



## Review

## Consumption of fleshy fruit: Are central European carnivores really less frugivorous than southern European carnivores?



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## ABSTRACT

Frugivory in carnivores in Central Europe is widespread and common. Therefore, the concept of gradient in regard to the share of fruit in the diet of carnivores in the northern and southern regions of Europe should be revised. The following hypotheses can be set: (1) carnivores from Central Europe consume amounts of fleshy fruit similar to those consumed by the same carnivore species from the southern regions of the continent; (2) the only difference between the central and southern parts of the European continent is the variety of fleshy-fruit species consumed by carnivores; (3) regardless of latitude, there is a strong relationship between the amount of fruit consumed and richness of fruit species in the diet. In total, 158 papers on the diets of carnivores inhabiting Europe were examined, spanning the period 1970–2010. Subsequently, in preparing this paper, data from 78 publications on the most generalist diets (badgers 25, foxes 21 and martens 32) were chosen for further statistical analysis. Analysis of standardised data from the literature did not confirm that frugivory in carnivores (with special attention to the martens *Martes marten*, *M. foina*, the red fox *Vulpes vulpes* and the badger *Meles meles*) varies between latitudes and longitudes in Europe. These results contradict previous findings. One reason for this is that data concerning dry fruit were excluded from the analysis. There were strong correlations between the number of fleshy-fruited plant species eaten by carnivores and the percentage of occurrence of such fruit in the diet, regardless of latitude and longitude.

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## Introduction

The diet of carnivores varies according to geographical gradient and is mainly expressed in terms of the proportion between shares of animal components and of plant material, depending mostly on latitude (Goszczyński et al., 2000; Zalewski, 2004). The presence of 'plant material' (in the broadest sense) in the diet of different carnivore species is characterised by a very wide range (Willson, 1993). This material may include either the green parts of plants (blades of grass) eaten in order to improve digestion, accidentally present in the diet, or obtained while devouring prey (Sládek, 1972), or residue from pericarps and seeds (Goszczyński, 1976, 1986). The presence of fleshy fruit in the diet of some carnivores is due to its high nutritional value and the treatment of this type of food as an important component of the diet (Martinoli et al., 2001; Posłuszny et al., 2007). This is typical for the guild of species characterised by consumption of a wide range of food, such as the badger *Meles*

*meles*, the pine marten *Martes marten* and the red fox *Vulpes vulpes* (Sidorovich et al., 2000).

A high share of frugivory in carnivores has usually been associated with a warmer southern climate (Herrera and Pellmyr, 2002). In Europe most of the research papers concerning fruit diets originate from the Mediterranean region (Herrera, 1989; Herrera and Pellmyr, 2002; Traba et al., 2006; Fedriani and Delibes, 2009; Fedriani et al., 2009; Rosalino and Santos-Reis, 2009; Guitián and Munilla, 2010; Matías et al., 2010). It is generally acknowledged that overall diversity of diet, including fruit and plants, decreases as one moves north (Goszczyński et al., 2000; Zalewski, 2004; Lozano et al., 2006; Vulla et al., 2009). This is a result of the decreasing species richness and periods of availability of this type of food in northern latitudes. The same mechanism also applies to invertebrates and vertebrates hibernating during the most severe (in terms of weather) part of the year. Although frugivory in carnivores in Central Europe (temperate climate) is known to be widespread and common (Rzebik-Kowalska, 1972; Goszczyński, 1976, 1986; Tryjanowski, 1997; Goszczyński et al., 2000; Schaumann and Heinken, 2002; Posłuszny et al., 2007), there are few specific studies summarising existing data on fleshy-fruit fractions in the diet of carnivores from Central Europe. This is likely

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to have resulted in an underestimation of the share of fleshy fruit in the diet of carnivores in these temperate zones in comparison to more southern latitudes. Therefore, the concept of gradient in regard to the share of fruit in the diet of carnivores in the northern and southern regions of Europe should be revised and requires a more detailed and systematic approach.

This review presents data from the literature about fleshy-fruit diets in carnivores inhabiting the temperate region of Europe. The aim of this article is to review and systematise data on the share (in terms of quantity and quality) of fleshy fruit in the diets of carnivores from Central Europe in comparison to the Mediterranean region. On the basis of the analysed literature, the following hypotheses can be set:

- (1) Carnivores from Central Europe consume amounts of fleshy fruit similar to those consumed by the same carnivore species from the southern regions of the continent, given the assumption that only data from corresponding phenological periods are to be compared. Studies dealing with the geographical diversity of the overall diet of carnivores emphasise the existence of a larger share of fleshy fruit in the diets of those from warmer and southern areas (Goszczyński et al., 2000; Zalewski, 2004; Lozano et al., 2006; Vulla et al., 2009). The species diversity of fleshy-fruited plants in the Mediterranean region that are available most of the year is higher than in the northern latitudes. This affords Mediterranean carnivores an opportunity to use these resources for a longer time, as reflected in the higher year-round occurrence of faeces containing fruit remains. Differences between latitudes in the frugivory of carnivores should not be so distinct when comparing corresponding periods of the year.
- (2) The only difference between populations of carnivores from the central and southern parts of the European continent is the variety of fleshy-fruit species consumed. The diversity of fleshy-fruited plant species of southern Europe create more opportunities to increase the species richness of fleshy fruit in diet than in northern latitudes.
- (3) Regardless of latitude and longitude, there is a strong relationship between the amount of fruit consumed (expressed as a percentage of occurrence and biomass) and species richness in the diet.

## Material and methods

Studies describing dietary composition were identified through web searches in Google Scholar and Web of Science. Other data sources were also searched for suitable studies containing information about the trophic ecology of carnivores, especially papers not available on the Internet. In total, 158 papers concerning the diet of carnivores inhabiting Europe were examined, spanning the period 1970–2010. Subsequently, in the preparation of this paper, data from 78 records about the most generalist diets (badgers: 25 studies covering 18 different study areas, foxes: 21 studies covering 19 different study areas and martens: 32 studies covering 22 different study areas) were chosen for further statistical analysis (Appendix A). Papers containing information about more than one carnivore were also included. There were no restrictions used to the minimum sample size for papers included to the database.

To verify hypotheses concerning the share of fleshy fruit in the diet of carnivores (the stone marten *Martes foina*, the pine marten *M. martes*, the red fox *Vulpes vulpes*, and the badger *Meles meles*) depending on the geographical gradient, the present work also includes data from other regions of the continent ranging from the Mediterranean basin to central Scandinavia. Special attention was paid to even geographical distribution of the data. Only

Iberian Peninsula was poor in proper data about martens. Identification of the Central Europe region tends to be variable, so for the purposes of this article, data from eastern Germany, Hungary, the Czech Republic, Slovakia, Belarus, the Baltic States (Lithuania, Latvia, Estonia) and Poland were included. In this study, the focus was on continental Europe, excluding data from the British Isles. The data used in this study came from an area between 37° and 61°N (the Iberian Peninsula to central Scandinavia) and 8°W and 31°E (the Iberian Peninsula to north-eastern Belarus). In terms of the environmental gradient, data came from the Mediterranean area and the temperate (Central Europe) and boreal zones (Scandinavia).

During the collection and selection of material, special attention was paid to maintaining comparability of data. For subsequent statistical analyses, all data were standardised regarding:

- (1) the species included in the analyses. In this paper, information about only two species of martens (taken together or separately, depending on whether the authors identified the species), foxes and badgers were included. Other species of carnivores were excluded from the analyses due to their rarity and the fragmentary nature of data on their diets.
- (2) height above sea level. Only data for areas located not more than 800 m above sea level were taken into account.
- (3) appropriate time period for the data published in the literature. In some papers data were pooled annually, seasonally, or both. For further analysis two databases were created: for annual data (in which case the influence of phenological differences between latitudes was included) and seasonal data (for the summer–autumn period, the influence of phenological differences between latitudes was excluded). For each group, subsequent analyses were performed independently. The beginning of the fruiting period varies between the northern and southern latitudes of the continent range by from none to one or two months (Herrera, 1984; López-Bao and González-Varo, 2011). It is common for different authors to identify summer and autumn in very different ways, creating serious difficulties in the selection of data for further analysis; therefore, many papers were excluded. In preparing data, it was necessary to allow one or two months of tolerance in order to standardise data for comparison. In the case of published data from several seasons, values were averaged.
- (4) type of fruit consumed. In many studies, especially those from southern Europe, the authors compiled data for both dry and fleshy fruit. In this paper we also considered data from studies in which dry fruit (i.e. *Corylus*, *Juglans*, *Castanea*, *Zea*, *Quercus*) was treated along with fleshy fruit, but only if its share did not exceed 5%. In the case of higher shares of dry fruit, the data were not included in the analyses. This statement does not take into account publications containing overly broad categories of food, such as 'fruit', a much broader concept than 'fleshy fruit'.
- (5) dietary composition, which had to be assessed through analysis of the stomach and/or faeces. In preparing this article we have collected published data respecting the diet of carnivores based on analyses of faeces and of stomach content. From a methodological point of view it is permissible to compare data from both stomach and faeces analyses (see Zhou et al., 2011), especially when it concerns seeds characterised by a very low rate of digestibility.
- (6) the total number of analysed scats (100%), which contained sufficient information to calculate the frequency of occurrence (0%). Another useful measure was the percentage of food biomass consumed (B%). Many authors use measures other than 0% and B%, i.e. RF, or relative frequency of occurrence, expressed as the percentage of occurrences of one food item in relation to the total occurrences of all food items. Papers with indicators other than 0% and B% were rejected from subsequent

analysis. In general discussions about the relevance of fruit in the diet of Central European carnivores, data on other species were included, though only martens, foxes and badgers were used for statistical analysis.

Different reports concerning the same areas were also taken into account, as it is known that the share of fleshy fruit in the diets of carnivores may vary from year to year. It is preferable to use data from different seasons, even if they derive from the same area, as this approach modifies the effects of certain exceptional years. In this paper, data from different authors from different periods of research for the same area were included to the extent possible. In some cases there was more than one paper concerning a single carnivore species from similar study sites. On the basis of such standardised data, the following parameters were derived from each study: (1) number of fleshy-fruit species consumed; (2) frequency of occurrence (O%) and biomass (B%) for the same phenological period (summer–autumn) and for the entire year ( $O_{ey}\%$ ,  $B_{ey}\%$ ); (3) approximate latitude and longitude (in degrees). If not available in the published study, coordinates were assessed from maps available through Google Earth 3.0.0548 software.

## Data analyses

Our purpose in this study was to examine frugivory in carnivores according to geographical gradient. Prior to statistical tests, the data were transformed with logarithmic or exponential functions to obtain a normal or at least symmetrical distribution. We explored the effects of two explanatory variables, namely, geographical latitude ( $^{\circ}$ N) and longitude ( $^{\circ}$ E), on the response variables, i.e. percentage of fruit occurrence (O%) and percentage of biomass (B%), with both characteristics computed for similar phenological periods and for the entire year ( $O_{ey}\%$ ,  $B_{ey}\%$ ), and the diversity of fleshy fruits in the diet of the selected carnivores (badgers, foxes, martens) using multiple regression. In order to be more informative, the figures present raw data. Pearson correlation was used to test, regardless of geographic variation, whether any relationships existed between O%, B%,  $O_{ey}\%$ ,  $B_{ey}\%$  and the number of fleshy-fruited plant species detected in the diets of the selected carnivores. ANOVA was computed to compare parameters of fleshy-fruited diet between martens, badgers and foxes. The significance level was set at 0.05. All statistical analyses were performed using Statistica 8.0.

## Results

For carnivores inhabiting Central Europe, 35 different fruit types could be identified, 25 of them to species level (Table 1). In the diet of the pine marten *Martes martes* and the red fox *Vulpes vulpes*, fruits of 18 fleshy-fruited plant species were detected. In the case of the stone marten *Martes foina* and the badger *Meles meles*, 15 and 16 fruit species were detected, respectively. It seems that the important fruits in the diet of carnivores belong to domestic tree cultivars from the genus *Prunus* sp. (*P. cerasus*, *P. domestica*, *P. cerasifera*, but also *P. spinosa* and *P. padus*) as well as *Malus* sp. and *Pyrus* sp. Also eaten are the fruits of *Rubus* sp., *Sorbus aucuparia*, *Frangula alnus*, *Fragaria* sp., *Rosa* sp. and *Vaccinium myrtillus*. Other fleshy-fruited plant species are noted more incidentally.

Among carnivores analysed from Central Europe, the most frugivorous (in terms of O% and B% computed for summer and autumn) were martens ( $O=41.8 \pm 26.4$ ,  $O_{max}=100\%$ ,  $B=30.6 \pm 18.3$ ,  $B_{max}=67.5\%$ ) and badgers ( $O=38.0 \pm 25.6$ ,  $O_{max}=82.5\%$ ,  $B=16.3 \pm 16.5$ ,  $B_{max}=47.4\%$ ). The fleshy-fruit consumption of Central European foxes constituted  $O=27.8 \pm 22.6$  ( $O_{max}=81.0\%$ ) and  $B=14.3 \pm 10.5$  ( $B_{max}=33.4\%$ ) of the diet ( $O$ :  $F=0.009$ ,  $p=0.991$ ,  $B$ :  $F=0.043$ ,

$p=0.958$ ). Similar model is expressed for entire year for martens ( $O_{ey}=29.2 \pm 14.4$ ,  $O_{max}=66.7\%$ ,  $B_{ey}=18.6 \pm 15.5$ ,  $B_{max}=47.2\%$ ), badgers ( $O_{ey}=27.6 \pm 17.8$ ,  $O_{max}=66.7\%$ ,  $B_{ey}=19.9 \pm 17.8$ ,  $B_{max}=56.3\%$ ) and foxes:  $O_{ey}=24.4 \pm 18.2$ ,  $O_{max}=54.1\%$ ,  $B_{ey}=11.5 \pm 6.7$ ,  $B_{max}=18.7\%$  ( $O_{ey}$ :  $F=0.006$ ,  $p=0.994$ ,  $B_{ey}$ :  $F=0.034$ ,  $p=0.967$ ). Also, there were no significant difference in mean number of fleshy-fruited plant species in carnivores' diet: martens:  $6.6 \pm 3.6$ , badgers:  $7.2 \pm 3.0$ , foxes:  $6.7 \pm 4.9$  ( $F=0.173$ ,  $p=0.842$ ).

Overall multiple regression, showed significant dependence of occurrence of fleshy fruits O% in carnivores' diet (foxes, badgers, martens) in geographical gradient ( $R^2=13.7\%$ ,  $F=3.81$ ,  $p=0.029$ ), but not in case of the biomass B% ( $R^2=14.0\%$ ,  $F=1.63$ ,  $p=0.221$ ). In detailed results occurrence O% of fleshy fruits in the diet of foxes, badgers and martens showed significant dependence only on latitude (hypothesis 1, Table 2, Fig. 1). Interestingly, no significant relationships were obtained from year-round data, i.e.  $O_{ey}\%$  ( $R^2=3.9\%$ ,  $F=0.73$ ,  $p=0.487$ ) and  $B_{ey}\%$  ( $R^2=0.7\%$ ,  $F=0.05$ ,  $p=0.949$ ), for either latitude or longitude (Table 2).

The highest numbers of fleshy-fruited plant species were found in the diet of carnivores in southern Europe, while slightly lower values were derived from the regions to the north (Fig. 1). The north-south gradient is marked by an insignificant but negative relationship between the richness of fleshy-fruited plant species in the diet and latitude (hypothesis 2,  $R^2=7.1\%$ ,  $F=1.34$ ,  $p=0.274$ , Table 2). It is worth noting that between locations with very similar coordinates there are distinct differences in the richness of fleshy-fruited plant species. The number of fleshy-fruited plant species in similar locations but from different studies varied by as many as 12 species. There was no significant relationship between longitude and the number of fleshy-fruited plant species whose fruit remains or seeds were found in the diet of carnivores. This relationship (however insignificant) is much weaker than in the case of latitude (respectively, Beta = 0.128, Beta = -0.325, Table 2).

A close to significance correlation between the number of fleshy-fruited plant species (estimated on the basis of fruit remains or seeds) found in the diet of carnivores and their frequency of occurrence (O%) was noted for summer and autumn (hypothesis 3,  $r=0.912$ ,  $p=0.088$ ). However, there were no significant correlations for B%,  $O_{ey}\%$  and  $B_{ey}\%$  (Table 3).

## Discussion

Opinions on the increase in fruit content in the diet of carnivores over the north-south gradient contained in the literature are common and indicate variations in the shares of the 'plant material' and 'animal' categories (Zalewski, 2004; Lozano et al., 2006; Vulla et al., 2009; Zhou et al., 2011). These publications include data collected over a wide range of geographical coordinates, usually based on year-round dietary information (e.g. Bojarska and Selva, 2011). The longer growing and fruiting seasons in the southern parts of the continent provide carnivores with opportunities to use this source of food for proportionately longer periods during the year than in areas with typically shorter warm periods and with more severe and snowy winters (central and northern Europe). In view of the long lifespan of fruit in the south, its frequency and biomass per year attains higher values in comparison to regions characterised by more severe climates, therefore painting a picture of a relatively larger proportion of fruit in the diet of carnivores. This is demonstrated by significant differences in the share of fruit between warm and cool regions (Vulla et al., 2009). On this basis, there is a tendency to claim that predators inhabiting the southern part of the continent consume more fruit, which seems to suggest their particular preference for this type of food in comparison to predators inhabiting northern latitudes. However, the share of individual components

**Table 1**

Seeds from fleshy-fruited plant species occurred in the diet of carnivores in Central Europe. Alien species in bold. Archeophites and cultivars (genus: *Prunus*, *Cerasus*) grouped with native species.

Species	<i>Meles meles</i>	<i>Vulpes vulpes</i>	<i>Martes sp.</i>	<i>Martes martes</i>	<i>Martes foina</i>
<i>Vaccinium myrtillus</i>	•	•	•	•	
<i>Vaccinium vitis idaea</i>		•		•	
<i>Oxycoccus palustris</i>				•	
<i>Prunus spinosa</i>		•	•	•	
<i>Prunus cerasus</i>	•	•	•	•	
<i>Prunus cerasifera</i>	•	•	•		
<i>Prunus domestica</i>	•	•	•		
<i>Prunus padus</i>		•	•	•	
<i>Prunus sp.</i>	•	•		•	
<i>Cerasus vulgaris</i>			•		
<i>Rubus sp.</i>	•	•	•	•	
<i>Rubus caesius/fruticosus</i>			•		
<i>Rubus idaeus</i>			•	•	
<i>Sorbus sp.</i>	•			•	
<i>Sorbus aucuparia</i>		•	•	•	
<i>Pyrus sp.</i>	•	•	•	•	
<i>Malus sp.</i>	•	•	•	•	
<i>Ribes uva-crispa</i>			•		
<i>Ribes nigrum</i>			•		
<i>Ribes sp.</i>	•				
<i>Taxus baccata</i>			•		
<i>Fragaria sp.</i>	•		•		
<i>Frangula alnus</i>		•	•	•	
<i>Juniperus communis</i>	•	•			
<i>Rosa canina/Rosa sp.</i>			•	•	
<i>Sambucus nigra</i>	•		•		
<i>Sambucus racemosa</i>	•				
<i>Cornus sp.</i>					•
<i>Crataegus sp.</i>		•	•	•	
<i>Convallaria majalis</i>			•		
<i>Viscum album</i>			•		
<b><i>Morus sp.</i></b>					•
<b><i>Fragaria ananassa</i></b>	•				
<b><i>Vitis vinifera</i></b>		•	•		•
<b><i>Prunus serotina</i></b>	•	•	•		
Total of species detected	16	18	25	18	15

**Table 2**

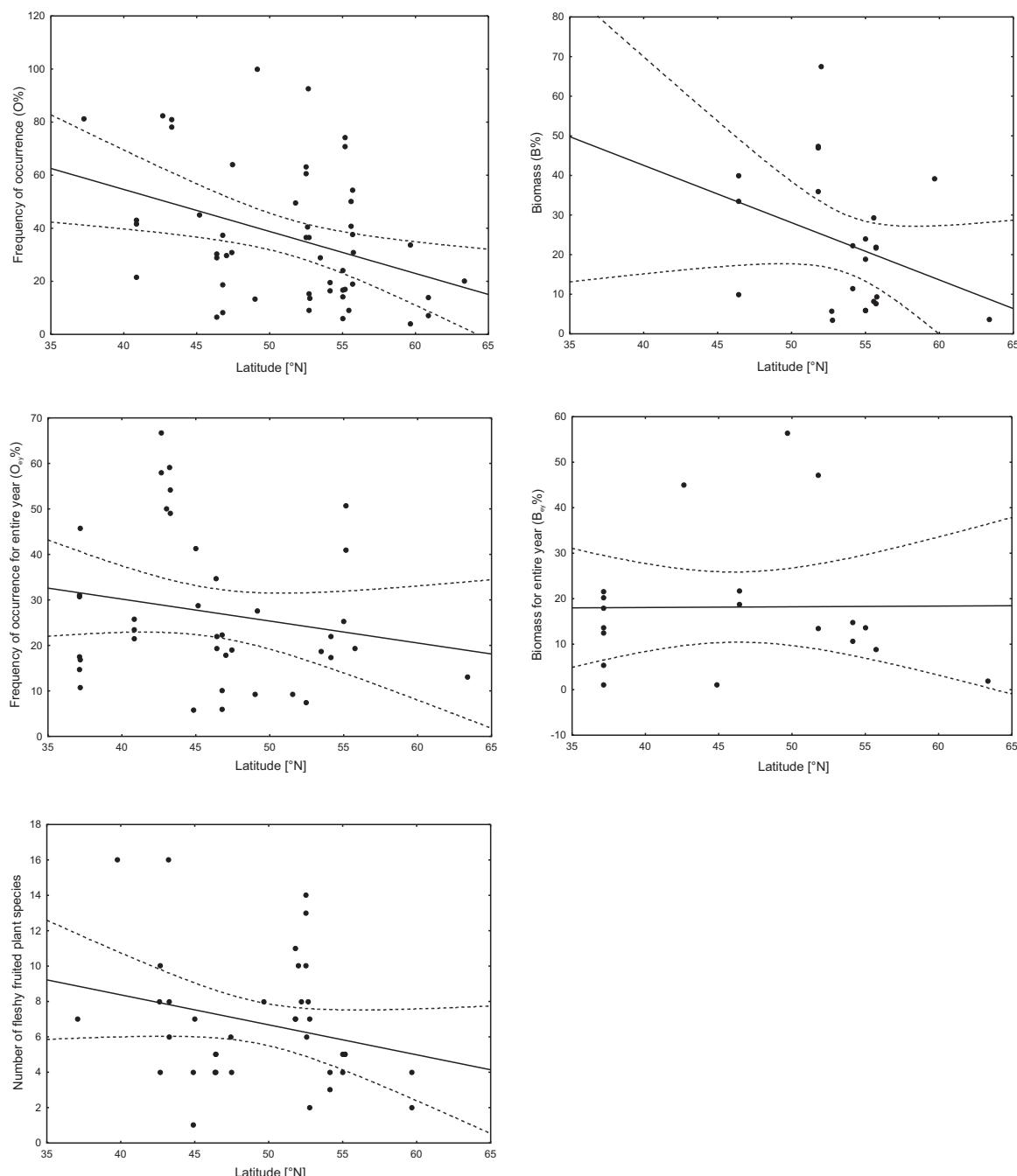
Summary of the multiple regression analysis of the percentage of occurrence (O%) and biomass (B%) for corresponding periods, percentage of occurrence and of biomass for the entire year (O<sub>ey</sub>%, B<sub>ey</sub>%) and number of fleshy-fruited species. Statistical significance in bold.

Dependent variable	Independent variable	Beta	SE (Beta)	b	SE (b)	t (114)	P
O%	N	<b>-0.372</b>	<b>0.173</b>	<b>-0.450</b>	<b>0.209</b>	<b>-2.152</b>	<b>0.036</b>
	E	0.004	0.173	-0.004	0.167	0.022	0.982
B%	N	-0.279	0.218	-0.443	0.346	-1.279	0.215
	E	-0.178	0.218	-0.244	0.299	-0.815	0.425
O <sub>ey</sub> %	N	-0.168	0.211	-0.194	0.243	-0.798	0.430
	E	-0.042	0.211	-0.045	0.223	-0.200	0.843
B <sub>ey</sub> %	N	-0.090	0.331	-0.085	0.315	-0.270	0.790
	E	0.014	0.331	0.015	0.353	0.042	0.967
Species number	N	-0.325	0.206	-0.373	0.236	-1.580	0.123
	E	0.128	0.206	0.141	0.226	0.622	0.538

of the diet (fruit, plants, insects, cold-blooded vertebrates) is the result of their availability, depending on local climate and environmental conditions (Roper and Mickevicius, 1995; Zalewski, 2004; Bojarska and Selva, 2011), rather than specific preferences. Based on the analyses included herein of phenologically identical periods, we may assume that carnivores inhabiting various latitudes within the study area utilise fruit resources equally, provided they are available. It should also be noted that every latitude has significant variations in the frequency and biomass of the fruit consumed between various environments (Goszczyński et al., 2000) and in respect of the age and sex of predators as well as the availability of prey (Zalewski, 2007).

Researchers from southern Europe also include dry fruit in their analysis of fruit in the diets of carnivores (Rosalino and Santos-Reis,

2009). The often high share of dry fruit in the diets of mammals may inflate the values of the "fruit" category as generally understood, which may exaggerate the differences between regions in light of the tendency of northern European researchers to regard fruit as strictly fleshy fruit. Scientific literature often fails to provide accurate definitions of 'fruit', by including papers that cover dry fruit, or creating a category labelled 'plant material', which includes material other than fruit (e.g. green parts of plants). These inaccuracies among researchers in the approach to the 'fruit' category may result in erroneous conclusions regarding the varying share of fruit over the gradients of latitude and longitude. The analyses included here indicate that gradients (both north-south and west-east), at least between southern Spain and the Baltic states, reveal weak trends in the share of fruit in the diet of carnivores. Other authors also show



**Fig. 1.** Species number and content of fleshy fruit in the diet of carnivores (martens, badgers and foxes) in relation to latitude [ $^{\circ}$ N] expressed as frequency of occurrence (O%) and biomass (B%) for the same phenological period (summer–autumn) and for the entire year ( $O_{ey}\%$ ,  $B_{ey}\%$ ).

that these relationships are not always essential or clear (Virgós et al., 1999; Diaz-Ruiz et al., 2011). The best solution would be to separate dry and fleshy fruit in quantity analysis of carnivores' diet.

In addition to variability over the north-south gradient, some researchers point to the variability of fruit components in the diet of carnivores over the west-east gradient, with the proportional share of fruit usually increasing as one moves eastward (Rosalino and Santos-Reis, 2009; Diaz-Ruiz et al., 2011). The review of literature presented herein does not confirm these regularities. Large-scale studies, including data from a large geographic area, are influenced by differences arising from the diversity of flora along geographical gradients. It must therefore be emphasised that the variable representation of fruit in the diet of carnivores within the same areas may

**Table 3**

Pearson correlations of the number of fleshy-fruited plant species in the diet of the analysed carnivores and percentage of occurrence and biomass for corresponding periods (O%, B%) and for the entire year ( $O_{ey}\%$ ,  $B_{ey}\%$ ).

Variable	$r(X, Y)$	$r^2$	$t$	$P$
O%	0.912	0.833	3.154	0.088
B%	0.377	0.142	0.576	0.623
$O_{ey}\%$	0.662	0.439	1.250	0.338
$B_{ey}\%$	0.346	0.120	0.521	0.654

be affected by different habitat types. As shown by the collected data, preferences in this regard are fixed geographically, and fruit presents an important source of food virtually everywhere, given the opportunistic feeding habits of the carnivores studied herein

(Erlinge, 1986; Roper and Mickevicius, 1995; Zhou et al., 2011). Variations independent of latitude gradient indicate a higher proportion of fruit in boreal forests than temperate forests (Bojarska and Selva, 2011).

Southern Europe is characterised by a greater diversity of species, including plants that produce fleshy fruit, which is reflected in the diversity of the diets of carnivores in southern regions compared to the North (Virgós et al., 1999; Zalewski, 2007). In addition to geographic variation, locations with similar coordinates also demonstrate a high variability of fruit in the diet depending on its local availability (Roper and Mickevicius, 1995; Padial et al., 2002; Schaumann and Heinen, 2002; Sidorovich et al., 2006; Bojarska and Selva, 2011). This is because the diversity of fruit plants in Central Europe is strictly dependent on the local diversity of plant communities found at similar latitudes. Badgers feeding outside forests on agricultural land (which is converted land) are more dependent on a vegetarian diet of fruit and cereals (Goszczyński et al., 2000). On the other hand, predators inhabiting the natural forests of Central Europe (Białowieża Forest) have a lower share of fruit in their diet compared with those found in environments characterised by greater human impact (Jędrzejewska and Jędrzejewski, 1998). The converse of this relationship between fruit availability and degree of environmental conversion has been observed by Herrera (1989) in the Mediterranean. It can therefore be assumed that the share of fruit in the diet of predators is a secondary phenomenon resulting from landscape transformations due to human activity (cultivation of fruit trees, mosaics of forest and

open environments). Fruit-eating is a relative trait in predators, revealing wide variation on the local scale between environments, and does not depend directly on latitude and longitude (Roper and Mickevicius, 1995).

A positive correlation was evidenced between the percentage of occurrence (O%) and the diversity of fleshy-fruit species in the diet of carnivores, thereby confirming hypothesis 3. Note that this concerns only O% for the same phenological periods. This study provided data showing that while the diversity of species of plants producing fleshy fruit does not depend on latitude or longitude, wide variation is observed locally. The diversity of species of fruit plants inhabiting communities where faeces were sampled has a significant impact on estimating the degree of frugivory in animals inhabiting the area (regardless of geographical coordinates). Some plant communities are characterised by a great diversity of fruit species (particularly ecotonal scrub environments on the border between forest and open areas) which differentiates the fruit diet of predators on a local scale.

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## Appendix A. Data source used in statistical analysis

Data source	Species	°N	°E	Plant species number	O%	B%	O <sub>ey</sub> %	B <sub>ey</sub> %
Lanszki (2004)	Badger	46.40	17.45	4	6.5	9.8		
Goszczyński et al. (2000)	Badger	52.72	23.90		15.4	5.7		
Goszczyński et al. (2000)	Badger	51.80	19.88	7	49.6	47.4		
Sidorovich et al. (2000)	Badger	55.69	29.42		54.4	21.6		
Virgós et al. (2004)	Badger	40.84	-3.70		41.5		23.4	
Virgós et al. (2004)	Badger	40.84	-3.70		42.9		21.5	
Virgós et al. (2004)	Badger	40.84	-3.70		21.4		25.8	
Sidorovich et al. (2011)	Badger	55.75	30.33		30.9	9.4	19.4	8.9
Revilla and Palomares (2002)	Badger	37.15	6.43				31.1	20.2
Revilla and Palomares (2002)	Badger	37.15	6.43				17.5	12.4
Fedriani et al. (1999)	Badger	37.15	6.43				30.7	13.6
Kauhala et al. (1998)	Badger	60.88	26.78		14.0			
Kurek (2012)	Badger	52.50	20.97	13	63.0			
Barea-Azcón et al. (2010)	Badger	37.28	3.65		81.2			
Fedriani et al. (1998)	Badger	37.17	6.38				45.8	17.9
Fedriani et al. (1998)	Badger	37.17	6.38				16.8	21.6
Fedriani et al. (1998)	Badger	37.17	6.38				10.8	1.0
Bove and Isotti (2001)	Badger	42.60	11.8	8				
Pigozzi (1991)	Badger	42.65	11.08	4			66.7	45.0
Canova and Rosa (1993)	Badger	44.90	8.60	4				
Lanszki et al. (1999)	Badger	46.77	17.87		8.3		5.9	
Pigozzi (1992)	Badger	42.65	11.08	10	82.5		57.9	
Broseth et al. (1997)	Badger	63.37	10.75		20.0	3.6	13.0	1.9
Myslajek et al. (2013)	Badger	49.68	19.02	8				56.3
Rodriguez and Delibes (1992)	Badger	37.10	-2.05	7				
Baltrūnaitė (2001)	Martens	55.15	25.33	5	70.9		41.0	
Posłuszny et al. (2007)	Martens	51.80	19.88	11			47.0	47.2
Posłuszny et al. (2007)	Martens	51.80	19.88	7			36.0	13.4
Helldin (2000)	Martens	59.67	15.50	4	33.7		39.2	
Goszczyński (1976)	Martens	52.00	16.80	10			67.5	
Schaumann and Heinen (2002)	Martens	52.67	13.07	8	92.6			
Schaumann and Heinen (2002)	Martens	52.58	13.08	6	40.5			
Lanszki (2003)	Martens	46.38	17.95	4			34.7	
Baltrūnaitė (2006)	Martens	54.16	24.19	3	16.3	22.2	17.3	14.8
Baltrūnaitė (2002)	Martens	55.57	24.82		50.0		29.3	
Sidorovich et al. (2005)	Martens	55.00	29.00	5	24.1	24.0	25.3	13.6
Sidorovich et al. (2005)	Martens	55.00	31.00	4	14.1	5.9		
Apáthy (1998)	Martens	47.48	19.06	4	64.0			
Sidorovich et al. (2000)	Martens	55.69	29.42		37.5		21.8	
Jędrzejewska and Jędrzejewski (1998)	Martens	52.75	23.94	7			78.0	49.1
Serafini and Lovari (1993)	Martens	43.30	11.08	8				
Jędrzejewski et al. (1993)	Martens	52.75	23.92	2	13.6	3.4		

Data source	Species	°N	°E	Plant species number	O%	B%	O <sub>ey</sub> %	B <sub>ey</sub> %
Zalewski (2007)	Martens	52.72	23.90		9.2			
Zalewski (2007)	Martens	52.72	23.90		36.6			
Bertolino and Dore (1995)	Martens	45.17	4.90		45.0		28.8	
Kurek (2012)	Martens	52.50	20.97	14	60.7			
Lanszki et al. (2007)	Martens	46.40	17.45	5	30.2	40.0	19.3	21.8
Rödel and Stubbe (2006)	Martens	52.21	12.02	8				
Ryšává-Nováková and Koubek (2009)	Martens	49.17	16.67		100.0		27.5	
Lode (1994)	Martens	47.43	2.23	6	30.9		18.9	
Lode (1994)	Martens	47.02	1.77		29.9		17.9	
Romanowski and Lesiński (1991)	Martens	44.87	28.95				5.7	1.0
Helldin (1999)	Martens	59.67	15.50	2				
Genovesi et al. (1996)	Martens	43.23	11.18	16			59.1	
Balestrieri et al. (2011)	Martens	45.02	8.07	7			41.3	
Lanszki et al. (1999)	Martens	46.77	17.87		37.3		22.3	
Storch et al. (1990)	Martens	59.67	15.42		4.0			
Sidorovich et al. (2006)	Fox	55.00	31.00		6.0	5.9		
Sidorovich et al. (2006)	Fox	55.00	29.00		16.8	18.9		
Baltrūnaitė (2001)	Fox	55.15	25.33	5	74.3		50.7	
Baltrūnaitė (2006)	Fox	54.16	24.19	4	19.6	11.5	21.9	10.7
Baltrūnaitė (2002)	Fox	55.57	24.82		40.8	8.1		
Von Schantz (1980)	Fox	55.42	13.25		9.0			
Sidorovich et al. (2000)	Fox	55.69	29.42		19.0	7.7		
Serafini and Lovari (1993)	Fox	43.30	11.08	6	81.0		54.1	
Cavallini and Volpi (1996)	Fox	43.00	10.50				50.0	
Fedriani et al. (1999)	Fox	37.15	6.43				14.7	5.3
Lanszki et al. (2007)	Fox	46.40	17.45	5	28.9	33.4	22.0	18.7
Kauhala et al. (1998)	Fox	60.88	26.78		7.0			
Kurek (2012)	Fox	52.50	20.97	10	36.5			
Jankowiak et al. (2008)	Fox	51.57	17.67				9.2	
Canova and Rosa (1993)	Fox	44.90	8.60	1				
Lanszki et al. (1999)	Fox	46.77	17.87		18.8		10.1	
Goldyn et al. (2003)	Fox	52.45	16.95				7.4	
Hartová-Nentvichová et al. (2010)	Fox	49.00	13.60		13.2		9.2	
Jensen and Sequeira (1978)	Fox	55.16	9.05		17.0			
Papageorgiou et al. (1988)	Fox	39.79	21.60	16				
Drygala et al. (2013)	Fox	53.49	12.94		28.8		18.6	

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