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Research Article

Diet composition of the invasive raccoon dog (*Nyctereutes procyonoides*) and the native red fox (*Vulpes vulpes*) in north-east Germany

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Abstract

Invasive alien species pose a great threat to the integrity of natural communities by competition with and predation on native species. In Germany the invasive raccoon dog (*Nyctereutes procyonoides*) and the native red fox (*Vulpes vulpes*) occupy a similar ecological niche. Therefore, the aim of our study was to discover the extent of exploitative diet competition between these two generalist carnivores. Carcasses of red foxes (n=256) and raccoon dogs (n=253) were collected throughout Mecklenburg Western-Pomerania (north-east Germany) and stomachs contains were analysed. Frequency of occurrence and biomass share indicate that both canids are omnivorous and pursue opportunistic feeding strategies. Small mammals and edible plant material were the most important food resources for red foxes and raccoon dogs. Nonetheless, interspecies differences were recorded for edible plant material, small mammals and insects. While red foxes mostly feed on voles, raccoon dogs consumed mice and shrews as often as voles. Only raccoon dogs preyed on amphibians. There were no differences in carrion consumption, both species scavenged on wild boar and we found clear competition for carrion year-round. Moreover, there was evidence that two red foxes foraged on raccoon dogs and vice versa. The mean annual interspecies diet overlap index was relatively high. The diets determined for raccoon dogs and red foxes were quite similar and a similar food niche breadth was recorded. However, only minor competition is assumed to take place since differences in feeding habits do exist.

Introduction

Introduced species can, through competition, displace native species which occupy a similar ecological niche. Some reports have indicated that in Japan, native carnivores such as the red fox (*Vulpes vulpes*) and the raccoon dog (*Nyctereutes procyonoides viverrinus*) are decreasing in areas where the raccoon (*Procyon lotor*) has been introduced (Ikeda et al., 2004; Hayama et al., 2006). In Australia there is a strong potential for exploitative competition between native spotted-tailed quolls (*Dasyurus maculates*) and introduced red foxes and wild dogs (*Canis lupus* ssp.) (Glen and Dickman, 2008).

In Europe the raccoon dog was introduced as a game species (Heptner and Naumov, 1974). To maximize the chances of success of the introduction programme, more than 9000 raccoon dogs originating from the Far East were released over a time span of about 30 years (from the 1920s to the 1950s). The species exhibited high dispersal ability and within 50 years (1935–1984), a territory of 1.4 million km^2 was colonised (Helle and Kahuala, 1991; Sutor, 2008). Today, the raccoon dog is widespread in northern and Eastern Europe and is one of the most successful alien carnivores on the continent (Kauhala and Saeki, 2004; Kowalczyk et al., 2008).

An important factor behind the raccoon dog's success is its high ecological plasticity (Kauhala and Kowalczyk, 2011). In Poland (Białowieża Forest), the index of food niche breadth for raccoon dogs was nearly twice as high as that of the red fox (Jedrzejewska and Jedrzejewski, 1998). Moreover, the diet of the raccoon dog varies from area to area and season to season, according to the availability of food sources (e.g., Ivanova 1962; Nasimovič and Isakov 1985; Sutor et al. 2010.

In general, the red fox is more of an active predator and consumes more vertebrate prey (mammals and birds), while the raccoon dog feeds frequently invertebrates, carrion and plants (Kauhala, 1996; Kauhala et al., 1998; Drygala et al., 2000; Sutor et al., 2010). As a successful generalist, the red fox has one of the largest distribution ranges of any terrestrial mammal and is adapted to a wide variety of habitats (from arctic to subtropical regions) suggesting a high degree of ecological flexibility (Nowak, 1999).

However, both species are opportunistic omnivores (Ansorge, 1991; Kauhala et al., 1993) and might compete in the various overlapping environments throughout Europe. For instance, in southern Finland, some overlap has been found in the diets of the two species (Kauhala et al., 1998), and female foxes have actually become more carnivorous since the arrival of the raccoon dog (Viranta and Kauhala, 2011). This change in behaviour leads to the conclusion that foxes and raccoon dogs have competed to some extent for food resources (Kauhala and Kowalczyk, 2011).

To understand competition between non-native and native carnivores, overlap in their food habits must be examined. Accordingly, the main objective of this study was to determine the diet of the two canids in order to assess the degree of competition for food items between them. This is the first ever investigation to compare the food habits of the red fox and the raccoon dog in Central Europe.

Material and Methods

Study area

Hunted and road killed carcasses of 253 raccoon dogs and 256 red foxes for diet analyses were collected in various areas of Mecklenburg Western-Pomerania (north-east Germany) from August 2004 to January 2007. The human population density (71 inhabitants/km^2) in the

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province is the lowest in Germany. The climate is temperate with an average annual temperature between 2004 and 2006 of 9.3° C, ranging from a mean of -0.3° C in January to a mean of 15.6° C in July. (German Weather Service/Laage, 2008). Raccoon dogs and red foxes are frequently hunted in our study area.

Diet analyses and determination of food items

After dissection, which was carried out at the Friedrich-Loeffler-Institut (BFA) Wusterhausen, Germany, the stomachs were filled with ethanol (70%) and frozen at -20° C. The diets of the raccoon dogs and red foxes were analysed at the Institute of Zoology, University of Rostock. Stomach contents were examined by rinsing them with water and collecting food items in a sieve (0.1 mm). Thereafter we successively put contents of the sieve into a Petri plate and examined small food items (e.g. single earthworm *Lumbricus* sp. chaetae) using a binocular microscope (32× magnification). Hairs from fur remains were determined using a microscope, according to the hair analysis key of Teerink (1991). Grass and deciduous leaves, plastic and mineral materials were excluded from further analysis. Larger food items were dried in Petri plates for 24 hours at 60-70° C for further determination. We used published descriptions, personal experience and the zoological collection held at the Institute of Zoology, University of Rostock to identify food items. To determine fruits we developed a sample collection. Seeds were compared with the "cereal" catalogue of Wagner et al. (2006). Insect were determined using the keys of Stresemann (1995); Bellmann (1999) and Chinery (1984) and exhibits from the zoological collection Rostock. Remains of amphibians were macerate and determined using the lilium bone and the keys of Beurton (1973); Boehme (1977) and Schaefer (1932). Remains of birds (feather, bill, and feet) were compared to exhibits of the zoological collection Rostock and determined using the descriptions of Busching (1997) and Hume (2002). We divided the year into seasons (spring: March-May, summer: June-August, autumn: September-November, winter: December-February) for diet analysis.

Frequency of occurrence (FO)

With FO, the presence or absence of a certain category was recorded in each stomach sample, and the results were expressed as the percentage of samples which had that category in relation to the total number of samples, that is: $FO(\%) = \frac{100n}{N}$, where:

$FO(\%)$: Relative frequency of occurrence of a food category

n : Number of samples with occurrence of a food category

N : Total number of stomach samples analyzed

Twenty-eight raccoon dogs and three red foxes were excluded from the seasonal analysis because we did not know the month the animal died. FO was estimated for small mammals, brown hare (*Lepus europaeus*), rabbit (*Oryctolagus cuniculus*), carrion, unidentified mammals, red fox, raccoon dog, birds, amphibians, reptiles, fish, insects, snails, earthworm and edible plant material (i.e. maize, crops and seed and fruits) with small mammals, carrion, birds, insects and edible plant material divided in subcategories.

Biomass share (BS)

We calculated quantitative mean annual and seasonal biomass indices following a method used in previous diet analyses (Ansorge, 1991, 1998) according to which food items are valued according to the live weight of the animals consumed (e.g. 7 g for *Sorex* sp., 30 g for *Microtus* sp. and 20 g for *Rana* sp.), regardless of their state of digestion and the extent to which they were consumed. The average stomach capacity of red foxes and raccoon dogs was calculated to be 102.04 g ± 102.58 SD and 111.26 g ± 140.27 SD, respectively. We used this benchmark to calculate the biomass share of food items that we were unable to count. Large ungulates, hares, rabbits, red foxes, raccoon dogs, large birds and edible plant material (i.e. fruits and maize) were thus valued to have been consumed to the average stomach capacity of the canids.

For standardisation, we calculated a mean biomass weight (g) for red fox and raccoon dog stomachs contents within different seasons. Thereafter we estimated the mean percentage share of each diet category for each season according to the standardised weight. We calculated the seasonal BS of seven food categories: small mammals, carrion, birds, amphibians, insects, fruits and maize corn (*Zea mays*). Twenty-seven raccoon dogs and 40 red foxes were excluded from the BS analysis because their stomachs were empty, but were considered in the statistical analysis. Where evidence of digested earthworm (*Lumbricus* sp.) was found by records of chaetae, one specimen per stomach was deemed to be present for the purposes of calculation. Evidence of small mammal species recorded by fur remains, was also counted as one specimen per species and stomach. We could not identify 9.9% and 7.6% of the mammals found in the stomachs of red foxes and raccoon dogs, respectively. Hence we decided to exclude unidentified mammals from the calculation of biomass share.

Food overlap and food niche breadths

The overlap in diet categories between red foxes and raccoon dogs was calculated according to the Pianka index (a_{jk}) formula (Pianka, 1973), where P_{ij} and P_{ik} are the proportions of the diet item in the total diet of species j and k, respectively:

$$a_{jk} = \frac{\sum P_{ij} P_{ik}}{(\sum P_{ij}^2 \sum P_{ik}^2)^{\frac{1}{2}}} \tag{1}$$

When the overlap index value a_{jk} is equal to 0, the diets of species j and k do not overlap at all, whereas when a_{jk} is 1, their diets overlap completely.

To compare the food niche breadths of the two canids, the Levins' index B was calculated for 10 food categories following Levins (1968):

$$B = \frac{1}{\sum n p_i^2} \tag{2}$$

where p_i is the frequency of food category i and n is the number of food categories.

Statistical analysis

We used SPSS 15.0.1 for statistics. To test for interspecies differences of the distributions of food items for BS and FO we used the two-sample Kolmogorov-Smirnov (K-S) test. To verify interspecies differences of BS for food items within seasons and for BS differences within food categories we used the nonparametric Mann-Whitney-Wilcoxon signed rank-test (M-W). To test for interspecies differences of FO for food items we used the χ^2-test, with a significance ($p < 0.05$) threshold at $\chi^2 > 3.84$ (Lind and Scheid, 1998; Sachs, 2004).

Results

Annual diet composition

Food items among species were equal distributed for BS (K-S, D = 0.28, $p = 0.43$) and FO (K-S, D = 0.33, $p = 0.22$). Small mammals (BS = 31.2, FO = 38.7) and edible plant material (BS = 51.3, FO = 63.1) were the most important food resources for red foxes and raccoon dogs, respectively. Interspecies differences of BS were recorded for edible plant material (M-W, $p = 0.02$), small mammals (M-W, $p <$

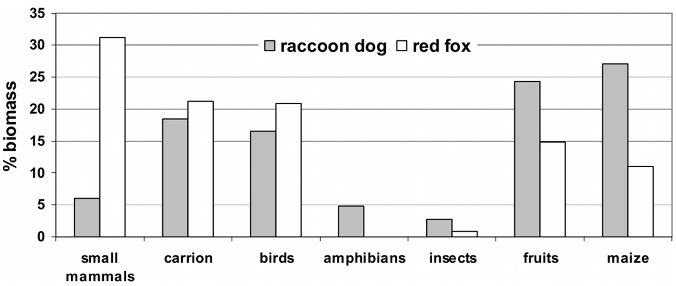

Figure 1 – Annual biomass share of food items found in the stomachs of raccoon dogs (n=226) and red foxes (n=216).

Table 1 – Frequency of occurrence (FO) of food items in red foxes (r.f. n = 253) and raccoon dogs (r.d. n = 225) and food niche overlap index according to Pianka (1973). 1 equals 100% and 0 equals 0% overlap.

Item	**Spring**		**Summer**		**Autumn**		**Winter**		**All seasons**	
	r.f. n=27	r.d. n=34	r.f. n=38	r.d. n=53	r.f. n=67	r.d. n=78	r.f. n=121	r.d. n=60	r.f. n=253	r.d n=225
Small mammals	37.0	20.6	31.6	17.0	43.3	12.8	47.5	21.7	38.7	17.3
Shrews and moles	-	11.8	-	3.8	1.5	2.6	-	11.7	0.4	6.6
Voles *Microtidae*	25.9	5.9	31.6	15.1	35.8	11.5	40.8	2.5	35.6	9.8
Mice *Muridae*	18.5	2.9	-	3.8	9.0	10.2	18.3	2.5	8.7	6.2
Brown hare *Lepus europaeus*	-	-	5.3	1.9	4.5	3.8	3.3	1.7	3.6	2.2
Rabbit *Oryctolagus cuniculus*	-	-	-	-	4.5	-	-	-	1.2	-
Carrion	22.2	17.6	21.1	18.9	23.9	21.8	21.7	38.3	22.1	24.4
Wild boar *Sus scrofa*	7.4	8.8	5.3	7.5	8.9	5.1	9.2	11.7	8.4	8.0
Red deer *Cervus elaphus*	-	2.9	-	-	1.5	-	2.5	5.0	1.6	1.7
Roe deer *Capreolus capreolus*	7.4	-	-	-	1.5	-	0.8	10.0	1.6	2.7
Domestic ungulates	-	-	2.6	-	-	-	-	-	0.4	-
Unidentified mammals	14.8	11.8	13.2	1.9	6.0	7.8	10.0	10.0	9.9	7.6
R.f. *Vulpes vulpes*	-	-	-	1.9	-	-	-	1.7	-	0.4
R.d. *Nyctereutes procyonoides*	3.7	-	-	1.9	-	-	0.8	-	0.8	0.4
Birds	40.7	32.4	28.9	17.0	25.4	24.4	30.0	31.7	29.6	25.8
Passeriformes	-	2.9	2.6	3.8	1.5	-	2.5	6.7	2.0	3.1
Ducks *Ardeidae*	3.7	-	-	1.9	1.5	1.3	4.2	1.7	2.8	0.9
Geese *Anseriformes*	-	2.9	-	-	-	-	-	1.7	-	0.9
Doves *Columbidae*	-	-	-	1.9	-	1.3	-	1.7	-	1.3
Domestic fowl	14.8	2.9	13.2	1.9	13.4	6.4	13.3	3.3	13.4	4.0
Unidentified birds	18.5	17.6	7.9	9.4	6.0	16.7	10.0	16.7	9.5	13.3
Amphibians	- 17.7	-	30.2	-	12.8	-	6.7	-	16.0	
Reptiles	-	5.9	-	7.5	-	1.3	-	-	-	2.2
Fish	3.7	-	7.9	1.9	1.5	-	1.6	1.7	2.8	0.9
Insects	48.1	38.2	55.2	84.9	32.9	48.7	11.7	40.0	27.7	53.3
Coleoptera	29.6	26.5	31.6	75.5	28.4	48.7	4.2	13.3	17.4	42.7
Other insects	3.7	14.7	23.7	24.5	16.4	23.1	1.7	13.3	9.1	19.6
Insect larvae	14.8	38.2	23.7	24.5	14.9	19.2	7.5	26.7	12.6	25.3
Snails	-	5.9	-	18.9	-	3.8	-	6.7	-	8.4
Earthworm *Lumbricus* sp.	3.7	23.5	-	11.3	1.5	20.5	-	21.7	0.8	19.1
Edible plant material	48.1	79.4	31.6	50.9	47.8	61.5	27.5	66.7	35.6	63.1
Maize *Zea mays*	25.9	61.8	2.6	22.6	11.9	29.5	10.0	45.0	11.1	36.9
Crops and seeds	14.8	35.3	5.3	15.1	10.4	15.4	11.6	11.7	9.9	17.3
Fruits	11.1	5.9	26.3	24.5	31.3	55.1	10.8	15.0	18.6	29.8
Niche overlap (Pianka's index)	0.72		0.77		0.72		0.54		0.72	

0.001) and insects (M-W, p = 0.005) (Fig. 1). We found differences between species in the FO for maize (χ^2 = 16.40, df = 1, p < 0.01), insects (χ^2 = 23.43, df = 1, p < 0.005), small mammals (χ^2 = 10.56, df = 1, p < 0.01) and fruits (χ^2 = 7.29, df = 1, p < 0.05) (Tab. 1). Red foxes mostly preyed on voles (FO = 35.6), whereas raccoon dogs consumed mice (FO = 6.2) as often as voles (FO = 9.8). Shrews, in contrast, were almost avoided by red foxes (FO = 0.4) while raccoon dogs (FO = 6.6) fed on them in all seasons. However unlike red foxes, raccoon dogs did not use small mammals intensively (BS = 6.1, FO = 17.3). Only raccoon dogs preyed on amphibians (BS = 4.9, FO = 16.0); mostly common brown frogs *Rana* sp. and toads *Bufo* sp. Edible plant material in stomachs consisted almost exclusively of maize and fruits (apple, pear, plum and cherry) for both species. Digestible plants and fruits (BS = 25.9) were found in 35.6% of red fox and in 63.1% (BS = 24.3) of raccoon dog stomachs. Insects (mostly beetles) were consumed more frequently by raccoon dogs ($F0$ = 53.3, BS = 2.8) than by red foxes ($F0$ = 27.7, BS = 0.8) but had no significant impact on the total biomass eaten. Insect larvae (mostly maggots Diptera sp.) were found in 25.3% of raccoon dogs and 12.6% of red foxes stomachs. Other invertebrates were of less importance to the red fox diet, but 8.4% and 19.1% of the analysed raccoon dogs feed on snails and earthworms, respectively.

There were no differences (M-W, p = 0.29) in carrion consumption between red foxes (BS = 21.2) and raccoon dogs (BS = 18.2). Both red foxes (FO = 8.4) and raccoon dogs (FO = 8.0) scavenged on wild boar. Moreover, there was evidence that two red foxes foraged on raccoon dogs and vice versa. In one raccoon dog stomach we found intraspecies hair, skin and tissue. Birds were eaten by red foxes (BS = 20.9, FO = 29.9) and raccoon dogs (BS = 16.5, FO = 28.5), without interspecies differences (M-W, p = 0.05). However, only red foxes preyed on domestic fowl (FO = 13.4), though to a limited extent.

Seasonal diet composition

No interspecies differences of BS (n = 7 food categories) composition was recorded within seasons (M-W, U = 21.5-23, p < 0.05 for all seasons). Raccoon dogs fed intensively on maize, and used birds and carrion to some extend in spring. For red foxes, carrion, edible plant material (i.e. fruits, maize, crops and seed) and birds were important diet categories in spring. Roe deer was found in red foxes' diet in spring and in raccoon dogs' diet in winter (Tab. 1, Fig. 2). No significant interspecies differences of percentage BS for different food items were recorded in spring (M-W, p > 0.05). Raccoon dog mostly consumed fruits and maize but also fed frequently on amphibians in summer. Red foxes consumed mostly small mammals and carrion in summer. There were no significant inter-specific FO differences for all food categories in summer, except for insects (χ^2 = 6.00, df = 1, p < 0.05) that were regularly consumed by red foxes and raccoon dogs. Only raccoon dogs preyed on amphibians in summer. In autumn we found an interspecies difference for the BS (M-W, p = 0.01) and FO (χ^2 = 4.51, df = 1, p < 0.05) of maize, when raccoon dogs extensively fed on fruits and red foxes on small mammals, fruits and carrion. In winter raccoon dogs mainly rely on carrion and maize whereas red foxes mainly fed on small mammals, birds and carrion. However, we found differences of FO for carrion (χ^2 = 4.16, df = 1, p < 0.05) and maize (χ^2 = 12.16, df = 1, p < 0.01) and there were significant differences for the BS of maize (M-W, p = 0.01), small mammals (M-W, p < 0.01) and insects (M-W, p < 0.01) between species in winter.

Diet overlap and food niche breadths

Overall, seasonal Pianka's indices of interspecies diet similarity were high (a_{jk} > 0.72) except during winter (a_{jk} = 0.54), however also the mean annual diet overlap index (a_{jk} = 0.72) indicates competition. (Tab. 1). The mean annual food niche breadths were B = 2.0 for red foxes and B = 1.1 for raccoon dogs.

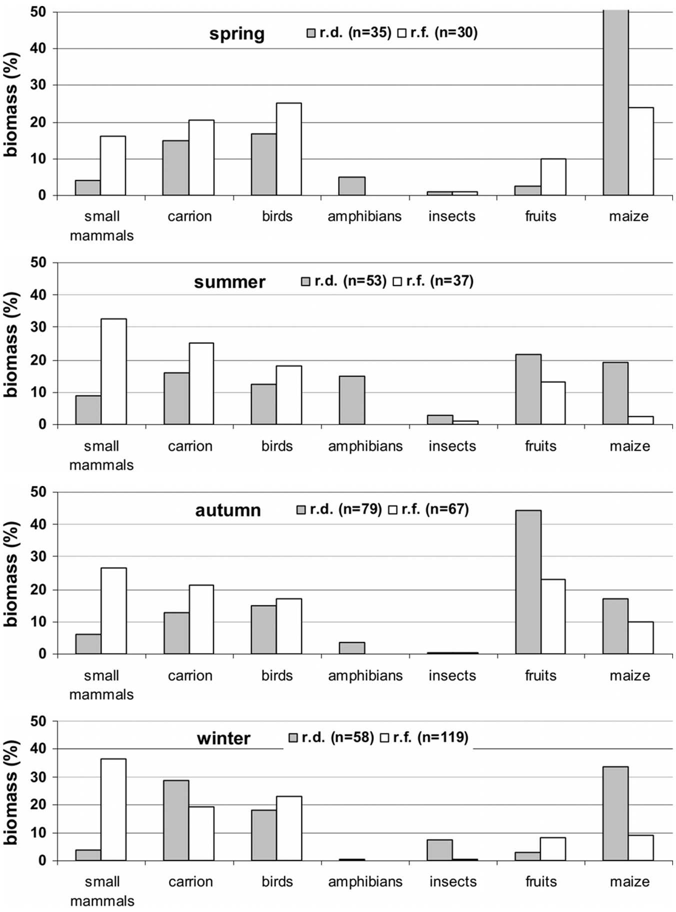

Figure 2 – Seasonal biomass share of food items found in the stomachs of raccoon dogs (grey) and red foxes (hollow) (n=animals).

Discussion

Present results and previous diet analyses (Barbu, 1972; Ansorge, 1991; Cavallini and Volpi, 1996; Ansorge, 1998; Drygala et al., 2000; Bertolini et al., 2001; Goldyn et al., 2003; Rika and Keiji, 2009; Sutor et al., 2010) indicate that both canids are omnivore and that both pursue an opportunistic feeding strategy. Some resources were exclusively used by the raccoon dog and avoided by the red fox and vice versa. Moreover our food niche overlap estimation corresponds to previous studies (Jedrzejewska and Jedrzejewski, 1998; Kauhala et al., 1998) and suggests that these canids can coexist.

Food niche breadths and preferences for food categories were similar. This indicates that competition between the species may occur in areas with very high raccoon dog density. However, competition for food between the species is eased by their omnivorous character and by dietary differences (Viro and Mikkola, 1981). Red foxes and raccoon dogs are sympatric in the original distribution area (East Asia) of the latter (MacDonald and Reynolds, 2004; Kauhala and Saeki, 2004) and have adapted to coexist. This may lead to the conclusion that competition between the species, if it takes place at all, is not crucial.

Studies carried out in north-eastern Europe (Poland, Belarus and Lithuania) into interspecific diet competition confirmed a high level of overlap in winter but low overlap indices in summer (Jedrzejewski et al., 1989; Sidorovich et al., 2000; Baltrunaite, 2002). In northern Belarus, for example, the native, generalist predator populations began to decline after the raccoon dog reached a level of high population density. Competition for carcasses in winter was proposed as a factor in the observed decline, particularly in the case of polecats (*Mustela putorius*), but also, to a lesser degree, in red foxes (Sidorovich et al., 2000). Raccoon dogs are able to hibernate and well adapted to a long period of food deprivation in northern areas (Asikainen et al., 2002; Kauhala and Kowalczyk, 2011) therefore sever diet competition between raccoon dogs and red foxes is improbable during winter. However, correlative data from Finland showed that when raccoon dogs were heavily hunted and their population decreased, the fox population started to increase (Kauhala, 2004). In the temperate climate of Central Europe, omnivorous, medium-sized predators face no food limitation in winter. For example, raccoon dogs did not hibernate and only at temperatures below -5° C they reduced their activity and sometimes stopped foraging for short periods in north-east Germany (Zoller and Drygala, 2013).

Small mammals (rodents and shrews), carrion (especially the innards left over from game hunting) and edible plant material (fruits, maize from bait stations) are assumed to be highly abundant and birds are available year round in our study area. Raccoon dogs frequently catch sick or injured birds left behind by hunters (Samusenko and Goloduško, 1961; Pavlov and Kiris, 1963; Barbu, 1972; Naaber, 1974; Viro and Mikkola, 1981; Kauhala et al., 1993) and may occasionally prey on ground-nesting birds such as waterfowl (Barbu, 1972; Włodek and Krzywiński, 1986; Schwan, 2003; Sutor et al., 2010). Red foxes in contrast, are considered a major predator of ground-nesting colonial birds and their effect on game-bird populations can be significant. They are adapted to pounce on their prey with great precision (MacDonald and Reynolds, 2004) and thus are much more skilful predators than raccoon dogs. Although, there is not much difference in the biomass estimated for birds, it is probable that red foxes killed most of the birds but raccoon dogs consumed most of them as carcasses. Moreover, insect larvae (i.e. carrion fly maggots), that were accidentally consumed and found more often in raccoon dog than red fox stomachs, point to scavenging behaviour. Interspecies predation among defendable, predators of equal size is improbable but adult red foxes are capable of preying on juvenile raccoon dogs (Heptner and Naumov, 1974). Hence, the two records of raccoon dogs eaten by red foxes and vice versa indicate scavenging behaviour or adult foxes that have killed raccoon dog pups.

In general, the diets determined for both species were fairly similar. Nevertheless, the competition involved is assumed to be minor since differences do exist: red foxes consumed more small mammals (i.e. voles) and less edible plant material (i.e. fruits and maize) than raccoon dogs. Moreover, raccoon dogs used food resources (e.g. amphibians, invertebrates and shrews) that were avoided by red foxes. This coincides with a study in Finland were the red fox is a more active predator and consumes more vertebrate prey (mammals and birds) than the raccoon dog, which feeds more frequently on shrews, invertebrates, carrion and plants (Kauhala, 1996; Kauhala et al., 1998).

Our results indicate broad food niche overlap throughout the year. However, dietary overlap may not necessarily be indicative of direct inter-specific competition, because as long as food is sufficiently available, the degree of competition is low (Rika and Keiji, 2009). We assume that the high level of habitat diversity (e.g. natural forests, wetlands and agricultural areas) in north-east Germany, together with distinct differences in habitat preferences between species (Drygala and Zoller, 2013) offers a high availability of food resources to both canids. Consequently exploitation competition is likely to be low to nonexistent. Similarly, the raccoon dog is not reported to have had any negative impact on native predators in Poland (Kowalczyk et al., 2008).

It can be concluded that though exploitation competition between the invasive raccoon dog and the native red fox might take place in Central Europe, it is unlikely to be severe enough to lead to a significant decline in either species.

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