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Toxic fruits in the diet of carnivores in Poland

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There is a lack of documentation on the consumption of toxic fruits by carnivores. To quantify the importance of toxic fruits in the diets of badgers (*Meles meles*), foxes (*Vulpes vulpes*) and martens (*Martes* sp.), we collected faeces of these animals along nine transects (total 30.4 km long, 2 m wide) during the fruiting seasons (June–November) in 2010 and 2011. From 619 faecal samples we found seeds of 16 fleshy-fruited plant species, including four species with toxic fruits. Surprisingly, the fruit of *Convallaria majalis* having a high content of toxic substances was also eaten by these animals. Fruits of *C. majalis* were found in faeces in late summer/autumn after early frost when maturing processes had reduced the content of toxic substances in the mesocarp. Toxic fruits were detected in 6.3% of all faeces sampled ($n = 619$). The proportion of toxic fruits in the diet was the highest (up to 10.5%) in martens as compared with that in badgers and foxes (2.2% and 0.7%, respectively).

Introduction

Numerous carnivores in the temperate zone are foraging opportunists (Erlinge 1986, Jędrzejewska & Jędrzejewski 1998). This is a result of the periodic occurrence of certain important prey species of cold-blooded animals: amphibians, reptiles and arthropods. As a consequence, carnivores are faced with periodic shortages of animal food and might be expected to show a trend towards generalised feeding habits (Erlinge 1986). Fruits, which also occur seasonally, may act as a critical diet supplement in the temperate forests of central Europe (Kwit *et al*. 2004). In general, a fruit is very nutritious, rich in energy, and accessible (Herrera 2002), making it a valuable and important source of food for carnivores (Herrera 1989, Posłuszny *et al*. 2007). Frugivory in badgers, martens, genets and foxes is very common in the Mediterranean region (Herrera 1989, Virgós *et al*. 1999, Fedriani & Delibes 2009, Diaz-Ruiz *et al*. 2011). Fruits often occur in the diet of carnivores in Poland as well, but the data concerning this phenomenon are still scarce. Many aspects of fruit consumption by this guild of animals are still not widely recognised and information about this behaviour is scattered among several reports about the general diets of individual species (e.g. Rzebik-Kowalska 1972, Goszczyński 1976, 1986, Goszczyński *et al*. 2000, Sidorovich *et al*. 2000, Schaumann & Heinken 2002, Posłuszny *et al*. 2007).

One very interesting issue is the occurrence of seeds of toxic fruits in the fleshy-fruited diet of carnivores. Secondary toxic metabolites in the pulp of fleshy fruits perform many tasks in plant tissue protection and dispersal mechanisms. In general, their presence is explained as a consequence of plant defence against herbivores or against fruit and seed pests such as fungi or invertebrates (Herrera 2002). Some toxins also have laxative properties, which influence the retention time of seeds in the digestive tract, a feature which may be highly relevant to their ability to germinate (Murray *et al.* 1994). It is well known that especially birds are able to feed on toxic fruits (Ehrlén & Eriksson 1993), thanks to their morphological and physiological adaptations (Herrera 2002). On the other hand, among European fruit-producing plant genera, the average number of bird and mammal species that eat these fruits is significantly lower for toxic than for edible genera, and it is believed that toxic fruits remain uneaten while coexisting plant crops are being exhausted (*see* Herrera 1982). The presence of toxins, i.e. saponins and glycosides, in the pulp of fleshy fruits may reduce their attraction for mammalian consumers (Schaumann & Heinken 2002) and create a disadvantage for the dispersal process. However, toxicity of fruit decreases during the growing season (Frohne & Pfänder 1983, Barnea *et al.* 1993), and thereafter toxic fruits may occur in the diet of carnivores. As this may be a result of the maturing process in fruits, low temperatures, or availability of non-toxic and edible fruits, it enables us to discuss coinciding factors that may affect the occurrence of toxic fruits in the diet of carnivores.

Based on the literature, it seems that to a certain extent toxic fruits are ignored by mammals and occur in their diet very rarely and in low quantities; however, some authors reported the presence of toxic fruits in the diet of carnivores, e.g. *Frangula alnus* in *Vulpes vulpes* and *Martes martes* (Baltrūnaitė 2006). There is also a lack of data about other toxic fruits from species of the family *Liliaceae*, whose fruits are widely available, but have not, to our knowledge, been reported in the diet of carnivores (Willson 1993, Schaumann & Heinken 2002). Despite the great availability of toxic fruits during the fruiting season in central Europe, reports on their presence in the diets of predatory mammals are still scarce. Small number of cases also results in a small sample size and makes conclusions speculative. To address this issue, the presence of toxic fruits in carnivores' diets should be recognised in more extensive studies. The aim of this study was to contribute to the knowledge on toxic fruits in the diets of medium-sized carnivores. We considered the diets of the badger *Meles meles*, the red fox *Vulpes vulpes* and the marten *Martes* sp. (faeces of *M. foina* and *M. martes*, both occurring in the research area, were combined) in Poland.

We posed the following questions: What is the role and significance (quantity and quality characteristics) of toxic fruits in the overall diet of carnivores? Why (as food or medicine, i.e. against parasites?) and when (upon a decrease in resources or in the fruits' toxicity?) are these fruits eaten? Is the same pattern observed for all carnivores?

Material and methods

Study area

The Kampinos National Park (KNP) is situated north-west of Warsaw, the capital of Poland, at 52.26°–52.40°N, 20.28°–20.88°E, covering an area of ca. 385 km^2. Altitudes range between 68 and 106 m a.s.l. The mean annual temperature and precipitation are 7.7 °C and 550 mm, respectively, with the vegetation period lasting on average 185 days. The first autumn frosts generally occur in the research area in the second half of September (after 15 September), but in 2010 the first frost 5 cm above ground level was recorded on 4 September. Forests, which cover 73% of the KNP's area, are dominated by oligotrophic and sandy habitats of *Pinus sylvestris* (80.9% of the forested area). At lower elevations, wet habitats occur, featuring *Alnus glutinosa* (13.6% of the forested area). In small areas between wet and dry habitats, oak–hornbeam forests have developed on more fertile soils (Andrzejewski 2003). The average age of the tree stands in the KNP is 67 years; however, stands older than 100 years cover 15% of the KNP area. Several settlements and small villages, abandoned in the 1970s and 1980s and surrounded by orchards and fallows, are scattered across the forests.

In the group of fleshy-fruited plants, *Frangula alnus* is the most common species. Less abundant, but also common, are *Sorbus aucuparia*, *Juniperus communis*, *Viscum album* and an invasive species, *Prunus serotina*. The remaining fleshy-fruited shrubs and trees are rare in the study area: *Sambucus nigra*, *S. racemosa, Viburnum opulus*, *Prunus spinosa*, *Cornus sanguinea, Ribes nigrum*, *Ribes uva-crispa*, *Rhamnus cathartica*, *Berberis vulgaris*, *Rosa* sp., *Euonymus europaeus*, *E. verrucosus*, *Cerasus avium*, *Crataegus* sp. In the herb layer, the most common fleshy-fruited species are *Vaccinium myrtillus*, *V. vitis-idaea*, *Convallaria majalis* and *Rubus* spp. Some cultivated trees, *Prunus domestica*, *P. cerasifera*, *Malus domestica* and *Pyrus* sp., are distributed in connection with the abandoned settlements.

Scat collection and analysis

Scats of badgers *Meles meles*, foxes *Vulpes vulpes* and martens *Martes* sp. were collected every month from June to November in 2010 and 2011 along nine parallel transects located every 500–800 m. Transects were mostly selected on dirt roads, but also off roads. Each transect was ca. 4 km long and 2 m wide, and crossed heterogeneous habitats (from wet to dry) and landscapes (open and forested). It was not possible to identify marten species from faeces (Posłuszny *et al*. 2007, Jędrzejewski & Sidarowicz 2010), so faeces of *M. foina* and *M. martes* were combined. Badgers' faeces were found in latrines localised within transects. Taking into account that the faeces of red fox and martens could be confused (Davison *et al*. 2002), samples that could not be assigned to species were used only in the joint analyses of animals. Straight, cigar-shaped faeces with a characteristic acuminate tip and a diameter greater than 1.5 cm were considered typical for foxes. Faeces with a smaller diameter (1.0–1.5 cm), not fragmented, and often deposited on logs were considered typical for martens (Jędrzejewski & Sidarowicz 2010).

The collected samples were dried in paper envelopes, then the dry samples were searched for seeds using a stereo microscope. All seeds were counted and their origins in terms of species were determined. Seeds were identified by plant species using our own seed reference collection and the seed atlas by Cappers *et al*. (2006). Phenological data about the fruiting period are based on our own observations. Climatic data (date of the beginning of the frost period and mean temperature) came from the meteorological station in the Kampinos National Park (Table 1). Having no data on toxicity of the studied fruits to carnivores, we classified the fruits as toxic to vertebrates according to information from Samuelsson (1973), Ehrlén and Eriksson (1993) and Zoltani (2012). We assume that the same fruits that are toxic to taxonomically-unrelated birds and mammals, are also toxic to humans (Herrera 1982), so it is likely that our adoption of the human point of view regarding fruit's edibility is not a major error. On the basis of the number of seeds in the analysed scats, we estimated the minimum number of fruits eaten by carnivores. Data on the number of seeds per fruit type were obtained from Ehrlén and Eriksson (1993) and first author's unpublished data. We excluded *Sambucus nigra* from the analysis, because its mature fruit is edible (Herrera 1982), although fruit extracts may interfere with cell physiology (Bratu *et al*. 2012).

Statistical analyses were performed using R ver. 3.0.2 (R Development Core Team 2011). A χ^2-test of independence ($\alpha = 0.05$) was used to

Table 1. Number of faeces samples collected during the two seasons 2010–2011. Data on mean temperatures (°C) during the research period come from the meteorological station of Kampinos National Park.

	June	July	Aug.	Sep.	Oct.	Nov.	Total
All samples	158	91	65	89	116	100	619
Samples containing seeds	53	45	32	28	30	20	208
Samples containing seeds from toxic fruits	1	1	12	13	1	11	39
Mean temperature	17.8	19.5	18.6	13.2	6.9	4.0	

Table 2. Minimum number of fruits eaten estimated from the maximum number of seeds in faeces during the two seasons in 2010–2011. The range of seed numbers detected in the scat is given in parentheses. n = number of samples with toxic fruits. S = total number of seeds from toxic fruits.

Plant species	Seeds per fruit*	Fox (n = 1)	S	Badger (n = 3)	S	Marten (n = 30)	S	Unidentified species (n = 5)	S	All samples (n = 39)	S	Percentage of seeds (n = 985)	Occurrence
Convallaria majalis	3.9	1 (1)	1	1 (1)	1	3 (3–11)	14	22 (10–83)	152	22 (1–83)	168	17.1	7 (17.9%)
Frangula alnus	2.0	1 (1)	1	1 (1)	1	55 (5–109)	741	12 (13–24)	37	55 (5–109)	780	79.2	26 (66.7%)
Viscum album	1.0	0	0	0	0	15 (1–15)	36	0	0	15 (1–15)	36	3.7	6 (15.4%)
Sambucus racemosa	3.0	0	0	1 (1)	1	0	0	0	0	1 (1)	1	0.1	1 (2.6%)
Total number of seeds			2		3		791		189		985		
Percentage of seeds (n = 985)			0.2		0.3		80.3		19.2				
Proportion to all faecal samples		1/137 = 0.007		3/138 = 0.022		30/285 = 0.105		5/59 = 0.085		39/619 = 0.063			
Proportion to faecal samples containing seeds		1/50 = 0.020		3/87 = 0.034		30/173 = 0.173		5/29 = 0.172		39/340 = 0.115			

* Source: Ehrlén and Eriksson (1993) and first author's unpublished data.

examine differences in abundance of the faeces of martens, red foxes and badgers containing seeds from toxic fruits and all faeces containing seeds (table 2 × 3). Spearman's rank correlation was applied to evaluate the correlation between the number of samples with seeds from toxic fruits and the number of samples containing seeds during the season.

Results

In 2010–2011, a total of 619 faeces of red foxes (n = 137), badgers (n = 138) and martens (n = 285) were collected. An additional 59 samples were unidentified as regards species. Changes in total sample sizes and the number of faeces containing seeds are presented in Table 1. The sampled faeces contained seeds of 16 fleshy-fruited plant species. Among them, 39 samples (6.3%) contained seeds of four toxic fleshy-fruited plants: *Frangula alnus* (26 occurrences), *Convallaria majalis* (7 occurrences), *Viscum album* (6 occurrences) and *Sambucus racemosa* (one occurrence) (Table 2). One scat sample from a fox contained seeds from toxic fruits of two plant species. A total of 985 seeds of toxic fruits were detected in the faeces. Most of the identified samples (n = 26, 66.7%) containing the seeds of *F. alnus*, and most of the samples containing seeds from toxic fruits belonged to martens (n = 30, 76.9%). Of all the seeds from toxic fruits detected in faeces (n = 985), 80.3% (n = 791) were found in the faeces of martens (Table 2). The seeds of *F. alnus* were also the most numerous in comparison with the total number of seeds from toxic fruits detected in the faeces (79.2%, n = 780). Seeds of other species usually occurred in lesser abundance and quantities, from one to a few seeds per sample. Only in the case of martens did seeds from toxic fruits occur more abundantly, in up to 17.3% of faecal samples containing seeds, in comparison with the other carnivores (red foxes and badgers), which were characterised by an unexpectedly low share of toxic fruits in their diets: 2.0% and 3.4%, respectively (χ^2 = 13.390, df = 2, p = 0.001, Table 2). There was no correlation (p = 0.231) between number of samples with seeds from toxic fruits and number of samples containing seeds.

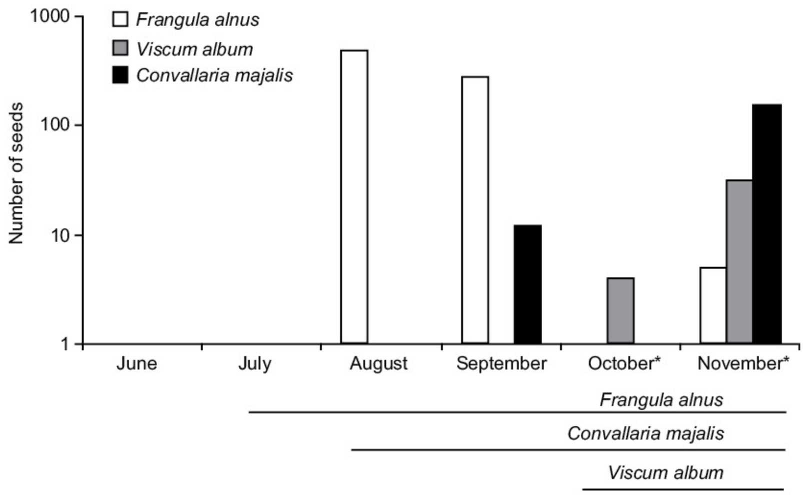

Fig. 1. Seasonal distribution of seeds from toxic fleshy-fruited plants detected in carnivores' faeces (martens, foxes and badgers are combined). An asterisk (*) indicates months with early frosts (data from the meteorological station of the Kampinos National Park). The horizontal lines indicate the fruiting and availability period of the toxic fruits of three plant species. A logarithmic scale was used on the *y*-axis. *S. racemosa* was excluded due to the extremely low number of seeds.

In general, faeces containing seeds from toxic fruits were collected in August–November (Fig. 1). A single seed of *Sambucus racemosa* found in June was the only exception. For most species (*Frangula alnus*, *Viscum album*, *Sambucus racemosa*), the presence of their seeds in faeces coincided with their fruiting/availability period (Fig. 1). Despite availability at the beginning of early summer, most seeds of *Convallaria majalis* were detected in faeces in late autumn after the first frost, when the mean monthly temperatures decreased (Table 1).

Discussion

Martens consumed the greatest amount of toxic fruits in comparison with red foxes and badgers. This finding seems to be consistent for martens throughout their entire geographical range (Zalewski 2004, Koike *et al*. 2008, Tsuji *et al*. 2011), where they are the most frugivorous carnivores. Likely, this reflects the fact that martens are able to climb to reach fruits on trees and shrubs (Koike *et al*. 2008). Foxes and badgers were characterised by a much lower intake of toxic fruits, both in terms of the number of plant species and the number of seeds detected in their faeces.

Regardless of other plant organs, toxins are highly concentrated in seed endosperms, while fruit pulp contains the lowest (though not necessary a low) quantity of toxins (Ehrlén & Eriksson 1993). From an evolutionary point of view, this is a compromise between attaining the toxicity level needed for protection against pathogens and maintaining the necessary capacity for endozoochorous seed dispersal (Cipollini & Levey 1997). Small numbers of seeds from toxic fruits (excluding *F. alnus*) detected in some faeces of carnivores indicate that these animals ingested toxic fruits in small quantities despite their wide accessibility in the habitat, and that these fruits could not be considered a source of food. Some authors suggest that the anti-parasitic properties of toxic fruits are the main reason for their consumption by carnivores (Murdoch *et al*. 2009).

The abundance in faeces of the seeds of most plant species mentioned in this research (*F. alnus*, *V. album* and *S. racemosa*) coincided with their fruiting period. Also, the fruits of these species are characterised by secondary metabolites of lesser toxicity in comparison with fleshy-fruited species from the family *Liliaceae*, such as *C. majalis*, which contains cardiovascular-active glycosides (Zoltani 2012), and whose fruits are characterised as the most toxic for livestock. Its seeds were detected in faeces only 7 times, but as many as 21 berries may have been consumed in the course of foraging. Still, however, information about the consumption of toxic fruits of the family *Liliaceae* by carnivores is scarce (Schaumann & Heinken 2002). Furthermore, in North America, the corresponding *Liliaceae* genera (e.g. *Convallaria*) are not known to be consumed by mammals (Willson 1993).

Although *C. majalis* fruits are available at the beginning of August, in most cases (five out of seven samples) its seeds were found in faeces in late autumn (November). Such late consumption of the *Liliaceae* fruits seems to be related to the fact that toxicity decreases with the ripeness of a fruit (Ehrlén & Eriksson 1993, Cipollini 2000), while its nutritional content increases (Schaefer & Ruxton 2011). In several species it has been found that toxins were present in high concentrations in unripe fruits but gradually disappear from the pulp as the fruits matured (Frohne & Pfänder 1983, Barnea *et al.* 1993). However, this is not true in all cases, because some plants, such as *Atropa belladonna* or *Solanum* sp., retain lethal levels of secondary compounds in ripe fruits (*see* Cipollini 2000). Ripening of *C. majalis* fruits also coincides with the occurrence of the first early frosts. Low temperatures can affect toxin levels in fruit: e.g., Barnea *et al.* (1993) reported that in January the toxin content in plants is lower than in November/December. This enabled us to assume that frost may also affect the quality of toxic fruits (reducing or deactivating toxins) and render them edible for mammals. However, we do not have clear evidence for this.

There are many hypotheses about the importance of toxins in plants (Cipollini 2000). In the case of ingestion (endozoochory), the presence of toxic or irritant substances, either in the seeds or in the fleshy parts of a fruit, has been connected with a defensive mechanism on the part of the plant (e.g. unripe or soft seeds) to prevent digestion by animals (Snow 1971). Fruit toxins acting as laxatives confirm this hypothesis (Murray *et al.* 1994), as in some plant species, prolonged retention in the digestive tract may reduce the ability of seeds to germinate (*see* Barnea *et al.* 1993). Thus it seems that toxins may play a relevant role in seed dispersal processes. Laxative reactions (determined on the basis of the consistency of faeces) were detected in the cases of *V. album*, *F. alnus* and *C. majalis* (concerning mostly shapeless and unidentified samples), in which faeces were full of seeds and remains of fruits. This applies especially to martens, whose faeces contained seeds of only *F. alnus*, with no traces of the remains of other prey. Secondary metabolites also prevent animals from eating too much fruit in a single round of foraging. This may explain why, in many cases, faeces contained only a few seeds from toxic fruits: high toxin content decreases the rate of fruit consumption (Schaefer & Ruxton 2011). This may have further important consequences for seed dispersal by preventing seed concentration in one place (Barnea *et al.* 1993).

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