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Source: Folia Zoologica, 67(3-4) : 165-172

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v67.i3-4.a3.2018

Folia Zool. – 67 (3–4): 165–172 (2018) DOI: 10.25225/fozo.v67.i3-4.a3.2018

The importance of natural food in wild boar (*Sus scrofa*) diet during autumn and winter

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Received 14 March 2018; Accepted 24 August 2018

Abstract. The diet of wild boar (*Sus scrofa*), a native and problematic species of European ecosystems, highly reflects the management of the species as well as the level of its damaging effect. This study focuses on the importance of natural dietary components in the diet of wild boar over the autumn to winter season (i.e. the main hunting season) in four predominantly oak forests in the Czech Republic. We also studied the effect of supplementary feed, especially maize, on feeding preferences. The oak acorn was always preferred, regardless of other natural or supplementary feeds available. Both acorns and maize are highly nutritional, energy rich foods and boars always consumed at least one of these energy-rich foods. If acorns were not available, supplementary feed, and especially maize, was actively searched for, whereupon they often substituted for acorns nutritionally. The wild boar is the dominant competitor for acorns and can potentially exploit the whole forest crop, depending on the size of the acorn crop, the wild boar population density and the density of other ungulates in the forest. When the acorn biomass was exhausted, supplementary feed (predominantly maize) was always preferred.

Key words: food preference, acorn, maize, seasonal diet, supplementary feeding

Introduction

The wild boar (*Sus scrofa*), a problematic game species in many countries, has been the subject of much debate in the Czech Republic in recent years (Bartoš et al. 2010), and indeed in Europe as a whole. Of particular interest has been their behaviour in relation to damage to field crops, forest stands and protected ecosystems and transmission of diseases (Baubet et al. 2004, Klein et al. 2007, Schley et al. 2008). The diet of wild boar is highly diverse, which allows the species to not only survive in a wide range of environments but also to create viable populations (Rosell et al. 2001, Baubet et al. 2004, Irizar et al. 2004). In habitats where it can obtain high-quality food throughout the year, the negative impacts are increased still further as the population density can increase considerably. As an opportunist omnivore, wild boar diet will be determined by the availability and abundance of food items (Schley & Roper 2003). In autumn, however, the food available to wild boar is wide and varied, with many fruit and field products available, along with acorns and beechnuts in mast years. On the other hand, winter is a critical season for the wild boar, along with other European mammals, as the natural food supply can be considerably limited by climatic conditions. In such cases, its survival is generally ensured through the provision of supplementary feed or by hunter's baiting, with maize being among the most frequently used baits to attract wild boar into hunting areas (Schley & Roper 2003, Bartoš et al. 2010). Supplementary feeding of wildlife during winter is obligatory under Czech law and is undertaken intensively throughout the country (Putman & Staines 2004). In the case of the wild boar, it has been suggested that consumption of such feed may increase their reproductive potential and contribute to the increase in their population density (Gortázar et al. 2000, Cellina 2008, Herrero et al. 2008, Ježek et al. 2016).

Wild boars always include at least one nutritious food component in their diet, especially acorns or some cereals (Schley & Roper 2003). Acorns are a very

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important resource as they are both nutritious (high in protein and sugars) and easy to digest (Herrero et al. 2004); however, they are only available in high numbers in mast years that only occur every three years or so (Bieber & Ruf 2005). In other years, the wild boar must adapt its diet to those foods currently available (Challies 1975, Wood & Roark 1980, Cellina 2008).

Thanks to their nutritional value, the acorn is also a favoured food of other woodland species and can also have a significant effect on their population dynamics (Massei et al. 1996, Ostfeld & Keesing 2000, Bieber & Ruf 2005). The rates of intake and the ability of wild boar to displace native wildlife species from feeding sites (Berger 1985) and obtaining a higher-quality diet by discarding acorn shells suggest that wild boar can compete effectively with wildlife for mast crops (Elston & Hewitt 2010).

In this study wild boar diet was analysed from four localities, all situated in forest dominated by oak in a good acorn harvest year in autumn-winter period. In all localities also supplementary food was given (mostly maize). Both these diet supplies (natural and supplemental) were compared as to nutritional content to see if this factor influence the food dominance. We presume oak acorns would be hypothetically dominant food over other food available, because of natural, energy-rich source. We also tracked the changes in wild boar food during half of the year (from late summer until the end of January) to know the food resources utilization dynamics in a site under intensive management (Soutok).

Study Area

Samples were collected during the autumn and winter of 2014 and January 2015 from four forest sites in the Czech Republic: Soutok (SO), Valtice (VA), Křivoklátsko (KR) and Domousnice (DO) (Fig. 1, Table 1, 2 and 4). All four sites were dominated by oak (*Quercus* sp.) forest and, while the natural food supply of acorn was similar, different supplementary food was supplied at each site. In all sites there was an intensive oak seed year. None of the sites suffered from substantial human disturbance or urbanisation.

Site SO is a game preserve situated in the floodplain forest aligning two large rivers, the Morava and Dyje. Open areas are mostly covered with alluvial grassland. The site contains numerous forest pools, cut-off meanders and channels. The forest stand comprises oak, European ash (*Fraxinus excelsior*), alder (*Alnus* sp.), poplar (*Populus* sp.) and willow (*Salix* sp.).

Site VA stands in a complex of production forest surrounded by farmland. The forest stand consists of oak, elm (*Ulmus* sp.), pine (*Pinus sylvestris*) and ash, often mixed with black locust (*Robinia pseudoacacia*). The surrounding farmland consists of wheat, maize, sunflower and barley. Roe deer (*Capreolus capreolus*) are common at the site.

Site KR represents a typical old oak stand mixed with hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). Forest-free land is covered by grassland.

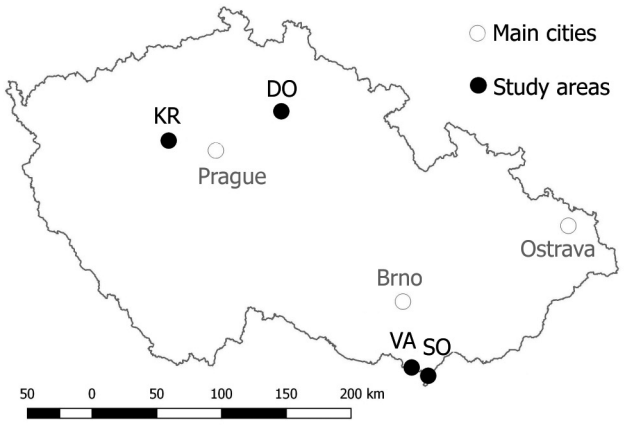

Fig. 1. Distribution of studied sites in the Czech Republic, locations are marked with solid point.

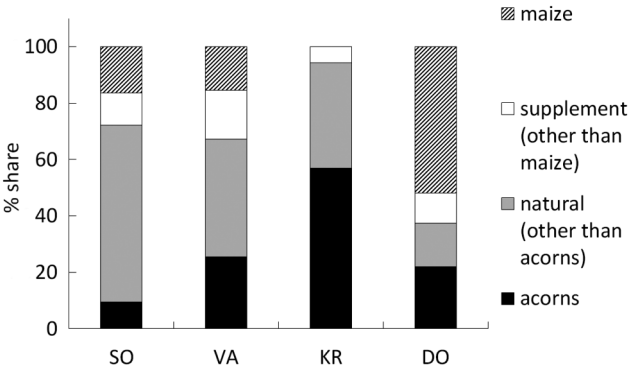

Fig. 2. The proportion of acorns, natural food and supplemented diet on locations (mean in %v).

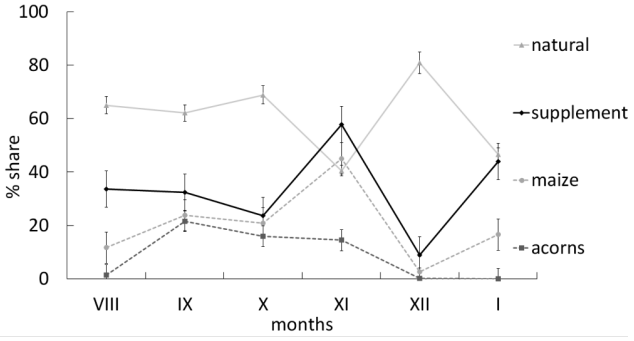

Fig. 3. The main diet components changes (natural food supply – natural; supplemented food supply – supplement; maize and acorn; in % of volume) during the monitored period in SO.

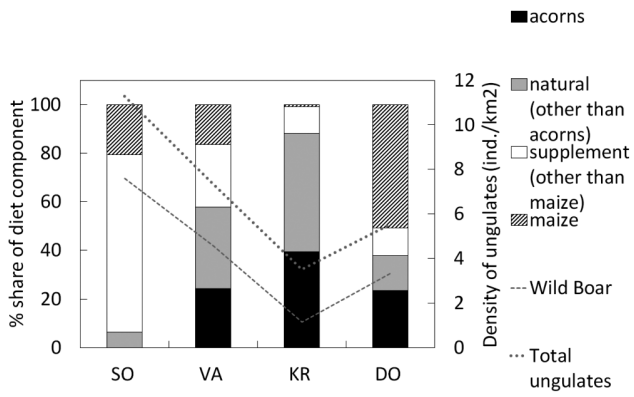

Fig. 4. Comparison of acorns consumption and ungulates densities in the localities in January.

Site DO is a mixed oak forest comprising several forest stands surrounded by farmland, where maize, rape and cereals are grown.

Data on wild boar density (ind. km^2) was obtained from the local hunting authorities, these figures being considered as more relevant than the official Czech game abundances (Table 2).

Material and Methods

Sampling

We took part in a number of drive hunts at each of the above-mentioned sites and were given permission to extract whole stomachs of all wild boars shot. All

Table 1. Description of study sites.

Location	Abbreviation in text	Character	Coordinates	Area (km^2)	Elevation (m a.s.l.)	Forest vegetation grade	Share of forest, fields, meadows and other areas (%)
Soutok	SO	flood plain forest	48.6734047 N, 16.9477844 E	63	160	oak	87/10/0/3
Valtice	VA	oak forest	48.7320886 N, 16.8236733 E	28	192	oak	86/11/1/2
Křivoklátsko	KR	oak forest	50.1096914 N, 13.9737511 E	193	465	oak beech	73/7/14/6
Domousnice	DO	mixed forest	50.3873000 N, 15.0808811 E	22	359	beech oak	63/24/8/5

Table 2. Game species present and supplemental foods provided at the study sites.

Location	Supplemental diet	Ungulate species	Wild boar density ind./km^2	Estimated total ungulate density ind./km^2	Share of oak forests (%)
SO	cereals, maize, beets	*Cervus elaphus*, *Dama dama*, *Capreolus capreolus*	7.6	11.3	67
VA	maize, beets	*Capreolus capreolus*	4.6	7.3	52
KR	cereals, beets	*Dama dama*, *Ovis musimon*	1.2	3.5	54
DO	maize, beets	*Capreolus capreolus*	3.3	5.5	48

Table 3. Nutritional content mean and standard deviation (in parentheses) of whole acorns (W), peeled acorns (P) and maize (M). Statistically significant differences are marked with asterisks (** = $p \leq 0.01$). (OM - organic matter, Nl – crude protein, NFE – nitrogen free extract, GE – gross energy).

g/kg	Whole acorn		Pealed acorn		Maize		W × P	W × M	P × M
OM	977.76	(0.67)	980.46	(0.22)	983.7	(0.30)		**	
Nl	69.10	(2.78)	61.86	(0.39)	106.6	(0.41)		**	**
Fat	34.18	(2.34)	65.84	(0.67)	45.2	(0.49)	**		
Fibre	23.82	(0.94)	11.36	(0.29)	22.5	(0.86)	**		
NFE	850.65	(2.82)	841.48	(0.51)	809.4	(1.07)	**		
GE	18.82	(0.67)	19.90	(0.36)	19.48	(1.44)	**		
Ash	22.24	(0.67)	19.54	(0.22)	16.2	(0.25)		**	

Table 4. Differences in food intake between areas (mean in %v).

%v	SO	VA	KR	DO
Animal food	7.00	8.41	15.77	11.20
Grass	11.80	7.19	14.30	1.69
Acorns	9.40	25.43	56.86	21.90
Fruit	11.80	3.83	0.00	1.96
Herbs	5.18	8.52	2.27	0.41
Roots	24.00	3.83	3.58	2.09
Beet	4.81	13.12	1.71	8.67
Cereals	6.66	3.95	3.93	0.20
Maize	16.37	25.70	0.00	51.81
Other	2.98	0.02	1.59	0.08

samples were collected in autumn 2014 to the end of January 2015. At SO sampling was continuous from the end of summer 2014 until the end of January 2015 (half of the year, every month), depending on the success of the hunters; at VA, KR and DO, samples were always collected during local hunts. After dissection the stomach was cut full length and a representative sample of 0.5 kg removed. Each sample was then placed in a polyethylene container labelled with sex, age, live weight and identification number of the individual. The samples were then transported to the laboratory where they were deep-frozen at –20 °C and stored for subsequent microanalysis. In addition, samples of maize and acorns from nature were collected in order to determine the chemical and nutritional content.

Stomach analysis

Food content from the stomach samples was analysed using the standard volumetric method (Zeman et al. 2016a). The relative volume (%v) of each item was then calculated from the food volume. The percentage frequency (%f) of each food item was calculated using the formula $\%f = 100\ f/\Sigma f$. Diversity (H') of food items in the diet was calculated on the basis of relative volume data using the Shannon-Wiener diversity index (H'; Shannon & Weaver 1964). As the wild boar occasionally peals the acorns while consuming them (Elston & Hewitt 2010), we focused in our analysis to see the fragmentation and proportion of the acorns in stomachs. In some individuals the entire acorn was in the stomach but in some only whitish mash with a minimum of shell (pericarp) was present. This is why chemical analysis was undertaken on peeled and unpeeled acorns (Zeman et al. 2016b). The nutritional quality of whole and peeled acorns and maize was assessed from dry matter, ground and mixed samples from four locations were prepared and being sent for laboratory analysis in order to determine organic matter (OM) content (nitrogenous substances N × 6.25 – crude protein (Nl), fat, nitrogen-free extract (NFE), fibre and gross energy (GE) (AOAC 1975).

To trace the changes in wild boar food during half of the year and record the degree of human influence on food composition at SO, stomach samples of shot wild boar were analysed every month from August to January (August – 4 samples; September – 14; October – 14; November – 13; December – 21; January – 13). Wild boar consumption of acorn, maize, supplementary feeding and natural sources of food were evaluated.

Data analysis

Non-parametric one-way ANOVA (Kruskall-Wallis test) was used to compare the expected values of natural food in stomachs at the four study sites. A non-parametric test was chosen as none of the localities provided normal data distribution. In order to compare the proportion of maize and natural foods in the stomachs, a correlation coefficient was calculated and tested using the correlation coefficient significance test. The Kruskall-Wallis test was also used to compare the expected values of food chemical components in whole acorns, peeled acorns and maize dry matter. This test was used due to the low number of samples in each group (always five).

To prove the influence of the wild boar densities on the oak acorn depletion we compared the amount (%v) of oak mast in the stomachs by Kruskal-Wallis ANOVA in all four localities under study. Non-parametric test was used due to small sample sizes in compared areas. The level of significance for all analyses was set at $\alpha = 0.05$, giving a confidence of 95 %. The STATISTICA 12 software package (StatSoft 2013) was used for all calculations.

Results

A total of 182 samples were collected from the four sites, 79 from SO, 39 from VA, 34 from KR and 30 from DO. Analysis of the samples detected a wide range of natural food components, including herbs, grass, wood, tubers, fruit, pine needles, tree leaves, roots, bark, moss, acorns, nuts, herb seeds, clams, beetles, rodents, a salamander, a feather, fish, earthworms and other indeterminate items of animal origin. Supplementary feeding components identified included maize, wheat, barley, oats, cereal husks and beetroot. The diet at all sites included an important proportion of acorns and maize. The comparison of

expected values for the proportion of natural food items in the stomachs at the four sites showed statistically significant differences ($H(3, 178) = 40.0682$, $p < 0.001$). The multiple comparison test indicated that identical proportions of natural food were only taken at SO and VA. Site KR had a statistically higher proportion of natural food than the other localities, where a large proportion of acorns was taken, and site DO had a statistically lower proportion (Fig. 2).

The proportions of maize and natural food in stomachs negatively correlate ($t(4) = -2.7978$, $p = 0.0489$) at –0.814, suggesting that the proportion of natural food decreased as the proportion of maize in the diet increased and *vice-versa*.

At SO, natural food was recorded most often (roots and grasses, both 18 % of relative frequency). The most frequently consumed item at VA were grasses (19 %f), followed by animal food, acorns and maize (all 14 % of relative frequency). At KR, animal food and acorns were eaten with the same high frequency (25 %f). At DO, maize was the most often eaten item (24 %f), followed by animal food. The diversity of the diet was highest at lowland localities (VA: H' = 2.01; SO: H' = 1.95). Samples from sites DO and KR had a relatively low diversity (H' = 1.42 and H' = 0.23, respectively).

Content of substances in dry matter

Statistically different results were obtained when comparing individual food components in peeled and whole acorns and maize. The most important component was Nl in maize. Peeled acorns had highest levels of fat and gross energy (GE), and the lowest fibre content express this good food quality (Table 3).

Dietary changes at SO (from late summer to January)

Our data indicate clear changes in food composition in the wild boar population at SO related to consumption of supplementary feed, natural food, acorns and maize over autumn and winter (Fig. 3). Supplementary food was supplied at all times; nevertheless, natural food was dominant in diet between August and October. Maximum acorn consumption occurred in September and lower in October and November. Supplementary food (from baiting stations) was dominant (approximately 60 %; mostly maize) in the diet in November, the most intensive period of the hunting season. In December, the situation was opposite, with supplementary food representing only 10 % of the diet. Acorn reserves had already been exhausted and roots were the dominant item taken. In January, supplemented food, such as maize (17 % of stomach content) and beetroot (16 %) were more intensively consumed.

Acorn exploitation

There was a noticeable difference in oak acorn exploitation between the study sites. Kruskal-Wallis ANOVA confirmed the percentage of acorns in diet of hunted wild boars was significantly different between studied locations ($p = 0.0074$). Difference was found between locations SO, with highest wild boar densities and acorn already depleted in January and KR with the lowest wild boar densities and acorns remaining an important food item (33 %) in January ($p = 0.0209$). No differences were found between the proportion of acorns in the diet at sites VA and DO (20 % in January). Acorn consumption by other ungulates at each locality depended upon their densities, with acorns soon exhausted in areas with high ungulate densities (Fig. 4).

Discussion

Our results indicate that both acorns and maize are very attractive sources of energy for wild boar. During mast years, acorns are sought after food over all other food components. If acorns are already consumed, maize is the first choice, where available. The importance of maize in the diet was also reported by Ballari & Barrios-García (2014). Presence of acorns in the diet correlated negatively with presence of maize, frequently given as supplementary food, as described by Fournier-Chambrillon et al. (1996). In localities without maize supplementation authors have described a negative correlation between acorns and grasses (Massei et al. 1996) and tubers, cereals or roots (Briedermann 1979, Herrero et al. 2004). Our data from SO confirm roots and grasses the most frequent items if no acorns were available.

The relationship between native wildlife, wild boars and mast crop species has been shown to be complex and incredibly interconnected. Wild boars can effectively compete with native wildlife for these resources and exploit mast crops that many species find unpalatable, increasing their competitive advantage through increased fertility and reproduction (Elston & Hewitt 2010). Wild boars have also been shown to actively search for acorns buried by granivorous small mammals, excavating significantly more locations with burrows (Focardi et al. 2000), thereby extending their competitiveness beyond other ungulates.

Chemical analysis of the three food components examined indicated that maize contains a high level

of Nl, making it a preferred food for ungulates (Bleier et al. 2017); acorns, however, also represent a very valuable food source, which, when present, will be sought after. According to Zeman et al. (2016b), the percentage of pericarp (shell) and cotyledon (nut) in whole acorn mass is 30 % and 70 %, respectively, while the percentage of dry matter is 53 % and 44 %, respectively. Wild boars peeled off the shell when consuming acorns if in feeding conditions without disturbance. If disturbed and in a hurry, however, they may swallow the whole acorn, which may be found undigested in stomach and also in the faeces (Elston & Hewitt 2010, Zeman et al. 2016b). Given the choice, therefore, the boar maximises its nutritional intake by discarding the less nutritious shell.

By continually collecting stomach samples from site SO from late summer to January it was possible to monitor changes in dietary composition over half a year's time. It was also possible to trace the human influence, particularly as regards to provision of supplementary feeding and baiting by hunters. Overall, maize was present in the diet, though acorns represented the highest proportion in the diet in September and October. According to Zeman et al. (2016b), the acorn crop is at its maximum in these two months and our results confirm that wild boars shift their diet and exploit this item intensively, it being the main food component for some individuals (up to 95 % of stomach content). In previous studies, however, forest fruits (mast) often represent between 22 to 68 % of dietary volume in (Schley & Roper 2003: a summary of wild boar diet data based on 21 European studies). In December, when acorn reserves were exhausted and supplemental foods were not available, wild boar shifted their diet toward natural foods such as roots (highest volume) and grasses (highest frequency). High diversity environment of lowland forests enabled them to exploit the food of the highest diversity from natural resources (Zeman et al. 2018). In January, supplementary food was used again intensively. It is evident that supplementary food can influence the whole feeding strategy of wild boar, especially in winter (Groot Bruinderink et al. 1994).

The high effect of acorn consumption and availability was demonstrated by the presence of acorns in the diet until January at those sites with lower density of wild boar population (VA, DO, KR), while at SO, where both wild boar and ungulate density was conspicuously higher, acorns had disappeared from the diet by December (Fig. 3). According to Kamler et al. (2016), wild boar populations are able to consume around 92 % of the acorn crop in lowland forest stands in South Moravia, though the percentage consumed by other animals and the percentage of successful germination must also be taken into account when using such figures. At such high rates of consumption, natural forest reproduction/regeneration may become almost impossible (Gómez et al. 2003). Only in mast years, when the acorn crop is abundant, will natural forest reproduction be possible, though only if the wild boar population density in such oak woods is kept at a suitable level and the overwintering population does not consume the entire crop (Kamler et al. 2016).

The availability of high quality food during autumn, when ungulates are storing energy reserves, can contribute significantly to successful overwintering and the condition of the animals following the long period of food deprivation. In such cases, productive oak stands and regular mast years can significantly increase the carrying capacity of the environment, thereby influencing both the diet and feeding habits of wild boar and potentially affecting other traits such as population dynamics, habitat use, dispersal, reproduction and interactions with other species (Massei et al. 1996, Bieber & Ruf 2005, Frauendorf et al. 2016). When mast is abundant, the overall body mass of the population will increase, thereby increasing individual fertility and, eventually, population size (Massei et al. 1996). Furthermore, a number of authors have shown that, when acorns are available in winter, the increase in nutrition over this period can contribute to an earlier start of the reproduction season (Massei et al. 1996, Schley & Roper 2003, Övergaard et al. 2007). Other researchers have also confirmed that forest tree mast years, and their increased frequency, have a strong influence on wild boar invasion capacity (e.g. Schley & Roper 2003, Övergaard et al. 2007). A previous study at KR by Nováková et al. (2011) clearly demonstrated a permanent increase in wild boar numbers as a result of increased supplementary feeding over autumn and winter (especially maize and waste cereals). When this feeding occurred in combination with good oak and beech mast years, there was a clear increase in the numbers of wild boars hunted in the subsequent year. It was explained by increased food offer positively influencing reproduction. Similarly, other authors have shown a significant increase in wild boar numbers following years with a combination of mild, warm above-average winters and good oak and beech mast (Briedermann 1979, Groot Bruinderink & Hazebroek 1995, Massei et al. 1996, Cahill & Llimona 2004), while Neet (2014) recorded an increase in population

size the year after the area sown with maize in adjoining fields was increased.

Conclusion

Our diet analysis data suggests that the provision of supplementary food strongly influences both wild boar feeding strategy and its habitat use, especially in winter, suggesting that humans can strongly influence levels of wild boar impact. Our observations confirmed the supplementary feeding as harmful and that law should be modified accordingly. Further, mild winters, changes in surrounding crops, forest productivity and an increase in the number of mast years can all significantly increase the carrying capacity of the environment, thereby influencing both wild boar diet and feeding habits, and potentially other traits such as population dynamics, habitat use, dispersal, reproduction and interactions with other species. As such, careful analysis of wild boar diet and the availability of food items should prove a useful tool for predicting, and perhaps controlling, wild boar impact on the environment.

Acknowledgements

This research was undertaken with supported by the Specific University Research Fund of the FFWT Mendel University in Brno (reg. number: LDF_PSV_2016013). We also thank Kevin Roche and Ladislav Čepelka for improving the English language and for comments to an earlier version of the manuscript.

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