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Cooccurrence and food niche overlap of two common predators (red fox *Vulpes vulpes* and common buzzard *Buteo buteo*) in an agricultural landscape

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Abstract: The mechanism of coexistence and interspecific relationships between 2 predatory species has been an important topic in ecology for many years. To date, researchers have focused mostly on very similar species, such as 2 mammals or 2 birds of prey, occupying the same habitat. However, the situation where a predatory mammal may live sympatrically with a common bird of prey is probably more common. A good example is the coexistence of the red fox and the common buzzard. The relationship between these species with respect to spatial distribution, the abundance of a potentially important prey species (common vole), diet, trophic niche breadth, and niche overlap was studied in western Poland during 2006–2009. The distances between fox dens and buzzard nests were significantly shorter than would be expected by chance. The abundance of common vole was higher in sites where both predators were present than in the control sites, where neither predator was recorded. The trophic niche overlap between both predators was moderate (62.1%). However, the trophic niche breadth of the common buzzard was narrower (2.733) than that of the red fox (3.875), which implies that the fox is a more generalist predator.

Key words: Red fox, common buzzard, coexistence, cooccurrence, diet

1. Introduction

Predators play an important role in influencing prey population size, as well as in modifying whole ecological communities (Holt and Huxel, 2007), but the density and distribution of predators depends on the availability and abundance of their prey (Goszczyński, 1977; Jędrzejewska and Jędrzejewski, 1998). The majority of studies on predation have focused only on the single predator–prey relationship, without any context of the effect of other predatory species living in the same area (Barbosa and Castellanos, 2005). However, in ecological communities there are usually several predatory species, and one predator may even consume another (e.g., intraguild predation; Polis et al., 1989; Barbosa and Castellanos, 2005). Therefore, simple predator–prey interaction is far from the reality, which includes more complex situations such as the interactions of 2 predators and their prey (Barbosa and Castellanos, 2005). The interspecific relationships of predators foraging on the same prey are popular subjects of many studies, especially those of mammalian carnivores (Palomares and Caro, 1999; Aunapuu et al., 2010) and avian predators, both diurnal raptors and owls (Sergio et al., 2007; Riegert et al., 2009).

Among previous studies (e.g., Goszczyński, 1986; Riegert et al., 2009) there is much information on the coexistence of 2 or more predators from the same taxonomic group (birds, mammals). On the other hand, it has been shown that interactions between predators from distinct taxonomic groups may arise (Goszczyński, 1977). Competition for food resources between predatory mammals and birds of prey seems to be even stronger than between 2 mammalian or avian predators and therefore affects the diet niche overlap between them (Goszczyński, 1977; Jędrzejewska and Jędrzejewski, 1998). For example, a study conducted in southern Finland revealed that red fox (*Vulpes vulpes*) negatively affected the goshawk (*Accipiter gentilis*) population by limiting the grouse population (Selås, 1998).

The major ecological niche theory says that niche segregation reduces exploitive competition and allows coexistence (Pianka, 1969). Coexistence could be facilitated by differences in size of predators (Rosenzweig, 1966), prey species (Schmidt et al., 2009), prey sizes (Gittleman, 1985; Scognamillo et al., 2003; Gliwicz, 2008), activity patterns (Fedriani et al., 1999), habitats (Fedriani et al., 1999), and use of space (Durant, 1998). Red fox and

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common buzzard (*Buteo buteo*) are 2 of the most numerous predators occurring sympatrically in Europe and northern Asia (Newton, 1978; Goszczyński, 1995). Especially in conditions where prey density is relatively low, predators have an important influence on prey populations, as well as on ecosystem functioning (e.g., Goszczyński, 1974). Although both species have been intensively studied (e.g., Goszczyński, 1995; Graham et al., 1995; Wuczyński, 2005), the spatial and diet interactions between these 2 species have been not thoroughly investigated. Studies on the feeding habits of red fox in central Europe indicate that their major prey are rodents and birds (Goszczyński, 1974; Kožena, 1988; Gołdyn et al., 2003; but see for exception Kidawa and Kowalczyk, 2011). The main prey of common buzzard in agricultural central Europe are also rodents and birds (Goszczyński and Piłatowski, 1986; Skierczyński, 2006). Both predators are generalists; in other regions, their populations might subsist by focusing their predation upon other prey (Graham et al., 1995; Leckie et al., 1998; Fedriani et al., 1999). The population of these 2 predators in central Europe depends on the fluctuating changes in vole densities (Goszczyński, 1974; Goszczyński and Piłatowski, 1986; Jędrzejewski and Jędrzejewska, 1992; Jędrzejewski et al., 1994; Graham et al., 1995). Common vole (*Microtus arvalis*) is the most abundant rodent in the agricultural landscape of central Europe (Goszczyński, 1977). Because of the preference for voles, we predict that both species would choose sites where common voles are most abundant. We might expect that foxes and buzzards inhabiting the same area could act antagonistically, including competition or even intraguild predation, despite factors that may allow them to coexist, e.g., distinct activity patterns (night vs. day, space uses).

The aim of this study was to evaluate factors that might affect the coexistence of the predators: 1) spatial cooccurrence, 2) density of their common prey, and 3) food niche overlap.

2. Material and methods

2.1. Study area

The study was conducted between May 2006 and August 2009 near the town of Odolanów, Wielkopolska Province, western Poland (51°34′N, 17°40′E). The study area was characterized by farmland with a mosaic of arable fields, meadows, small woods, and scattered trees and shrubs of different ages, with a dominance of white willow (*Salix fragilis*), birch (*Betula pendula*), black poplar (*Populus nigra*), and Scots pine (*Pinus sylvestris*). The study area is about 220 km^2 and is characterized by a low proportion of woods (22% of area) in relation to meadows (39%) and arable fields (39%).

2.2. Spatial cooccurrence

To investigate whether the spatial cooccurrence between the red fox and the common buzzard was higher than could be expected by chance, the distances between buzzard nests and fox dens were compared to the distances between buzzard nests and randomly selected points. If red foxes dig dens independently of common buzzard nests (and vice versa), there should be no difference in distances between dens and nests and between randomly selected points. Before analysis, red fox dens and common buzzard nests were located using a GPS device (Garmin GPSMap 76) and added to a digital map. Only the nests in whose vicinity (within 250 m) 1 or more dens were found were included in the analysis. Sixteen buzzard nests and 26 fox dens were studied. Using Quantum GIS software (2010), circle buffers of 500 m in diameter were created around the 16 nests. As a control, we created a random set of 26 points (virtual dens) contained within the above buffers, assuming that the red fox dens and common buzzard nests were within forests. The 26 real and 26 virtual distances were log-transformed and had normal distribution. To test differences, we used analysis of covariance. To avoid a bias caused by forest size (ranging from 0.61 to 66.7 ha), we used forest area as a covariate. Proportion of the forest area was arcsine-transformed.

2.3. Density of voles

Common vole abundance was estimated from an index of density (Romankow-Żmudowska and Grala, 1994) based on the counts of holes that were conducted every spring season (April–June) in 2006–2009. The counts were performed at each of the selected sites in 3 main habitats: arable field, meadow, and other grassland (mainly unfarmed field margins and abandoned areas). In each given habitat, 3 randomly selected 3 × 3 m quadrates were chosen. The vole indexes were created as a sum of the number of holes across the habitat. To confirm that the distribution of predators was clumped according to the distribution of vole "hot spots", we estimated common vole abundance in fox/buzzard territories and in control sites where neither fox nor buzzard occurred. Predators' territories were determined according to their breeding dens/nests. Results were divided into 2 groups: where a predator occurred, and where it did not occur.

2.4. Diet

The diet of foxes was examined by analyzing their feces (scats). Scats were collected regularly between May 2006 and August 2009 across the whole study area and the areas around dens. Droppings were placed in plastic bags and stored for later analysis. Prey were identified to the species on the basis of macroscopic remains (mainly bones and teeth; Pucek, 1984). Identified food remains were classified into the following categories: rodents, insectivores, birds, lagomorphs, other mammals (mainly carrion), reptiles and amphibians, invertebrates, plants, fruits and seeds, and garbage. The composition of the diet was characterized using 3 methods: relative frequency of occurrence, R% (number of prey of a given food category / total number of prey × 100); frequency of occurrence, O% (number of occurrences of each prey items / total number of feces × 100); and the percentage of fresh biomass, B% (dry weight of remains of a particular prey type × a factor characterizing the coefficient of digestibility / total biomass × 100). Coefficients of digestibility were obtained from the literature (Lockie, 1959; Goszczyński, 1974). In addition to the fecal analysis, prey remains in the vicinity of breeding dens and nests were also collected.

The diet of common buzzard was determined from pellets, remains of prey, and whole prey found under nests and in their immediate surroundings. During check visits all pellets and remnants of prey were collected, placed in plastic bags, and stored for later analysis. The prey were identified to the species on the basis of the characteristics of the skeleton, pelage, and plumage (Dziurdzik, 1973; Pucek, 1984; Brown et al., 1999). Diet items were classified into the same categories as for red fox and by the same 2 methods, R% and O%, and by the percentage of fresh biomass, B% (number of each prey type × the mean weight of the appropriate food taxa / total biomass × 100). Jędrzejewska and Jędrzejewski (1998) suggested that if a predator consumed large prey, stomach capacity (66 g for common buzzard) should be taken into account to calculate biomass. Prey remains of both predators found in the field were included in the analysis of niche breadth and niche overlap. The G-test was used to compare differences of R%, O%, and B% in diet components between red fox and common buzzard.

Trophic niche breadths of red fox and common buzzard were calculated for 4 years using the Levin index (Krebs, 1989): $B = 1/\sum p_i^2$, where p_i is relative frequency of occurrence of the *i*th taxon. Prey were grouped into the following 10 food taxa: rodents, insectivores, birds, lagomorphs, other mammals (mainly carrion), reptiles and amphibians, invertebrates, plants, fruits and seeds, and garbage. Trophic niche overlap was calculated by means of the Renkonen index: $P_{jk}=\Sigma^n(\text{minimum } P_{ij}, P_{ik})\times 100$, where P_{jk} is the percent overlap between species j and species k, p_{ij} and p_{ik} are the proportion of resource i represented within the total resources used by species j and species k, and n is the total number of resource taxa (Krebs, 1989). Seasonal differences between species were evaluated by a Wilcoxon matched pairs test.

Statistical analyses were performed using the R package (R Development Core Team, 2005).

3. Results

3.1. Spatial cooccurrence

The mean distance between fox dens and buzzard nests was significantly lower (n = 26; mean = 155.5 ± 61.5 m [mean ± SE]) than that expected by chance (n = 26; mean = 266.1 ± 83.8 m; ANCOVA, df = 1, ms = 158,789, F = 4.7, P < 0.05). Moreover, the analysis of covariance showed that size of forest area included in buffers did not affect the result (ANCOVA, df = 1, ms = 7109, F = 0.2, P > 0.05).

3.2. Density of voles in places of predator occurrence

Common vole abundance was significantly higher in sites where common buzzards were present (median = 20.0; interquartile range = 9.8–34.5) than in sites where buzzards were not recorded (median = 0.0; interquartile range = 0.0–4.0; Mann–Whitney U test: n_1 = 42, n_2 = 51, Z = –6.50, P < 0.0001). A similar value was noted for red fox (median = 17.5, interquartile range = 5.8–31.0 in sites where red foxes were present; median = 0.0, interquartile range = 0.0–4.0 in sites where red foxes were not recorded; Mann–Whitney U test: n_1 = 50, n_2 = 43, Z = –5.44, P < 0.0001).

3.3. Diet

A total of 2344 prey items were identified in 1022 red fox scats. The most important component in the diet of red fox was rodents. Other common prey were birds and carrion (other mammals). Invertebrates and plants were frequently recorded, although biomass showed they were not important; other food components occurred rarely (Table). A total of 1035 prey items were identified in 546 buzzard pellets. The buzzard diet compared to the red fox diet was based much more on rodents; birds were less important. Other prey items were generally found only in low proportions (Table).

Based on calculations on the 10 main food categories, the trophic niche breadth of red fox was broader (3.875) than common buzzard (2.733). Trophic niche overlap between the 2 predators was 62.1%. Niches between predators differed significantly in all surveyed seasons (Wilcoxon matched pairs test: n_1 = 7, n_2 = 7, Z = 2.367, P < 0.05).

4. Discussion

Recent studies investigating why sympatric species coexist have focused on interactions between birds of prey (Sergio, 2007) or mammalian carnivores (Schmidt et al., 2009; Aunapuu et al., 2010). In our study, we examined coexistence and interactions between a mammalian carnivore predator and a bird of prey. Red fox and common buzzard appeared to cooccur in farmland. They chose sites with a higher abundance of voles. To reduce potential competition and to allow coexistence (Pianka, 1969),

Table. Food composition of red fox and common buzzard expressed as frequency of occurrence in scats/pellets (O%), relative frequency of occurrence in all prey (R%), and the percentage of fresh biomass (B%). Asterisks indicate significant differences in diet between red fox and common buzzard (G-test: * P < 0.05, ** P < 0.01, *** P < 0.001).

Food type	Red fox			Common buzzard		
	O%	R%	B%	O%	R%	B%
Rodents	70.4	45.4	26.1*	92.4	51.4	79.4*
Insectivores	2.4	1.1	0.0	4.2	1.9	4.5
Birds	25.5*	14.2*	24.8*	12.1*	5.1*	10.1*
Lagomorphs	2.9	1.3	1.7	0.2	0.1	0.3
Other mammals (mainly carrion)	13.5**	5.2	26.0***	2.5**	1.2	1.1***
Reptiles and amphibians	0.9	0.3	0.0	3.2	1.4	1.4
Invertebrates	23.9***	10.5**	0.4	69.1***	30.6**	2.8
Plants	33.2**	14.6	8.4**	14.8	6.5	0.3
Fruits and seeds	11.0*	5	12.6***	2.3*	1.8	0.1***
Garbage	5.4	2.4	0.0	0.0	0.0	0.0
Number of scats/pellets	1022			546		
Number of prey	2344			1035		

both predators may differentiate their prey preferences. It may also be achieved by various other factors such as different body sizes, antagonistic behavior (e.g., intraguild predation), hunting methods, and different hunting periods (buzzard is diurnal while fox is mainly nocturnal). Furthermore, these species use different dimensions, with the buzzards using the third dimension (vertical), which is not explored by the foxes, who have no arboreal abilities.

Red fox and common buzzard are the most numerous predators in the agricultural landscape in Poland (Goszczyński, 1995; Goszczyński et al., 2005), where their cooccurrence may by very common. Previous studies showed that both species select similar habitats: midfield woods for breeding and fields/meadows for hunting (Goszczyński, 1977). In our study area, due to a lack of large forests, both predators chose small woods adjacent to vole-rich hunting grounds as breeding sites. What permits their coexistence? Our results showed that despite high vole preferences, the species differ in their diet composition. Rodents, mainly common voles, are the most abundant prey items in the agricultural landscape in Poland for both species (Goszczyński, 1977). It is known that fox and buzzard biology depends on fluctuating changes in vole density, and that both species are generalist predators who can switch to alternative prey if the main food item declines (Leckie et al., 1998; Reif et al., 2001). The outcome of our diet study showed that common buzzard is a more specialized species than red fox. Moreover, Goszczyński (1977) denoted that both predators utilize voles of different weight classes (predatory birds hunt chiefly heavier and older voles, while foxes often dig up the earth and catch young voles directly in the nest, especially in the summer–autumn period). In that way, both species may reduce potential competition for the same food spectrum (voles), at least partially.

The diet of foxes is much more diverse than that of buzzards (rodents, birds, carrion, fruits, and garbage). The buzzard had a narrower niche breadth each year. The unique system of these predators and their diet differences may change over time, e.g., due to fluctuating vole and hare (*Lepus europaeus*) densities; this was not the focus of our study. Previous studies on both predators showed that the decline of the hare population in the 1990s was strongly matched by a decrease of hares found in their diets (Goszczyński, 1986; Goszczyński et al., 2005). Despite diet differences between the species, their niche overlap is quite high, which can affect competition between them. However, antagonistic behavior probably does not affect their cooccurrence, since there is no evidence of spatial avoidance.

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