f) for a given tree or shrub species as $V_d = L_d \times W_d \times P_d \times G_d$ or $V_g = W_g \times P_g \times G_g$, respectively.

To determine the mean dry mass of 1 cm^3 of bark, we collected 10 bark samples from freshly-cut logs (10–20 cm in diameter, the range most frequently seen for debarked trees) of the tree species that were most often debarked. Squares of the bark (10 × 10 cm) were carefully separated from the wood with a chisel. Their thickness was then measured with a calliper at the central point to the nearest 0.5 mm. Each bark sample was placed in a paper envelope, dried at 70 °C until it reached a stable mass, and weighed to the nearest 0.01 g. For rarely consumed species, we used the dry mass of 1 cm^3 of the bark calculated for common deciduous or coniferous species. These data were used to assess the bark consumption.

We used the dbh values of all debarked trees and the width of the debarked area to estimate the percentage of the phloem missing from the circumference of the tree.

To estimate consumption by browsing, thirty twigs were cut from a tree or bush at the point where they were normally bitten off by browsing wisents, and their diameters at the cut-off point were measured to the nearest 0.1 mm. Then, the twigs were placed in paper envelopes, dried at 70 °C until they reached a stable mass, and weighed to the nearest 0.1 g to calculate the mean dry weight of a twig. For rarely consumed species, we used the mean dry mass of a twig calculated for common deciduous or conifer-

ous species. The consumption by browsing was estimated by multiplying the mean dry mass of a twig by the number of eaten twigs.

To assess consumption of brambles, we set ten plots (1 × 1 m) at the formerly grazed (broken snow cover and visible signs of grazing) sites and ten plots (1 × 1 m) at sites which were not grazed by large herbivores. In each grazed plot, we counted all browsed twigs, and measured their diameters at the point where they were bitten off by wisents to the nearest 0.5 mm. From the ungrazed plots, we collected fully-leafed twigs by cutting them at the point where they were normally severed from plants by wisents. The number of collected twigs was equal to that of browsed twigs. We dried those samples at 70 °C until they reached a stable mass and subsequently weighed them to the nearest 0.1 g. The dry mass of consumed brambles per 1 m^2 was then calculated as the mean value of the dry mass harvested from ten un-grazed plots. This value was subsequently used to determine the amount of brambles eaten by wisents based on the area (m^2) overgrown by brambles that was grazed by wisents in a single foraging bout.

For other species of ground flora, we recorded the species (or genus/family if identification of the species at the vegetative stage was not possible) and the number of consumed twigs, specimens, or tussocks. The consumed dry mass was determined only for the sedge (*Carex sylvatica*). The same number of blades that were consumed by wisents from the nearest tussock were sampled from ten *C. sylvatica* tussocks, which were untouched by animals. Then, we dried the plant material at 70 °C until it reached a stable mass and subsequently weighed it to the nearest 0.5 mm 0.1 g. We calculated the consumption of the sedge as the sum of the dry mass of such samples multiplied by the number of grazed tussocks.

Since wisents rarely consumed other ground-flora species, only their occurrence (not consumption) in the wisent diet was recorded, and their proportion in consumed forage was regarded as negligible.

The effect of snow-cover depth on the proportion of woody species in the wisent diet was evaluated using linear regression. Calculations were performed with Statistica 10.

Results

Characteristics of food items consumed by wisents during periods with snow cover

The mean dry mass of bark (1 cm^2) of the most frequently debarked woody species ranged from 0.28 g cm^{-3} for the spruce to 0.53 g cm^{-3} for the common ash. The values were most variable for the grey alder and least variable for the fir. When browsing trees and bushes, wisents usually consumed only part of the annual growth of a twig. The mean diameter of twigs at the point where they were normally severed from plants by wisents depended on the species and ranged from 3.0 to 8.7 mm. The dry mass of an average single browsed twig was smallest for the sycamore (0.48 g) and highest for the grey alder (21.34 g). The dry mass of twigs with the same diameter varied considerably (*see* Table 2).

The branches consumed by wisents from fallen trees or timber leftovers at logging sites, were on average 13 and 15 mm in diameter for the mountain ash and the aspen, respectively. The respective mean ± SD dry mass values were 98.45 ± 25.3 g and 98.50 ± 23.4 g. From a patch of brambles (1 m^2), wisents consumed on average 105.3 ± 29.9 g dry mass, and from one sedge tussock they ate on average 11.3 ± 2.41 g dry mass.

Depth of snow and the proportion of ground flora and woody species in the wisent diet

During the entire studied period (continuous snow cover), 46.8% of the wisent diet consisted of woody species (browse and bark), and the remaining 53.2% were various ground flora species. However, there were differences in the diet composition in the two consecutive years. Woody species dominated in the 2011–2012 season (57.5%), and ground flora in the 2012–2013 season (65.7%).

Wisents foraged on woody species mainly by debarking (86.3% of dry mass), while gnawing and browsing were not common (12.6% and 1.1%, respectively). Of the dry mass of consumed ground flora, 99.1% were brambles.

Therefore, the two most important items in the winter wisent diet were tree bark and brambles, together comprising over 90% of the dry mass consumed (91.8% in 2011–2012 and 94.8% in 2012–2013) (Table 3).

The increase in proportion of woody species in the wisent diet was only partly explained by an increase in snow depth ($y = 0.0224x - 0.11$, $r^2 = 0.4152$), which during the study ranged between 7.5 and 45.0 cm (except during one tracking session). There were, however, cases of wisents foraging solely on ground flora at snow depths of 20–30 cm. Wisents also foraged on very high proportions of woody species (> 80%) when there was 17–25 cm of snow on the ground. At snow depths ≤ 15 cm, the proportion of consumed woody forage was always below 6%. Attempts of wisents trying to dig through deep snow to gain access to ground flora were observed frequently. In such cases, animals frequently reached their goal by pushing the snow down from steep creek banks, which are often densely overgrown with brambles in the Bieszczady Mountains.

Plant species consumed by wisents during periods with snow cover

The absolute majority of food (> 99.0%) consumed by wisents from the forest floor consisted of brambles, while sedges provided only about 0.9% of dry matter. Other species, appearing incidentally in the diet, were raspberry (*Rubus idaeus*), rush (*Juncus* sp.) and various grasses (Poaceae). However, their contribution was insignificant, and they were included with sedges in the category of 'other green plants'. Wisents were also obviously searching for beechnuts by poking the forest litter, but estimation of the amount they consumed was not possible. During the two study seasons, wisents foraged upon 14 tree and 9 shrub species. Amongst all woody plants in the diet, 39.5% was the common ash, 22.9% the fir, 9.9% the sallow, and 7.6% the grey willow. The remaining 20.1% came from other species, whose proportions did not exceeded 5.0% of the dry matter consumed (Table 4).

Nineteen of the 23 tree and shrub species eaten by wisents were debarked. The diameter of debarked trees ranged between 2 and 35 cm (mostly between 10 and 20 cm). The proportion of food consumed by debarking did not differ much from the proportion of woody species in the total quantity of foraged species. Aspens (live standing trees) were an exception as they were not debarked but only browsed, providing 4.4% of the total foraged amount from trees and shrubs (Table 4).

Table 2. Mean ± SD dry mass of 1 cm^3 of tree bark, mean diameter of twigs at the point where they were normally bitten off by browsing wisents, and mean ± SD dry mass of twigs consumed by wisents.

	Bark	Twigs	
	Dry mass ± SD (g)	Mean diameter at cut-off point* (mm)	Dry mass ± SD (g)
Fraxinus excelsior	0.53 ± 0.03	6.4	6.44 ± 1.24
Acer pseudoplatanus	0.51 ± 0.03	3.0	0.48 ± 0.22
Alnus incana	0.41 ± 0.05	8.7*	21.34 ± 6.56**
Corylus avellana	0.51 ± 0.03	3.0	1.01 ± 0.20
Salix caprea	0.39 ± 0.02	–	–
Picea abies	0.28 ± 0.02	–	–
Abies alba	0.47 ± 0.01	3.8	2.06 ± 0.58
Sambucus nigra	–	4.1	1.19 ± 0.43
Frangula alnus	–	3.0	1.15 ± 0.33
Cerasus avium	–	3.0	1.15 ± 0.31
Mean value for deciduous species	0.47	4.5	4.68
Mean value for coniferous species	0.37	3.8	2.06

* the point where they were normally bitten off by browsing wisents.

** browsing on the grey alder was recorded only at the transect where wisents had access to supplemental food.

Four tree and six shrub species were browsed, and as much as 78.5% of the dry mass acquired by browsing were twigs of the fir. The contribution of the common ash and other woody species that consumed in the same manner was also considerable (14.2% and 7.3%, respectively).

Fallen trees, tree branches on the ground, and the logs of seven woody species were gnawed. As much as 82.3% of the whole dry mass of food consumed in this way came from the common ash and aspen (which was only consumed in this form). The consumption of the fir (13.7%) was also substantial. Moreover, the bark of all seven species was gnawed. Regarding the common ash and aspen, twigs greater than 10 mm in diameter were also consumed. All available specimens of those two species were gnawed, and most of the gnawing was observed on the branches and tree tops left at logging sites. Other species were randomly gnawed and often ignored by wandering wisents. Of the total quantity of food consumed from fallen trees and logs, 70.7% was bark and 29.3% were twigs (Table 4).

However, there were considerable differences in the contribution of various species to the wisent diet between the two consecutive seasons. Regarding debarking, the greatest differences were between the values for fir, alder and spruce trees, which were consumed in the 2012–2013 season in much smaller quantities than a year earlier. Moreover, the grey willow, which was not eaten during the 2011–2012 season, constituted 25.7% of the woody forage consumed by wisents during the 2012–2013 season. In both seasons, the common ash was very important among debarked species, but its proportion was much higher during the latter season. Among the browsed species, the fir was dominant in both seasons. The proportion of gnawed species differed greatly between seasons: in 2011–2012, the aspen (51.8%) was the most frequent, followed by the common ash (22.9%) and the fir (20.3%); while in 2012–2013, the common ash alone contributed 97.8% of the gnawed matter.

The effect of supplemental feeding on the selection of natural food

Data from one tracking session (2.4 km) were excluded from the analysis because along that transect supplemental food was available and an average snow cover depth reached 90 cm. Practically all (99.9%) food consumed by the six individuals registered along this trail came from natural sources (94.9% tree bark, 3.3% gnawed matter and 1.7% browse). The remaining 0.1% came from brambles (*see* Table 5).

At this transect, the very high percentage of the alder among browsed species (76.3%) was surprising because this species was not browsed at other transects. Despite unlimited access to supplemental food, including hay, beet, and special pellets containing tree bark, wisents debarked 214 trees and shrubs. The wisents attempted to gain access to ground flora several times, especially along the steep banks of creeks where they pushed snow down in an effort to reach green plants on the forest floor.

Discussion

When wisents were reintroduced to the Białowieża Forest in 1952, it was assumed that they required supplementary feeding in winter

Table 3. Proportions of food types in the dry mass consumed by wisents at the Bieszczady, during the periods with snow cover.

Seasons	Average depth of snow cover (cm)	Woody species			Ground flora	
		Bark from live trees (%)	Gnawed branches and logs (%)	Browse (%)	Brambles (%)	Other green plants (%)
2011/2012	31	49.5	7.3	0.7	42.3	0.2
2012/2013	20	29.9	4.2	0.2	64.9	0.8
Average	26	40.4	5.9	0.5	52.7	0.5

Table 4. Percentages of trees and shrubs in the forage consumed from woody species, and their proportions in various types of foraging (debarking, gnawing and browsing). Given are mean values for both studied seasons.

Species	Proportion in consumed woody species (% d.m.)	Proportion in debarking (% d.m.)	Proportion in browsing (% d.m.)	Proportion in gnawing (% d.m.)
1. *Fraxinus excelsior*	39.5	38.6	14.2	47.4
2. *Abies alba*	2.9	23.6	78.5	13.7
3. *Salix caprea*	9.9	10.9	–	3.3
4. *Salix cinerea*	7.6	8.8	0.7	–
5. *Alnus incana*	4.7	5.5	–	–
6. *Populus tremula*	4.4	–	–	34.9
7. *Corylus avellana*	4.2	4.8	2.1	0.2
8. *Picea abies*	3.1	3.6	–	–
9. *Tilia cordata*	1.2	1.4	–	–
10. *Cerasus avium*	0.9	1.0	–	–
11. *Acer pseudoplatanus*	0.5	0.6	0.2	–
12. *Malus sylvestris*	0.4	0.4	0.1	0.3
13. *Fagus sylvatica*	0.3	0.3	–	–
14. *Prunus spinosa*	0.2	0.2	0.2	–
15. *Quercus robur*	0.1	0.2	–	–
16. *Crateagus* sp.	< 0.1	< 0.1	–	–
17. *Frangula alnus*	< 0.1	< 0.1	1.1	–
18. *Carpinus betulus*	< 0.1	< 0.1	–	–
19. *Evonymus europaea*	< 0.1	< 0.1	–	–
20. *Sambucus nigra*	< 0.1	–	2.7	–
21. *Salix fragilis*	< 0.1	–	–	0.2
22. *Sorbus aucuparia*	< 0.1	–	0.1	–
23. *Padus avium*	< 0.1	< 0.1	–	–
Sum	100	100	100	100

(Krasińska & Krasiński 2007). Recently, in the Bieszczady Mountains, the winter feeding of wisents was applied solely as a management tool, mostly to prevent undesirable migrations or to bond the animals to a release site (Perzanowski & Marszałek 2012). However, it remained unclear (1) whether wisents were able to survive severe winters without human help, and (2) which plants were selected by wisents during periods of critically-reduced access to natural food resources. Answering these questions was also very important to ascertain if free-ranging wisents could pose a serious risk of damage to forest stands.

To maintain identical standards during our study, the same person performed all observations and measurements. According to Gębczyńska (1980) and Gębczyńska *et al.* (1991), studies of diet composition based on snow tracking overestimate the proportion of food coming from woody species as compared with analyses of rumen contents or scat. On the other hand, they eliminate errors resulting from animal access to supplemental feeding.

Studies of the wisent diet composition in the Białowieża Forest included direct observations

Table 5. Species composition (percentage of dry matter) of trees and shrubs being debarked, browsed, and gnawed by wisents, when supplemental food was available, and snow cover was exceptionally deep.

Species	Debarking (%)	Browsing (%)	Gnawing (%)
Fraxinus excelsior	56.6	23.7	–
Alnus incana	20.5	76.3	26.7
Corylus avellana	17.6	–	–
Salix caprea	2.7	–	73.3
Sorbus aucuparia	1.7	–	–
Prunus spinosa	0.9	–	–
Fagus sylvatica	0.1	–	–
Acer pseudoplatanus	< 0.1	–	–
Sum	100	100	100

of foraging animals, or rumen and scat analyses (Borowski & Kossak 1972, Gębczyńska *et al*. 1991, Jaroszewicz & Pirożnikow 2008, Kamiński *et al*. 2010, Kowalczyk *et al*. 2011), hence their results may not be directly comparable with ours. Nevertheless, our results for the season with higher snow cover (57.5% of food from woody species) correspond fairly well with the value (65%) reported by Kowalczyk *et al*. (2011) for the Białowieża Forest individuals that stayed away from the main herd and those that did not visit feeding stations. However, due to the lack of snow cover data, a direct comparison is not possible. Krasińska and Krasiński (2007) reported that during mild winters, wisents at Białowieża preferred natural food over supplementary feeding.

The proportion of woody plants in the diet of wisents in the Bieszczady Mountains varied greatly (0%–97.3%), and was to some extent dependent on snow-cover depth: it was low when there was less than 15 cm of snow on the ground, but exceeded 90% when the thickness of snow cover was more than 25 cm. This result is indirectly supported by Kaz'min and Smirnov (1992) who found that the proportion of ground flora in the diet of the wisents in the Caucasus Mountains was 59% at the beginning of winter when the snow was fairly shallow, and 6% during the second half of winter when the snow was deep. Same was also reported by Ahlén (1965) for red deer in southern Sweden, which tended to feed on ground vegetation under the canopy of old spruce trees; however, when the snow was deep and frozen, they switched to bark and browsing comprising 98% of their diet. According to the data collected in Poland by Bobek *et al*. (1992), snow cover of 50 cm may completely restrict red deer's access to ground flora. However, because of their body mass and strength, wisents are better able to cope with deep and frozen snow than deer. Furthermore, during the present study, deer were frequently observed feeding at sites formerly grazed by wisents, and they also followed paths trampled by wisent herds after snowfall.

The number of plant species (28) that were consumed by wisents in our study is much smaller than reported in other studies from the Białowieża Forest (93–454; Borowski *et al*. 1967, Borowski & Kossak 1972, Gębczyńska *et al*. 1991, Jaroszewicz & Pirożnikow 2008, Kamiński *et al*. 2010). However, those studies were conducted either during vegetative seasons or throughout the year. Moreover, some species found in winter diet were absent from the area but they were available to wisents through supplemental feeding, and they were also found in agricultural areas surrounding the forest.

There were also considerable differences in woody species consumption between the Bieszczady Mountains and lowland forests. The common ash dominated in the Bieszczady Mountains (39.5%), but it only constituted 2% of the wisent diet in the Białowieża Forest. This species was also among the most eagerly consumed in Lithuania (Balčiauskas 1999). On the other hand, the hornbeam and the hazelnut that were frequently eaten (about 50%) in the Białowieża Forest, were of marginal importance in the Bieszczady Mountains (Kowalczyk *et al*. 2011) (Table 5). If we exclude species which, like the fir, do not naturally occur in the Białowieża Forest (Michalczuk 2001, Jaworski 2011), differences in common ash, hazelnut or aspen consumption cannot be explained solely by their availability or palatability, since proportion of the common ash found by Jamrozy (1980) in the diet of the red deer inhabiting the same type of forest habitat to that in the Bieszczady Mountains was < 1%.

Consumption of brambles by wisents in the Bieszczady Mountains and the Białowieża Forest cannot be compared because in the latter two different, much less abundant species (*R. suberectus* and *R. caesius*) occur (Okołów *et al*. 2009). In the Bieszczady Mountains, *R. hirtus* forms large, dense patches providing up to 90% of the ground flora biomass, which allows herbivores to maintain very high consumption rates (Janik 1997). Its leaves, which are easily digestible and rich in proteins, remain green throughout the winter; therefore, this species is a very important diet component of all ruminants in the habitat (Jamrozy 1980, Nowakowska 1981, Bobek *et al*. 1992, González-Hernández & Silva-Pando 1999). Also, according to Kaz'min and Smirnov (1992), in the Central Caucasus this species is an important component of wisents' food in winter. Brambles in our study area are

mostly available in fairly young Scots pine and alder stands, in former agricultural areas, and within native beech–fir stands with loose canopy or within gaps in the stand. Therefore, these tree stand types are highly preferred by wisents in the Bieszczady Mountains (Wołoszyn-Gałęza 2005).

Differences in the diet composition between wisents dwelling in lowland forests (e.g. Białowieża Forest) and mountain ecosystems (e.g. the Carpathians) may also be explained by the concept of food blocks (Kossak (1976), according to which instead of particular plant species, herbivores prefer their groups specific to ecosystems and depending on the structure of a given phytocenosis.

Selection of some tree species like the willow or the birch by herbivores may depend on their specific chemical properties (i.e. occurrence of salicylic acid or compounds inhibiting digestive processes) (Rehbinder *et al*. 2002, Krauze–Baranowska & Szumowicz 2004, Grynkiewicz & Hennig 2010). On the other hand, differences in the diets of various large herbivores found in the Bieszczady Mountains result from factors such as their specific foraging patterns, digestion efficiency, and anatomical as well as physiological adaptations (Pytel 1969, Gębczyńska *et al*. 1974, Kowalczyk *et al*. 1976, Hofmann 1989). Nevertheless, the degree of overlap between the foraging niches of wisents and red deer in the Bieszczady Mountains is not high, and it reflects a difference between these two species regarding their potential impact on woody vegetation. Data from similar habitats in the Carpathians, collected using a similar method by Jamrozy (1980), show strong dominance of browse and tree bark in the winter diet of red deer (92%). In addition to a much lower proportion of woody species in the wisent diet, of all tissues tree bark was most commonly consumed by wisents (89.9%), while browse was preferred by red deer (70%). Therefore, the impact of these herbivores on young trees is quite different, and assessments of damage to young plantations should be carefully conducted if both species co-exist in the same area.

According to our data, in periods with continuous snow cover (i.e. when damage to tree stands is most likely to occur), about 50% of the wisents' food comes from woody species. However, this proportion is dependent to some extent on snow depth, and the proportion of twigs and tree bark in the diet decreases by several percentage points when animals have direct access to ground flora. This indicates that woody species are not the main food source for wisents. However, a specific, minimal proportion of fibrous matter is necessary for maintaining digestive processes in the rumen (Pytel 1969, Bobek *et al*. 1992). Therefore, in the Bieszczady Mountains, the best foraging conditions for wisents are not in a dominating forest type (i.e. mature beech–fir stands) but the in forecrop stands such as those of the Scots pine or the grey alder that grow in former agricultural areas that have rich bramble undergrowth. This combination of highly productive grazing grounds and habitats that provide good cover explains the less intensive use of open pastures by wisents in the Bieszczady Mountains as compared with animals from lowland forests.

Of the tree species that were important components of the wisent diet, only the fir is considered economically important for forestry (*see* Table 1). The common ash, with the exception of a few stands where it dominates, is only an admixture. Willows and alders occur only along watercourses, in gaps, or in earlysuccession stands, and are not economically important (Jaworski 2011, Matuszkiewicz *et al*. 2012). The data on the diameter of debarked trees from Belarus and Russia in Krasińska and Krasiński (2007: up to 10, 15 or 30 cm) correspond well with our observations (*see* Table 4).

We found that damage resulting from wisent browsing is marginal, but debarking may be a significant problem for certain species. For instance, the common ash is under especially strong pressure, because the same tree is often repeatedly debarked for several consecutive years (Szukiel 2001).

Wisents usually damage the bark along one-fifth to one-fourth of the tree trunk circumference, and the average length of the debarked area is 62 cm. However, a single debarked area by red deer is much smaller (2 × 23 cm on average) (Bobek *et al*. 1992). Such extensive damage to the bark triggers tree deformations and increases the risk of fungal or insect invasions (Starzyk & Łuszczak 1982, Szukiel 1986). According to the

data from the Baligród Forest District, maintenance of the common ash in tree stands within areas of wisent' concentrations during winter is not possible now. However, as compared with that of other ungulates the population of wisents in the Bieszczady Mountains is still generally not very high (about 270 *vs.* ~2900 red deer). Therefore, considering the size of their home range, wisents do not cause economically significant forest damage (Jamrozy 1973, Jamrozy *et al.* 1981, Perzanowski *et al.* 2008, Paszkiewicz & Januszczak 2010).

One tracking session was carried out under deep-snow conditions (90 cm), considerably exceeded the limit (65 cm) regarded by Van Camp (1975) as critical for American bison. Furthermore, that group of wisents visited a feeding station for red deer supplied with hay and beet. Despite unlimited access to good quality forage, those wisents intensively debarked surrounding trees. Such behaviour was frequently observed in the Bieszczady Mountains and around permanent feeding stations at the Białowieża Forest (Kowalczyk *et al.* 2010, Paszkiewicz & Januszczak 2010). This indicates that supplemental feeding in winter may not be an effective way of preventing damage to trees. However, a considerable amount of tree bark was gnawed by wisents from fallen trees, cut off branches and logs. This agrees with earlier results obtained in the Białowieża Forest (Krasińska & Krasiński 2007). Hence, debarking of economically important species could be significantly reduced by making timber remnants at logging sites accessible, and by adding attractive seedlings without economic value (e.g. willows or aspens) to forest plantations. A similar effect may be achieved by shifting the timing of thinning in younger stands to winter, and by leaving fallen trees on site to allow gnawing. Such measures were successfully applied to mitigate damage to Scots pine stands by moose (Komenda 2001, Szukiel 2001). Supplemental feeding may also be a factor disturbing seasonal-migration patterns typical to Carpathian wisents because the presence of attractive forage may delay their departure from summer ranges and keep them around feeding stations.

To conclude, our data show that during winter Carpathian wisents mostly forage on ground flora, even if it is difficult to access due to snow cover. The most important food item during that period, allowing them to meet their energy and protein requirements, was brambles, which wisents were able to locate even under deep snow. The tissues of woody species, mostly tree bark, were an important component of the wisent diet, but were consumed in larger quantities only when access to ground flora was severely limited. Damage to tree stands due to wisent foraging can currently be regarded as negligible, except for debarking of highly preferred species (e.g. ash), especially during periods of very deep snow cover or around feeding stations. Therefore, provision of supplemental food to wisents should be treated as an option for managing their spatial distribution rather than as an approach to improve their nutritional status during winter or as a measure against tree stand damage. Our results should be helpful when planning introductions of new free-ranging populations in mountain habitats.

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