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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 martes*, *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.

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 martes* 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 (O%). Another useful measure was the percentage of food biomass consumed (B%). Many authors use measures other than O% 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 O% and B% were rejected from subsequent