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Diet composition of the golden jackal and the sympatric red fox in an agricultural area (Hungary)

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Abstract. In order to better understand the ecology of the golden jackal (*Canis aureus*) and interspecific relationships among carnivores, we studied its dietary pattern and the diet of its main competitor, the red fox (*Vulpes vulpes*) over a three-year period. The study was carried out in an agricultural area in SW Hungary and was based on scat analysis (jackal n = 373, fox n = 268 samples). The jackal primarily consumed small mammals in all seasons (mean biomass consumed: 72 %). The secondary food sources were wild ungulates (in winter and spring; mainly wild boar *Sus scrofa*, including piglets) and plants (in summer and autumn; mainly wild fruits). The consumption of cervids in winter and in spring was only detected in low proportions. The fox also primarily consumed small mammals (50.3 % of trophic niche breadth, B), but their consumption dropped in summer and autumn. Two-thirds of the summer and autumn diet consisted of plants, while the bird consumption was higher in spring and summer. The diet compositions of both predators were similar. However, compared with jackal, the fox consumed significantly higher proportions of birds. The standardized trophic niche breadth (B_A) of these canids was very narrow (0.09), and the food overlapped in high proportions (69.8 %). The study confirmed the partial partitioning of food resources and opportunistic feeding of both canids.

Key words: *Canis aureus*, *Vulpes vulpes*, feeding ecology, trophic niche, opportunistic feeding, resource partitioning

Introduction

The golden jackal (*Canis aureus* Linnaeus, 1758), a developed social system living mesocarnivore species, is spreading mainly in areas of Central and South-East Europe, including Hungary (Arnold et al. 2012). Its population size is continuously increasing (Szabó et al. 2009), and recently there has been an increase of reproductive populations in northern regions of Europe (Rutkowski et al. 2015). There are many common beliefs about the jackal, especially on its feeding habits (Szabó et al. 2010, Mihelič & Krofel 2012, Bošković et al. 2013). The backgrounds of such beliefs are often unknown or can be easily misinterpreted lacking knowledge of real causes.

The golden jackal feeds upon a broad range of smaller sized prey, such as rodents, hares, birds, reptiles and arthropods (Demeter & Spassov 1993, Mukherjee et al. 2004, Lanszki et al. 2006, Jaeger et al. 2007), but also consumes plants (Demeter & Spassov 1993, Mukherjee et al. 2004, Aiyadurai & Jhala 2006, Borkowski et al. 2011), and scavenges on domestic animal remains (Macdonald 1979a, Poché et al. 1987, Lanszki et al. 2009, Giannatos et al. 2010, Lanszki et al. 2010, Borkowski et al. 2011, Bošković et al. 2013, Penezić & Ćirović 2015), and different kinds of wild ungulate carcasses left by large predators (Aiyadurai & Jhala 2006) or hunters (Lanszki & Heltai 2002, Bošković et al. 2013, Raichev et al. 2013, Lanszki et al. 2015). The group-living jackal successfully preys on medium- and larger-sized wild and domestic ungulates, especially fawns and calves (Demeter & Spassov 1993, Yom-Tov et al. 1995), or wounded, injured and weakened adults (Lanszki et al. 2006, 2015).

The red fox (*Vulpes vulpes* Linnaeus, 1758) is one of the most widespread and important mesopredators in the Northern Hemisphere (Macdonald & Sillero-Zubiri 2004). In agricultural areas the fox preys primarily on small mammals or hares, and periodically eats birds, carrion, plants and invertebrates (e.g. Englund 1965, Goszczynski 1977, Macdonald 1977, Jensen & Sequeira 1978, Goszczynski 1986, Jędrzejewska & Jędrzejewski 1998, Leckie et al. 1998, de Marinis

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& Asprea 2004). Due to the well known ecology as well as feeding habits of the red fox, it may represent a useful basis for comparison with less well studied competitors such as the jackal. The comparative dietary analyses can also facilitate exploring interspecific interactions (Lanszki et al. 2006). The red fox and the golden jackal are also considered to be generalist species for food and habitat (Macdonald & Sillero-Zubiri 2004). Because of the dramatic decline of large carnivore populations in Europe (Macdonald & Sillero-Zubiri 2004, Chapron et al. 2014), both have become top predators in a majority of the areas they occur in.

The differences between the golden jackal and the red fox arise for example from differing body mass (average of genders, jackal: 9.6-10.8 kg, fox: 5.4-6.3 kg; Heltai et al. 2010, Lanszki et al. 2015), body shape (jackal: longer legs, stronger toothing; Demeter & Spassov 1993, Heltai et al. 2010), activity period (jackal: arrhythmic, fox: nocturnal and crepuscular; Gittleman 1985, Heltai et al. 2010, Lanszki et al. 2015), and hunting techniques (Macdonald 1979b, Bekoff et al. 1984, Yom-Tov et al. 1995). Furthermore, the social system of the golden jackal, depending on the food resources is flexible (Macdonald 1979b, 1983). Although the cooperative hunting of jackals was only clearly proved in Africa (Kruuk 1972, Lamprecht 1978, Moehlman 1987) where they are separate *Canis* species (e.g. Rueness et al. 2011), the golden jackal can hunt not only solitary, but also in a pair, and in a smaller or larger family group with "helpers" and youngsters (Macdonald 1979b, 1983, Demeter & Spassov 1993). Cooperative hunting means competitive advantage compared to the solitary fox (Lloyd 1980) and could be related to habitat (Demeter & Spassov 1993). Larger and social carnivores (Bekoff et al. 1984, Gittleman 1985, 1989), such as the golden jackal, are more effective in preying on smaller or larger animals, because they can change the hunting techniques, while the smaller red fox preys on relatively smaller animals. Therefore, the jackal, unlike the fox, can be a pursuer hunter, not only a searcher hunter (Bekoff et al. 1984). The feeding habits besides prey size or abundance of food resources (e.g. Macdonald 1977, Jędrzejewska & Jędrzejewski 1998, Hungary: Lanszki et al. 2006, 2007), are influenced by numerous behavioural and ecological factors, e.g. zonation, habitat or environmental association of prey species (Gittleman 1985), which is less known in European carnivores. Therefore, in this study, behavioural and ecological features of consumed species are also compared between two sympatric canids.

Previous studies performed on agricultural areas in Hungary (periods examined: 1996-1997 and 2000-2004; Lanszki & Heltai 2002, Lanszki et al. 2006, Lanszki & Heltai 2010) showed similarity in diet composition and small mammal preference, trophic niche of both canids was narrow, but there were detectable characteristic differences as well. For example, more marked seasonal and inter-year differences were found in the diet composition of foxes than jackals, but area specific differences are less known. Better knowledge of intraspecific, interspecific and area related differences in diet compositions and feeding habits of these species may strengthen the biological basis of wildlife management.

Assuming, that the larger body massed, social predator takes larger prey more often than the smaller, solitary hunter (Bekoff et al. 1984, Gittleman 1985, 1989), the first prediction was, there should be considerable intraspecific differences in feeding habits, that is, the golden jackal should consume wild ungulates, meanwhile the red fox should consume small mammals in greater proportion. The second prediction was that the more varied diet jackal should be more food generalist than the fox. Based on the resource partitioning hypothesis (Hardin 1960, Rosenzweig 1966), the third prediction was that there should be a slight trophic niche overlap between the sympatric mesopredator species, because they use the resources (e.g. the prey species) in different ways, namely they partition it.

The aims of this three-year study performed in an agricultural area were 1) to evaluate the diet composition of the sympatric golden jackal and red fox, 2) to examine the trophic niche breadth and the intraspecific trophic niche overlap, 3) to investigate the feeding habits of canids based on the body mass, zonation, habitat association and environmental association of prey species in the diet, and 4) to examine the differences between the diet compositions of the golden jackal and the sympatric red fox in different areas based on Hungarian studies.

Material and Methods

Study area and study species

The study area is located in the Pannonian biogeographical region of SW Hungary (Vajszló region, centre: 45°51′N, 17°56′E), plains area, close (6 km) to the River Drava. Although it is an inland water hazardous area, most of the land is used for arable agricultural cultivation. The vegetation consists of a mosaic of different habitat types, i.e. cultivated lands [59-60 %, mainly cereals, less extent watermelon

(*Citrullus lanatus*), maiden grass (*Miscanthus sinensis*)], forests [29 %, mainly English oak (*Quercus robur*) and European hornbeam (*Carpinus betulus*), less extent poplar (*Populus*) and locust (*Robinia*)], and the 11-12 % of the total area is abandoned grasslands [partially covered by blackthorn (*Prunus spinosa*), common hawthorn (*Crataegus monogyna*), sedge (*Carex*)], common reed (*Phragmites australis*) and oxbow lakes covered by reed, bulrush (*Typha*), willow (*Salix*), alder (*Alnus*) and Canadian goldenrod (*Solidago canadensis*).

The study area lies on the continental climatic region, but there are some Mediterranean features (i.e. moderately warm and wet and relatively mild winter, Dövényi 2010). During the study period the mean annual temperature was 10.9 °C (winter 0.5 °C, summer 17.5 °C). The annual number of days with snow cover was 14-21, with the average snow depth of 5 cm (20 cm in February 2012) and the mean annual precipitation was 862 mm (less than 500 mm in 2011 and above 1000 mm in 2010 and 2013).

Hunting bag data (individuals/km^2, mean ± standard error SE) between the 2010/11 and 2012/13 hunting years were as follows: red deer (*Cervus elaphus*) 1.92 ± 0.25, roe deer (*Capreolus capreolus*) 0.80 ± 0.09, wild boar (*Sus scrofa*) 3.69 ± 0.33 and pheasant (*Phasianus colchicus*) 0.59 ± 0.23 (Csányi 2011, 2012, 2013, 2014). In the study area the big game management is less intensive than at some other game management units in SW Hungary (Lanszki et al. 2015).

The mean (± SE) golden jackal density of the area was 0.35 ± 0.08 group/km^2 plus 0.11 ± 0.01 individuals/km^2, calculated from records of five surveys between November 2010 and March 2013 by the stimulated calling method (Giannatos et al. 2005). The hunting bag density of the golden jackal between 2010 and 2013 was 0.28 ± 0.11 individuals/km^2, while that of the red fox was 0.24 ± 0.16 individuals/km^2. The area was also inhabited by several other predators, including the Eurasian badger (*Meles meles*), stone marten (*Martes foina*), pine marten (*Martes martes*), Eurasian otter (*Lutra lutra*) and white-tailed eagle (*Heliaeetus albicilla*). There was no grazing in the study area.

Scat collection and diet analysis

The diet composition and feeding habits of the golden jackal and the red fox were investigated by analysis of scats collected two times per season from July 2010 to May 2013. Scat samples (each corresponding to one scat and not to a pile, Macdonald 1979a) were collected on a 13.6 km long standard route within a 6.1 km^2 area, through agricultural land. Samples were frozen at –20 °C for three months prior to analysis. Jackal and fox scat samples were distinguished on the basis of odour, size and shape characteristics (Macdonald 1980). Stray dogs were very rare or not present in the area. Questionable samples (1-2 %) were not collected or excluded from the analysis.

A total of 373 golden jackal and 268 red fox scats were analyzed by means of a standard procedure (Jędrzejewska & Jędrzejewski 1998). Scats were soaked in water, then washed through a sieve (0.5 mm mesh) and finally dried. All food remains were separated, and using a microscope, all feather, bone, dentition, and hair specimens identified using keys from März (1972), Teerink (1991), Brown et al. (1993), and our own vertebrate, invertebrate and plant reference collections. Diet composition of the predators was expressed in two ways (Tables 1 and 3): relative frequency of occurrence (%O, number of occurrences of a certain food type divided by the total number of food occurrences of all food types and then multiplied by 100), and percentage of biomass consumed (%B). To estimate the fresh mass of food ingested (Reynolds & Aebischer 1991), all dry food remains were weighed separately (measured at the 0.01 g accuracy) and the food remain mass was multiplied by an appropriate conversion factor (i.e. coefficient of digestibility), as summarized from literature data by Jędrzejewska & Jędrzejewski (1998) for red fox (i.e. insectivores and small rodents × 23, medium sized mammals × 50, wild boar × 118, deer × 15, birds × 35, reptiles × 18, fish × 25, insects and molluscs × 5, fruit, seed and other plant material × 14, for both mesocarnivores). For wild boar and cervids we used various coefficients of digestibility, suggested by Jędrzejewski & Jędrzejewska (1992) and applied in other studies (e.g. Lanszki et al. 2006, 2010). Non-food (generally indigestible) substances ingested were not included in the calculation.

Recorded animal food types were classified according to body mass and behavioural or ecological variables (Gittleman 1985, Clevenger 1993, Lanszki et al. 2006, 2007, 2010). Firstly, prey species were classified on the basis of their mass (< 15 g, 15-50 g, 51-100 g, 101-300 g, 301-1000 g, and > 1000 g). The second classification was based on the “zonations” (behavioural feature) such as: terrestrial (and mainly terrestrial but sometimes arboreal); arboreal (and mainly arboreal but sometimes terrestrial); and aquatic (or water-related). Thirdly, they were classified on the basis of their typical habitat associations (or vegetation). Classes were: open field species (e.g. common vole *Microtus arvalis*); forest species or species living in dense shrubbery (e.g. bank vole *Myodes glareolus*); and habitat generalist species which may live both in open fields and in forests (e.g. *Apodemus* mice, European brown hare *Lepus europaeus*, wild ungulates). Fourthly, animal food species were classified on the basis of their typical environmental associations, such as: human-linked, wild, and mixed (which may live both near settlements and in the wild).

The following 11 food categories were used in the calculations related to the comparative analysis of the scat composition and the trophic niche for predator species: 1 – small mammals (insectivores and rodents), 2 – European brown hare, 3 – wild carnivores, 4 – wild boar, 5 – cervids, 6 – pheasant, 7 – other birds, 8 – reptiles and amphibians, 9 – invertebrates, 10 – domestic animals and 11 – fruits, seeds and other plant matter.

Data analysis

General log-linear likelihood tests were used on frequency of occurrence data to test for interspecific (between golden jackal and red fox) and intraspecific differences of two carnivore species for four seasons and three years. The unit of analysis was jackal and fox scats and the response variable was the presence or absence of the food item considered. The model was fitted using carnivore species, season and year as independent variables. Owing to the large number of comparison (11 food categories), we adjusted the level of significance to 0.0045 with a Bonferroni correction. The consumption of 11 food categories on the basis of the estimated percentage of biomass consumed (arcsin transformed %B values) was also compared between the two predators using paired samples t-test. Multivariate analysis of variance (MANOVA, Bonferroni post-hoc test, GLM procedure) was applied to explore intraspecific differences in consumption of fresh biomass of preys (arcsin transformed %B for both canids as dependent variables, season and year as fixed factors and weighed by food types).

Trophic niche breadth was calculated in accordance with Levins (Krebs 1989): $B = 1/\Sigma p_i^2$, where p_i is the relative frequency of occurrence or the percentage biomass proportion of the *i*th food item; and standardised across food items: $B_A = (B - 1)/(n - 1)$,

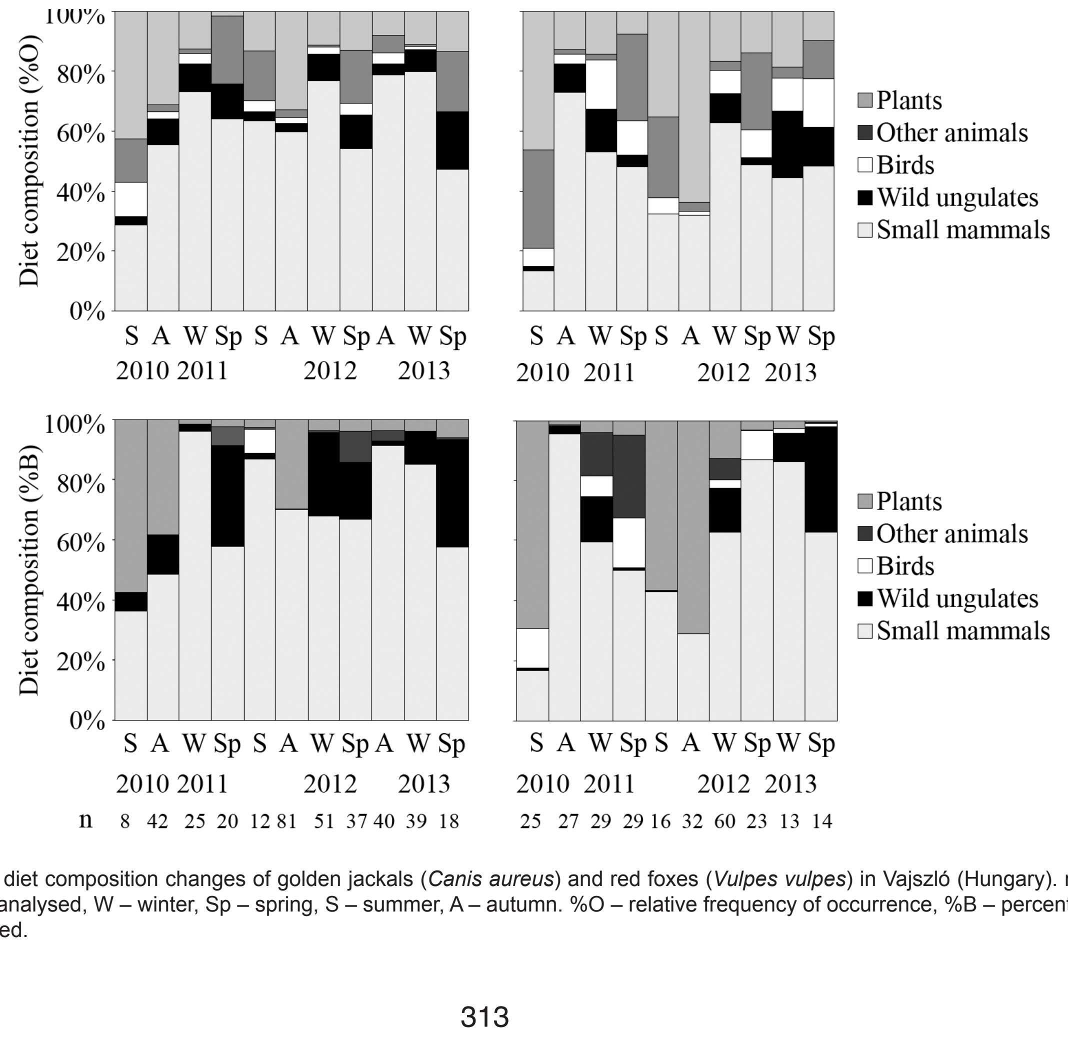

Fig. 1. Seasonal diet composition changes of golden jackals (*Canis aureus*) and red foxes (*Vulpes vulpes*) in Vajszló (Hungary). n – the number of scats analysed, W – winter, Sp – spring, S – summer, A – autumn. %O – relative frequency of occurrence, %B – percentage of biomass consumed.

Table 1. Seasonal and annual relative frequency of occurrence and biomass percentage of food items in scats of golden jackals (*Canis aureus*) in Vajszló, Hungary. Scat samples collected between July 2010 and May 2013, %O – relative frequency of occurrence, %B – percentage of consumed biomass, + – biomass under 0.05 %, B_A – standardized trophic niche breadth value.

Food items	Spring		Summer		Autumn		Winter		Annual	
	%O	%B	%O	%B	%O	%B	%O	%B	%O	%B
Microtus sp.	27.1	30.4	16.9	25.8	31.0	37.9	40.2	40.4	32.4	37.2
Bank vole (*Myodes glareolus*)	7.7	8.0	3.1	6.1	7.6	8.1	12.5	12.8	9.0	9.9
European water vole (*Arvicola amphibius*)	4.8	8.8			2.3	4.0	6.0	9.2	3.8	6.8
Apodemus sp.	10.6	9.8	15.4	21.5	17.6	16.5	15.1	13.1	15.4	14.2
Other small rodents	1.9	1.1	3.1	2.6	4.2	4.0	3.1	2.5	3.4	2.8
Shrews (Soricidae)	0.5	1.0	1.5	1.2	0.4	0.2	0.3	0.1	0.5	0.3
European mole (*Talpa europaea*)	2.4	2.7	4.6	5.8					0.7	0.7
European brown hare (*Lepus europaeus*)	1.0	1.4			0.6	1.1			0.5	0.6
European badger (*Meles meles*)	0.5	2.0					0.3	0.3	0.2	0.5
Domestic cat (*Felis catus*)	1.0	2.8							0.2	0.5
Wild boar (*Sus scrofa*)	4.8	19.3			3.0	3.1	2.6	11.0	3.0	8.9
Wild boar (*Sus scrofa*) juv.	2.9	5.2	3.1	4.2			0.6	3.3	0.9	2.4
Red deer (*Cervus elaphus*)	1.4	0.4			1.3	0.1	1.7	1.2	1.4	0.6
Roe deer (*Capreolus capreolus*)	3.4	1.4			0.2	+	2.6	1.8	1.6	1.0
Cervidae, indet.	1.0	0.8			0.4	+	1.1	0.5	0.7	0.3
Small birds (Passeriformes spp.)			3.1	+	1.3	0.1	0.9	+	1.0	0.1
Pheasant (*Phasianus colchicus*)			1.5	4.3	0.4	+			0.3	0.2
Other birds	1.4	+	3.1	+	0.4	+	0.9	+	0.9	+
Bird egg	0.5	0.1			0.2	+			0.2	+
Reptiles and amphibians	2.9	0.2	1.5	0.1	0.8	+			1.0	+
Invertebrates	14.0	0.2	13.8	0.1	1.9	+	0.6	+	4.5	+
Plum (*Prunus domestica*)			9.2	11.0	1.1	1.2	0.3	0.2	1.1	1.0
Blackthorn (*Prunus spinosa*)	1.9	1.4			9.3	16.4	0.6	0.1	4.6	6.6
Other fruits	0.5	0.1	4.6	8.3	4.9	3.1	0.6	0.2	2.7	1.6
Maize (*Zea mays*)	0.5	0.6	4.6	8.6	1.3	1.0	1.1	1.3	1.3	1.3
Other plants	7.2	2.3	10.8	0.4	9.6	3.0	9.1	1.8	9.0	2.3
Number of scats analysed	75		20		163		115		373	
Number of items	207		65		471		351		1094	
B_A	0.19	0.12	0.18	0.07	0.11	0.08	0.07	0.05	0.13	0.09

rating from 0 to 1. The trophic niche overlap was calculated by the Renkonen index (Krebs 1989): $P_{jk} = [\Sigma n(\text{minimum } p_{ij}, p_{ik})]100$, where P_{jk} is the percentage overlap between species *j* and species *k*; p_{ij} and p_{ik} are the proportion of the resource *i* which is represented within the total resources used by species *j* and species *k* (the minimum means that the smaller value should be used); n is the total number of the resource taxa (of the 11 categories listed above). The standardised trophic niche breadth values were compared with paired samples t-test. The consumption of animal food according to body mass and three behavioural or ecological features (zonation, habitat and environmental association) on the basis of percentage relative frequency of occurrence (%O) and estimated biomass (%B) values were compared using G-test.

Hierarchical cluster analysis (cluster method: between-groups linkage, interval of measure: Euclidean distance ranged between 0 and 100) was applied to compare diet composition among golden jackals and red foxes from different study sites in Hungary (Lanszki & Heltai 2002, Lanszki et al. 2006, 2015), including this study. Dendrogram was performed on the basis of arcsin transformed percentage relative frequency (%O) and consumed biomass (%B) data of 10 main food types (same food types as listed above, except

Table 2. Results of log-linear models for the frequencies of occurrence of food types in the scats of golden jackals (*Canis aureus*) and red foxes (*Vulpes vulpes*) during four seasons and three years (2010-2013) in Vajszló, Hungary, for the effect of years, seasons, and their interaction. *P* values (with Bonferroni corrections) in boldfaced type are significant. In case of pheasant (fox) was not enough data to perform the calculation.

Item	Effect	df	Golden jackal		Red fox	
			χ^2	*P*	χ^2	*P*
Small mammals	Year	2	3.04	0.2190	1.77	0.4131
	Season	3	2.67	0.4454	24.90	**< 0.0001**
	Interaction	6	29.67	**< 0.0001**	56.53	**< 0.0001**
Brown hare	Year	2	0.24	0.8878	3.92	0.1411
	Season	3	2.32	0.5081	0.43	0.9334
	Interaction	6	29.33	**< 0.0001**	60.66	**< 0.0001**
Carnivores	Year	2	0.01	0.9998	0.60	0.7414
	Season	3	6.10	0.1068	0.45	0.9307
	Interaction	6	29.11	**< 0.0001**	61.86	**< 0.0001**
Wild boar	Year	2	4.09	0.1294	18.61	**< 0.0001**
	Season	3	10.68	0.0136	8.02	0.0456
	Interaction	6	30.20	**< 0.0001**	57.74	**< 0.0001**
Cervids	Year	2	0.71	0.7017	0.85	0.6552
	Season	3	12.48	0.0059	1.00	0.8021
	Interaction	6	29.53	**< 0.0001**	62.22	**< 0.0001**
Pheasant	Year	2	0.36	0.8357		
	Season	3	4.62	0.2016		
	Interaction	6	28.95	**< 0.0001**		
Other birds	Year	2	3.91	0.1412	5.80	0.0549
	Season	3	6.81	0.0782	5.69	0.1278
	Interaction	6	28.48	**< 0.0001**	63.47	**< 0.0001**
Reptiles,	Year	2	1.29	0.5249	0.88	0.6438
amphibians	Season	3	11.77	0.0082	6.04	0.1098
and fish	Interaction	6	29.80	**< 0.0001**	61.93	**< 0.0001**
Invertebrates	Year	2	2.03	0.3622	1.88	0.3911
	Season	3	43.97	**< 0.0001**	63.42	**< 0.0001**
	Interaction	6	29.41	**< 0.0001**	58.27	**< 0.0001**
Plants	Year	2	5.83	0.0541	0.74	0.6908
	Season	3	24.85	**< 0.0001**	93.18	**< 0.0001**
	Interaction	6	24.50	**0.0004**	45.96	**< 0.0001**

pheasant and other birds were merged). The SPSS 10.0 for Windows (1999) and R (v. 3.2.3., R Development Core Team, Vienna, Austria) statistical package were used for data processing.

Results

Golden jackal diet

Small mammals were dominant in the diet of the golden jackal (annual mean, %O: 65.1 %, %B: 72.0 %, Table 1). Proportion of small mammal consumption ranged between 28.6 and 79.7 % (%O) or 36.1 and 95.8 % (%B) among seasons and years (Fig. 1) in the scat samples. The main prey was the common vole. Besides the common vole, important prey species were also field mice (*Apodemus* sp.), bank vole and European water vole (*Arvicola amphibius*). Carnivores (Eurasian badger, domestic cat) occurred rarely in the diet; European brown hares were eaten

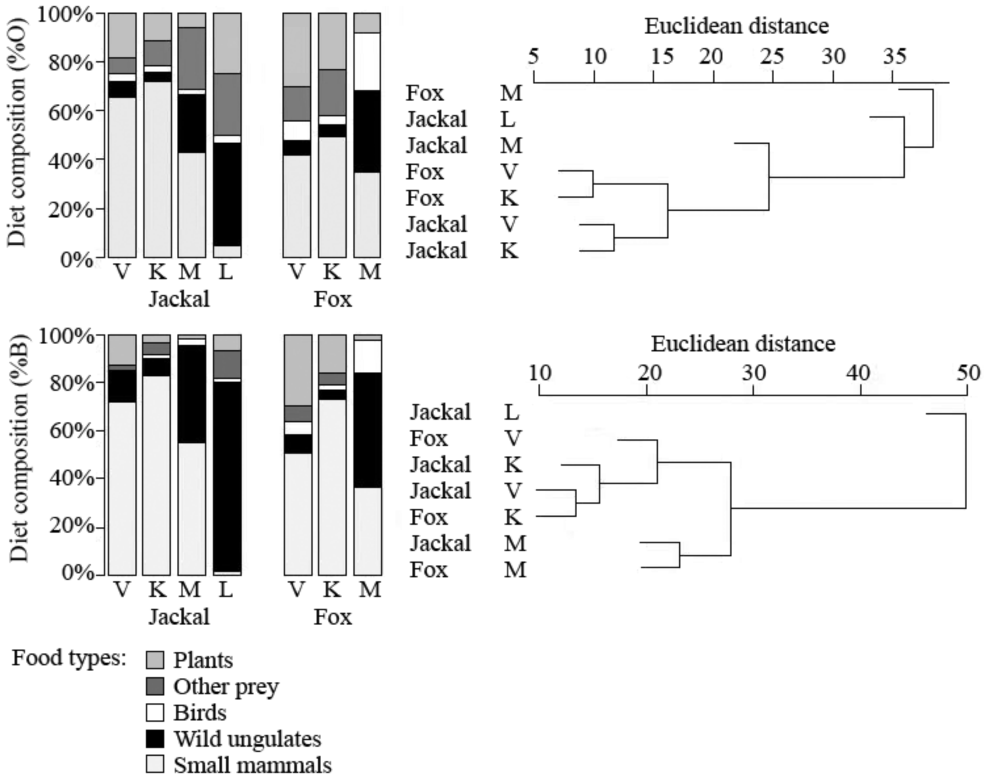

Fig. 2. Distribution of food types in the diets and similarity dendrogram of the Euclidean distances among general diet compositions of golden jackals and red foxes from different areas of Hungary. Sources: V – Vajszló (present study), K – Kétujfalu (Lanszki et al. 2006), M – Mike-Csököly (Lanszki & Heltai 2002), L – Lábod (Lanszki et al. 2015). For details see methods.

in small amounts. Wild ungulates were the second most important (%B) or third food type (%O, Table 1). The most important ungulate species was the wild boar (piglets in the spring and summer), consumption of which greatly fluctuated among seasons and years (Fig. 1). The presence of cervids in the samples was low (Table 1). Other vertebrates, such as birds, lizards, snakes, frogs, and invertebrates (mainly beetles) were consumed in low quantitative proportions. Depending on season jackals supplemented their diet mainly with wild fruits and corn (Table 1). In the analyzed samples inorganic materials (i.e. plastic, rag, gravel and paper) occurred very rarely (in 1-1 case).

Food item occurrence in the diet of golden jackal based on scat analysis showed only occasional significant differences (i.e. invertebrates, plants) among seasons (log-linear analysis, Table 2), while season × year interactions were significant in all food types. No significant differences were found in consumption ratios (%B) depending on season (MANOVA, $F_3 = 0.30$, $P = 0.825$), year ($F_2 = 0.20$, $P = 0.817$) or their interactions ($F_5 = 0.32$, $P = 0.901$). In the jackal diet, the role of small mammals was significant in all seasons, their consumption increasing from spring (%O: 55.1 %, %B: 61.9 %) or summer (%O: 44.6 %, %B: 63.0 %) to winter (%O: 77.2 %, %B: 78.2 %). The ungulates and the plants switched places with each other in the diet. The jackal consumed ungulates in spring and winter, while plants in summer and autumn in higher proportions.

Red fox diet

Small mammals were also the primary food type of the red fox (annual mean, %O: 41.9 %, %B: 50.3 %, Table 3) in the scat samples. Their consumption fluctuated between 13.4 and 73.0 % (%O) or 16.9 and 87.1 % (%B) among seasons and years (Fig. 1). Most important prey species were the *Microtus* voles (mainly common vole). In addition, important prey species were field mice and water vole. The brown hare occurred very rarely in fox scat samples but its consumption was occasionally (in spring 2011) relatively high (Fig. 1). Almost one third of the diet consisted of plants, these (especially the wild fruits) were a secondary important food item in the fox diet (Table 3). The consumption of plants showed great inter-year differences and varied over a wide range (Fig. 1). Third most important items of the fox were ungulates; the most important species was the wild boar (mainly piglets). The wild boar consumption

Table 3. Seasonal and annual relative frequency of occurrence and biomass percentage of food items in scats of red foxes (*Vulpes vulpes*) in Vajszló, Hungary. For abbreviations see Table 1.

Food items	Spring		Summer		Autumn		Winter		Annual	
	%O	%B	%O	%B	%O	%B	%O	%B	%O	%B
Microtus sp.	26.2	33.6	7.7	15.3	11.0	16.5	32.6	39.4	21.0	28.8
Bank vole (*Myodes glareolus*)	1.6	2.6	2.9	1.9	2.2	2.7	2.8	1.2	2.4	2.0
European water vole (*Arvicola amphibius*)	11.9	22.6	1.9	2.1	1.5	1.2	4.5	5.6	5.0	8.2
Apodemus sp.	5.6	2.5	3.8	1.6	14.7	10.3	9.0	8.1	8.6	6.1
Other small rodents	1.6	1.1			2.9	2.0	6.2	8.2	3.1	3.7
Shrews (Soricidae sp.)	0.8	0.1	1.9	1.2			1.7	2.0	1.1	1.0
European mole (*Talpa europaea*)	0.8	0.7	1.9	1.7			0.6	0.3	0.7	0.6
European brown hare (*Lepus europaeus*)	1.6	4.3					1.1	0.1	0.7	1.1
Small mustelids (Mustelidae)							1.1	8.4	0.4	3.0
Domestic dog and cat	1.6	7.1							0.4	1.7
Medium sized mammal, indet.	2.4	1.3							0.6	0.3
Wild boar (*Sus scrofa*)	2.4	0.5					6.2	5.9	2.6	2.3
Wild boar (*Sus scrofa*) juv.	1.6	9.7					2.2	7.8	1.1	5.2
Red deer (*Cervus elaphus*)	0.8	+	1.0	0.8			1.1	0.2	0.7	0.2
Roe deer (*Capreolus capreolus*)	0.8	+			2.2	+	3.4	0.4	1.8	0.2
Small birds (Passeriformes sp.)	2.4	0.5	3.8	0.4	1.5	+	5.1	1.0	3.3	0.5
Pheasant (*Phasianus colchicus*)							0.6	+	0.2	+
Anas sp.	0.8	0.9	1.0	0.1	1.5	0.4	0.6	+	0.9	0.3
Other medium sized birds	6.3	9.1	1.0	9.1	0.7	+	3.9	2.8	3.1	4.8
Bird egg	2.4	+					0.6	+	0.7	+
Reptiles	3.2	0.1	3.8	0.1					1.5	+
Invertebrates	15.1	0.2	26.9	0.1	4.4	+	0.6	+	9.9	0.1
Plum (*Prunus domestica*)			11.5	28.9	5.1	6.8			3.5	6.4
Blackthorn (*Prunus spinosa*)	2.4	1.2			23.5	36.5	10.1	7.7	9.7	11.2
Other fruits	1.6	1.5	26.0	35.6	11.0	17.9	1.1	+	8.5	10.3
Other seeds and plants	6.3	0.5	4.8	1.1	17.6	5.6	5.1	0.8	8.5	1.8
Number of scats analysed	66		41		59		102		268	
Number of items	126		104		136		178		544	
B_A	0.24	0.11	0.23	0.10	0.09	0.04	0.20	0.10	0.19	0.09

largely fluctuated during the study period (most in 3013; Fig. 1), while cervids were eaten in small amounts. The bird (mainly medium-sized species) consumption was considerable in spring and summer (Fig. 1). Other vertebrates, such as carnivores, lizards, snakes, snake eggs, and invertebrates were consumed in small amounts. The analyzed scat samples contained inorganic materials (i.e. pieces of plastic, gravel, textile and cigarette butts) very rarely (in 1-1 case).

The diet composition of the red fox showed occasional significant differences (i.e. small mammals, invertebrates, plants) among seasons (log-linear analysis, Table 2), the difference among years was significant only in case of the wild boar, season × year interactions were significant in all food types. No significant differences were found in consumption ratios (%B) depending on season (MANOVA, F_3 = 0.42, P = 0.741), year (F_2 = 0.47, P = 0.622) or these interactions (F_4 = 0.49, P = 0.740). In winter and spring the consumption of small mammals was (%O: 48.4-57.3 %, %B: 63.1-64.9 %), and it significant dropped in summer (%O: 20.2 %, %B: 23.8 %) and autumn (%B: 32.8 %, %O: 32.4 %), while consumption of plants increased (%O: 42.3-57.4 %, %B: 65.7-66.8 %).

Table 4. Distribution of animal food types in the diet of golden jackals (*Canis aureus*) and red foxes (*Vulpes vulpes*) on the basis of weight, zonation, habitat type and environment association of animal food species in Vajszló, Hungary. %O – relative frequency of occurrence, %B – percentage of consumed biomass. Significance was tested by G-test.

Prey characteristic		%O					%B				
		Jackal	Fox	G	df	*P*	Jackal	Fox	G	df	*P*
Weight (g)	< 15	10.8	19.7	2.66	1	NS	3.3	3.9	0.04	1	NS
	15-50	71.1	52.1	2.95	1	NS	70.5	53.4	2.37	1	NS
	51-100	1.1	1.8	0.18	1	NS	0.8	0.9	0.01	1	NS
	101-300	5.5	9.7	1.19	1	NS	8.2	14.7	1.87	1	NS
	301-1000	1.1	6.1	3.72	1	NS	0.2	11.8	14.46	1	< 0.001
	1000 <	10.3	10.5	0.00	1	NS	17.0	15.3	0.09	1	NS
Zonation	Terrestrial	92.6	80.5	0.84	1	NS	92.0	80.2	0.81	1	NS
	Arboreal	2.6	10.8	5.41	1	< 0.05	0.1	7.6	9.54	1	< 0.01
	Aquatic	4.8	8.7	1.11	1	NS	7.8	12.2	0.94	1	NS
Habitat type	Open	12.8	43.9	18.06	1	< 0.001	11.4	56.4	32.61	1	< 0.001
	Mixed	50.1	52.1	0.04	1	NS	54.1	40.6	1.93	1	NS
	Forest	37.1	3.9	30.89	1	< 0.001	34.5	3.0	31.24	1	< 0.001
Environment association	Wild	92.2	72.1	2.47	1	NS	98.1	85.8	0.83	1	NS
	Mixed	7.3	26.6	11.65	1	< 0.001	1.5	11.4	8.66	1	< 0.01
	House	0.4	1.3	0.44	1	NS	0.4	2.9	2.12	1	NS

Interspecific differences in dietary composition and trophic niche

Main effects of carnivore species (log-linear analysis, Bonferroni test) were significant in the consumption of "other birds" (all birds without pheasant; χ^2_1 = 9.52, P = 0.0020) or summarized data of birds (all birds, including pheasant; χ^2_1 = 8.17, P = 0.0043). Compared with jackal, the fox consumed more frequently birds. Main effects of season were significant in the consumption of small mammals (χ^2_3 = 18.28, P = 0.0004) and summarized data of reptiles and amphibians (χ^2_3 = 16.67, P = 0.0008), and main effect of year was significant only in the consumption of wild boar (χ^2_2 = 12.53, P = 0.0019), interactions were not significant. Compared with jackal, the fox consumed significantly higher proportions (%B) of "other birds" (paired samples t-test, t_9 = 3.39, P = 0.008) and invertebrates (t_9 = 2.59, P = 0.029).

Jackal and fox scat samples contained 33 and 32 different animal taxa (i.e. species or higher taxa), as well as 13-13 plant taxa, respectively. The standardized trophic niche (B_A, Table 1 and 3) of both predators was equally narrow (paired samples t-test, occurrences: t_9 = 2.01, P = 0.075, biomass data: t_9 = 2.01, P = 0.884) and the mean (± SE) trophic niche overlap value was high (biomass data: 69.8 ± 5.27 %, occurrences: 73.8 ± 2.77 %).

Small-sized, terrestrial, open field living or habitat generalist and wild living animals were the most important food for both predators (Table 4). Significant interspecific differences were found (Table 4) in consumption of 301-1000 g prey category (for %O data), in arboreal, open- and forest-living species and animals which may live both near settlements and in the wild. In general, jackal, consumed higher ratios of forest-living and lower ratios arboreal species than fox.

Area specific differences in diet compositions

On the basis of Euclidean distances (E_d) from the hierarchical cluster analysis (Fig. 2), the mean dissimilarity among overall diet compositions of jackal and fox from different studies from Hungary was 32.9 (%O data) and 41.1 (%B data). Mean E_d among all group pairs ranged between 9.9 and 58.1 (%O data) or between 13.2 and 80.5 (%B data). Independently of variable (%O or %B) jackal and fox from Vajszló and Kétújfalu, as they mainly consumed small mammals (Fig. 2), fell into one group and Lábod, where jackals consumed mainly viscera and carrion of wild ungulates, fell into another group. On Mike-Csököly area, jackals and foxes consumed wild ungulates (mainly from carrion) and small mammals as primary foods, so they fell into the third cluster for %B data, while foxes, due to frequent bird consumption fell into a separated group for %O data in the cluster analysis.

Discussion

The feeding habits of the golden jackal and the red fox in the studied agricultural area showed similarity in that their primary food was small mammals, and they consumed other food types in high proportions periodically. Therefore, the first prediction was partially supported by the differences found in dietary patterns. The diet of jackal was characterized by the dominance of small mammals in all seasons; the secondary food types were ungulates during winter and spring, and plants during summer and autumn.

The seasonal and inter-year variation of the diet composition was high in this study similarly as in the Balkans (Radović & Kovačić 2010, Markov & Lanszki 2012, Bošković et al. 2013, Penezić & Ćirović 2015), and it was higher than in a nearby (distance around 20 km) agricultural area, where abandoned fields were at a greater extent (Kétújfalu region, Lanszki et al. 2006). The fox dietary pattern showed greater differences among seasons than that of the jackal. Consumption of plants periodically exceeded (in summer and autumn) the small mammal consumption, however, other items, like ungulates (in winter and spring) and birds (in spring and summer) were considerable food sources too. The seasonal variation in fox diets was higher than in an earlier study in this region (Lanszki et al. 2006), and in research carried out in other agricultural areas (Lever 1959, Jensen & Sequeira 1978, Goszczynski 1986, Lanszki et al. 1999, Goldyn et al. 2003), seasonal and inter-year differences in fox diets were found to be just great.

Contrary to our expectations, the larger sized jackal consumed small mammals in higher proportion; despite the biologically important difference, it was supported statistically only for relative frequency (%O) calculation. Small mammal dominated diets are known mainly from agricultural areas where both the jackal (Khan & Beg 1986, Lanszki et al. 2006, Jaeger et al. 2007) and the fox occur (Englund 1965, Jensen & Sequeira 1978, Lanszki et al. 1999), however exceptions are also known (e.g. Lever 1959, Kožená 1988, Goldyn et al. 2003). The most important food was the agricultural pest, the common vole for both canids.

As we expected, interspecific difference in consumption of wild ungulates was significant. However, consumption ratio of ungulates was lower than experienced in other studies in southern areas (Demeter & Spassov 1993, Radović & Kovačić 2010, Bošković et al. 2013) and in intensively managed big game areas (Lanszki et al. 2015), or common beliefs (summary: Szabó et al. 2010). Within ungulates, for the golden jackal, the periodically important (secondary or buffer) food was the wild boar, while the cervids consumption was occasional. In studies where considerable ungulate consumption were found, golden jackals (Aiyadurai & Jhala 2006) or similar, medium-sized *Canis* species (Moehlman 1987), consumed prey remains of larger predators or eat carrion, which were usually remains left from official hunting or poaching (Lanszki & Heltai 2002, Radović & Kovačić 2010, Bošković et al. 2013, Lanszki et al. 2015, Penezić & Ćirović 2015), or the predation happened in a fenced area (Prerna et al. 2015). Although, the consumption of cattle calves (Yom-Tov et al. 1995) is known on open grass lands.

Regarding golden jackals, in addition to solitary hunting and scavenging (Macdonald 1983, Demeter & Spassov 1993), co-operative hunting probably also occurred on wild boar piglets or wounded ungulates. Due to limitations of the applied methodology (Reynolds & Aebischer 1991), it is not exactly known what proportion of wild boars or cervids were directly preyed on by predators, and what proportion was carrion. Carcasses (from natural mortality, sport hunting, road kill, poaching) and remains (e.g. viscera left by hunters) of wild ungulates are available in high quantity for predators in SW Hungary (Lanszki et al. 2015). Jackals might remove injured or dead ungulates within a night (Lanszki et al. 2006), and in these cases insect larvae in the scats cannot indicate the real scavenging activity. Because of these, in the case of the jackal, occasional occurrence of direct predation and predominance of scavenging indicates that the solitary red fox also consumed ungulates periodically in relatively high proportions, although the occurrence of direct predation could not be excluded for the foxes, either. Considerable periodical ungulate consumption (partially from scavenging) of the fox was shown in other European studies (e.g. Englund 1965, Fedriani & Traviani 2000, Baltrūnaitė 2002, Lanszki & Heltai 2002, Cagnacci et al. 2003, Lanszki et al. 2006, 2007).

Plants were the secondary (buffer) food for the golden jackals, while for the red fox they were temporarily the primary food source. In this food item, both canids consumed the seasonally ripening wild fruits (plum, blackthorn, cherry, pear) and corn. Although for the jackal, the plants consumption was periodically high in this study, in total, it was lower than that recorded in warmer climate areas (Mukherjee et al. 2004, Aiyadurai

& Jhala 2006), however, it was higher than in an earlier study in this region (Lanszki et al. 2006). Feeding temporarily based on plants, can help the omnivorous predator to survive in critical periods (Poché et al. 1987, Mukherjee et al. 2004), however also indicates competitive disadvantages, as in the case of the sympatric fox and jackal have experienced (Lanszki et al. 2006).

The bird consumption of both canids was similar to an earlier study performed in this region (Lanszki et al. 2006), and was lower than in other areas where birds are more abundant (golden jackal: Demeter & Spassov 1993, Lanszki et al. 2009, red fox: Lever 1959, Kolb & Hewson 1979, Goldyn et al. 2003, Lanszki et al. 2007). The bird consumption of the fox was substantially higher during nesting period. The differences in bird consumption found also indicate interspecific differences between the species.

Consumption of other food items was occasional. No predation on livestock, only consumptions of domestic cat and dog were detected in the golden jackal and the red fox scat samples. Studies on the feeding habits of the golden jackal across its geographical range indicate that domestic animals (poultry, ungulates, dog) are important food items especially in south-east Europe and Israel (Macdonald 1979a, Yom-Tov et al. 1995, Lanszki et al. 2009, Giannatos et al. 2010, Lanszki et al. 2010, Radović & Kovačić 2010, Bošković et al. 2013, Penezić & Ćirović 2015), but in these cases the carrion eating was dominant, as in the case of the fox in other studies (Englund 1965, Jensen & Sequeira 1978, Baltrūnaitė 2002, Cagnacci et al. 2003). In this study the detected domestic animal consumption was lower than in an earlier study in this region (Lanszki et al. 2006) which has likely arisen from lack of used nearby garbage dumps (Bino et al. 2010). The low brown hare consumption could depend mainly on the low hare density in this region (Csányi et al. 2014). Both predators consumed reptiles and amphibians rarely, arthropod frequently, but in low quantitative ratios. The second prediction was not supported because the trophic niche of both canids was similarly very narrow in this study, as in case of food specialist species (Hanski et al. 1991). However, in the case of generalist species (Kruuk 1989, Jędrzejewska & Jędrzejewski 1998), the diet of both canids was diverse, and feeding habits were flexible (Macdonald 1979a, Demeter & Spassov 1993, de Marinis & Asprea 2004), utilizing the seasonally available food resources. The third prediction was only partially supported. Due to similarities in diet compositions, the trophic niche overlap between the two predators was high. These results (diverse diet, opportunistic feeding, narrow trophic niche, high trophic niche overlap) are consistent with earlier studies carried out in Hungary (Lanszki & Heltai 2002, Lanszki et al. 2006). Despite high trophic niche overlap values, these two canids can undertake long term coexistence, which is supported by the national game management data (Szabó et al. 2009, Csányi et al. 2014). One of the most important reasons for this can be that they utilise many resource in varying degree at the same time.

According to the body mass and ecological features of consumed animals, the niche of the two canids differed, which confirmed partially our third prediction (food partitioning). However both canids consumed mainly small-sized, terrestrial, open field living and wild animals, but the jackal, compared to the fox, consumed a lower proportion of arboreal and higher proportions of forest and wild living species.

The hierarchical cluster analysis of diet composition of golden jackals and red foxes from different studies from Hungary identified three groups. Wild ungulate (carrion) consumption increased, while small mammal consumption decreased along a gradient with increasing forest coverage and intensity of big game management, i.e. from agricultural areas as Vajszló (forest coverage 29 %, present study area) and Kétújfalu (forest coverage 26 %, Lanszki et al. 2006), through Mike-Csököly (forest coverage 39 %, Lanszki & Heltai 2002) to Lábod (forest coverage 52 %, Lanszki et al. 2015) in case of both canids. Based on these studies, the diet compositions differed to a greater extent depending on the area (habitat type and/or wildlife management) rather than depending on the species (jackal or fox).

In conclusion, better knowledge of the ecological role of mesocarnivores, i.e. the spreading golden jackal and the most common wild canid, the red fox in food webs, may facilitate the choice of appropriate management approaches. Further field studies need to explore community level and area specific trophic interactions especially in human dominated habitats. The experienced temporary dietary specialization and the long-term generalization show high feeding flexibility of both canids. This is beneficial for the golden jackal to occupy new territories across Europe, and for the red fox to coexist with the jackal, as a larger-sized competitor.

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