

Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the Pannonian ecoregion (Hungary)

J. Lanszki, M. Heltai, and L. Szabó

Abstract: The feeding ecology of the golden jackal (*Canis aureus* L., 1758) and its interspecific trophic relationship with the sympatric red fox (*Vulpes vulpes* (L., 1758)) was investigated in an area of recent range expansion of the golden jackal in Hungary, central Europe. Diet composition was determined by scat analysis (over 4 years: jackal 814 scats; fox 894 scats). Compared with jackals, foxes consumed more small mammals (mean biomass consumed: jackal 77%; fox 68%) and to a lesser extent plant matter (6% and 18%, respectively). The importance of other prey, such as wild boar (*Sus scrofa* L., 1758), cervids, brown hare (*Lepus europaeus* Pallas, 1778), birds, reptiles, fish, invertebrates, and domestic animals, was minimal. Both mesocarnivores consumed primarily small animals (<50 g; 92% and 87%, respectively); this implies a typical searching and solitary hunting strategy. The trophic niche breadth of both species was very narrow and the fox proved to be more of a generalist. The food overlap index between the two canids was high (mean, 73%) and varied with the decreasing availability and consumption of small mammals. Based on prey remains found in scats, small-mammal specialization over a 2-year period and seasonal predation upon wild boar piglets (mainly by the jackal), seasonal fruit eating (mainly by the fox), and scavenging on wild or domestic ungulates (both predators) were found.

Résumé : Nous avons étudié l'écologie de l'alimentation du chacal doré (*Canis aureus* L., 1758) et sa relation trophique interspécifique avec le renard roux (*Vulpes vulpes* (L., 1758)) sympatrique dans une région récemment colonisée par le chacal doré en Hongrie, Europe centrale. Nous avons déterminé la composition du régime alimentaire par l'analyse des fèces (sur 4 années; chacal, 814 fèces; renards, 894 fèces). Par comparaison aux renards, les chacals consomment plus de petits mammifères (moyen de la biomasse consommée : 77 % chez le chacal, 68 % chez le renard) et moins de matière végétale (respectivement 6 % et 18 %). L'importance des autres proies, telles que le sanglier sauvage (*Sus scrofa* L., 1758), les cervidés, le lièvre brun (*Lepus europaeus* Pallas, 1778), les oiseaux, les reptiles, les poissons, les invertébrés et les animaux domestiques, est minimale. Les deux mésocarnivores consomment principalement des animaux de petite taille (<50 g : respectivement 92 % et 87 %), ce qui implique une recherche typique et une chasse solitaire. La largeur de la niche trophique des deux espèces est très étroite et le renard est le plus généraliste des deux. L'indice de chevauchement alimentaire entre les deux canidés est important (73 % en moyenne) et varie en fonction de la diminution de la disponibilité et de la consommation de petits mammifères. D'après les restes des proies retrouvés dans les fèces, on note une spécialisation pour la consommation de petits mammifères au cours d'une période de 2 ans avec une prédation saisonnière sur les carcasses des sangliers sauvages surtout par le chacal, une consommation saisonnière de fruits particulièrement par le renard et une utilisation des carcasses d'ongulés sauvages et domestiques par les deux prédateurs.

[Traduit par la Rédaction]

Introduction

The geographical range of the golden jackal (*Canis aureus* L., 1758) includes northern and eastern Africa, Asia Minor, the Middle East, the Caucasus, central and southern Asia, and southeastern Europe (Trense 1989; Krystufek et al. 1997; Mitchell-Jones et al. 1999). The Pannonian ecore-

gion (Hungary, central Europe) is on the northern edge of the jackal range, where the species became extinct by the beginning of the 20th century (Heltai et al. 2000; Heltai 2002). The red fox (*Vulpes vulpes* (L., 1758)) is widely distributed, being the most common mesocarnivore (i.e., medium-sized predator) in the northern hemisphere, and is an omnivore and habitat generalist that lives in all of the possible golden jackal habitats (Lloyd 1980; Macdonald 1983; Gittleman 1985, 1989).

Studies on the feeding habits of the golden jackal across its geographical range indicate that the major food items are wild ungulates, livestock, and small mammals (Van Lawick and Lawick-Goodall 1970; Kruuk 1972; Lamprecht 1978; Macdonald 1979; Poché et al. 1987; Demeter and Spassov 1993; Yom-Tov et al. 1995; Lanszki and Heltai 2002; Mukherjee et al. 2004). Besides these, the consumption of invertebrates and fruits could be seasonally important or

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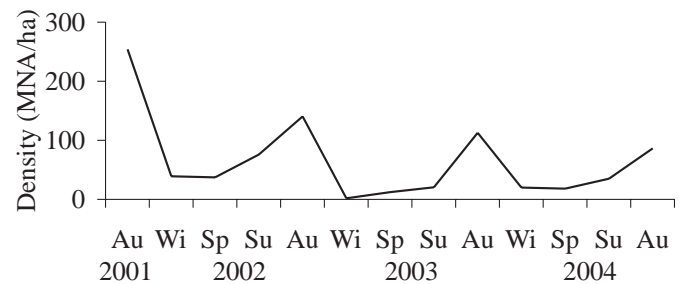
even dominant. The most important food of red foxes in European (Englund 1965; Jędrzejewska and Jędrzejewski 1998; De Marinis and Asprea 2004) and North American (Gosselink et al. 2003) agricultural areas are small and medium-sized mammals (e.g., rodents and lagomorphs), as well as periodically invertebrates, birds, carrion, and fruit. For both species, scavenging in garbage dumps and near human settlements is important. The spread of the jackal has raised numerous conservation and management questions (Giannatos 2004), while the emerging ecological role of the species in the area of recent range expansion is barely known. Trophic relationships between the golden jackal and the red fox have also received little attention (Lanszki and Heltai 2002; Scheinin et al. 2006).

The larger golden jackal (7–15 kg; Heltai et al. 2004) is able to take larger prey than the smaller red fox (4–7 kg; Corbet and Harris 1991), owing to differences in body mass, body form, activity, and hunting method (Macdonald 1979; Bekoff et al. 1984; Mills 1984; White et al. 1995). The golden jackal is a solitary hunter, just like the red fox (Lloyd 1980; Corbet and Harris 1991), but it also hunts in pairs or groups (Lamprecht 1978; Griffith 1980; Macdonald 1983; Gittleman 1989; Admasu et al. 2004), thus improving the likelihood of success when it tackles larger prey. It is also capable of preying on small animals, just like the red fox (Gittleman 1985). In this current paper we test two hypotheses. Our first hypothesis is that the interspecific differences in feeding habits would be considerable owing to the difference in body mass; the smaller red fox follows a typical hunting strategy of a searcher, while the larger golden jackal behaves like a searcher but also as a pursuer hunter. We predict that the jackal will prey more on ungulates and the fox more on rodents, and consequently, in the Pannonian ecoregion, the golden jackal will be more of a food generalist than the red fox.

Between sympatric canids in North America (Neale and Sacks 2001) or Africa (Loveridge and Macdonald 2003), high trophic niche overlaps were found; for example, between the coyote (*Canis latrans* Say, 1823) and gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)) and between the black-backed jackal (*Canis mesomelas* Schreber, 1775) and the side-striped jackal (*Canis adustus* Sundevall, 1847). Other studies (Gosselink et al. 2003; Kamler et al. 2003; Lavin et al. 2003) have also demonstrated that a new species entering a carnivore community, as in the case of the golden jackal in the present study, should affect the other species in that community. Therefore, our second hypothesis is that, as a consequence of possible interspecific competition and possible differences in feeding habits, the trophic niche overlap will decrease between coexisting mesopredators because resources will be separated and partitioned (Rosenzweig 1966). We predict that the niche of the returning and larger golden jackal will more likely overlap with that of the red fox, which had previously been the only canid in the carnivore community.

To investigate these hypotheses and to understand better the ecological role of the spontaneously repatriated golden jackal to the Pannonian region, and trophic relations between jackals and red foxes, we compared composition, trophic niche breadth, and interspecific overlap of their diets.

Fig. 1. Dynamics of the abundance of small mammals in the Pannonian ecoregion, Hungary. Small-mammal density based on minimum number alive (MNA) per hectare obtained by mark–recapture technique. Surveys were performed in winter (Wi), spring (Sp), summer (Su), and autumn (Au).



Materials and methods

Study area, food, and predator populations

The study area is located in the Pannonian ecoregion of southwestern Hungary (45°56'N, 17°41'E; 20.5 km²) and the main land use is arable agricultural cultivation. The vegetation consists of a mosaic of four principal habitat types: cultivated lands (34.5%, cereals and soybean (*Glycine soja* Sieb. & Zucc.)), abandoned fields (31.3%, species of *Eriogon* L.), oak–elm–ash (*Quercus* L. – *Ulmus* L. – *Fraxinus* L.) forests (26.5%), and shrubs (7.8%, willow (*Salix alba* L. and *Salix fragilis* L.) and blackthorn (*Prunus spinosa* L.)). The climate is continental; during the study from December 2000 to November 2004, the mean average winter temperature was between –1.9 and 2.8 °C. Duration of snow cover was between 4 and 48 days and snow depth varied between 6 and 84 mm. Temperature was between 19.4 and 22.6 °C in the summer and the mean annual precipitation was between 552 and 749 mm. During the study period, 2003 was an extreme year with an especially cold and long winter, a hot summer, and little rainfall as indicated by the recorded extreme values of precipitation. Intensive wildlife management (trophy hunting of cervids) was carried out in the study area. Hunting-bag data (individual/km², mean ± SE) between 2000 and 2004 were as follows: red deer or wapiti (*Cervus elaphus* L., 1758) 1.3 ± 0.16, fallow deer (*Dama dama* (L., 1758)) 0.1 ± 0.03, western roe deer (*Capreolus capreolus* (L., 1758)) 1.1 ± 0.21, wild boar (*Sus scrofa* L., 1758) 1.3 ± 0.19, common pheasant (*Phasianus colchicus* L., 1758) 1.5 ± 0.41, and estimated, provisionally nonhunted brown hare (*Lepus europaeus* Pallas, 1778) 0.2 ± 0.02 (Csányi 2001, 2002, 2003, 2004). Abundance of small mammals was determined from October 2001 to October 2004 seasonally, using the mark–recapture method (Krebs 1989). In each trapping period for four consecutive nights, 199–299 glass-doored wooden live traps were distributed to the four principal habitat types (cultivated land, abandoned field, forest, and shrub), with permission of the Directorship of the Danube–Drava National Park (for more detail about the method applied see Horváth and Pintér 2000; Lanszki 2005). Maximum small-mammal densities (86–254 individual/ha) were observed in autumn (October) and minimum densities (2–39 individual/ha) were observed at the end of winter (February) (Fig. 1; J. Lanszki, M. Heltai, and L. Szabó,

unpublished data). The calculated mean (\pm SE) relative abundance of jackals was 1.0 ± 0.20 collected scats/km route (method adapted from Kamler et al. 2003). A minimum of three different family groups were recorded by howling count during summer and autumn between 2000 and 2002, and by stimulated calling method (Giannatos et al. 2005) in 2003 and 2004 (J. Lanszki, M. Heltai, and L. Szabó, unpublished data). The calculated mean (\pm SE) relative abundance of red foxes was 1.1 ± 0.19 scats/km route and the minimum density was estimated at 2.4 ± 0.65 individuals/km² based on harvests, or 2.8 ± 0.36 individuals/km² based on den density (inhabited den \times 2) (J. Lanszki, M. Heltai, and L. Szabó, unpublished data). The area was also inhabited by several other carnivores, including the Eurasian badger (*Meles meles* (L., 1758)), European pine marten (*Martes martes* (L., 1758)), beech marten (*Martes foina* (Erxleben, 1777)), least weasel (*Mustela nivalis* L., 1766), European otter (*Lutra lutra* (L., 1758)), and wild cat (*Felis silvestris* Schreber, 1775). Domestic animal carcasses (cattle, pig) were deposited in dumps located 2.2 km from the study area. There was only summer grazing on stubble-fields with one flock of 100–120 domestic sheep in 2001 and 2004.

Scat collection

The diet composition of the golden jackal and red fox was studied by the analysis of scat collected monthly from December 2000 to November 2004. Scat samples were collected on a standard route (12.8 km in 2001, 21.3 km in 2002, and 22.7 km in 2003 and 2004) within a 650 ha area. Samples were frozen at -20°C for 3 months prior to analysis. Golden jackal and red fox scat samples were distinguished on the basis of odor, size, and shape characteristics (Macdonald 1980). Jackal scats were collected frequently in piles, within a circle of 1–1.5 m diameter (Macdonald 1979). Within the piles, individual jackal scats were separated in all cases based on actual age (if known), visible content, and (or) color of samples. Additionally, predator hairs collected from scats were morphologically identified (Debrot et al. 1982; Teerink 1991; our own reference collection). Stray dogs, which might cause error in the identification, were very rare or not present in the area. According to the Hungarian Game Management Act, gamekeepers may shoot any stray dog on sight within hunting areas. Collection of jackal and fox scats on transects were taken far from the surrounding settlements (1.6 ± 0.14 km) to avoid collecting dog scats by mistake. Finally, questionable samples (1%–2%) were not collected or excluded from the analysis.

Diet analysis

A total of 814 jackal (seasonal mean \pm SE, 51 ± 7.0) and 894 fox (seasonal mean 56 ± 7.1) scats were analyzed using a standard procedure (Jędrzejewska and Jędrzejewski 1998). Scats were soaked in water, then washed through a sieve (0.5 mm mesh) and dried. All food remains were separated and identified under the microscope with the aid of keys from Teerink (1991), März (1972), Brown et al. (1993), and

our own vertebrate, invertebrate, and plant reference collections. Diet composition of the predators was expressed in two ways (Table S1):² relative frequency of occurrence (%O) and percentage of biomass consumed (%B). Frequency of occurrence generally emphasizes the importance of small prey in the diets of predators (e.g., foxes frequently ate invertebrates, although only in small quantities; Lanszki 2005), and the estimation of actual biomass consumed provides a more realistic measurement of the nutritive value of a prey, emphasizing the importance of large prey. To calculate the relative frequency of occurrence, the number of occurrences recorded for the given food type was divided by the total number of food occurrences and then multiplied by 100. To estimate the fresh mass of food ingested (Reynolds and Aebischer 1991), all dry food remains were weighed and the mass data were multiplied by an appropriate conversion factor (i.e., insectivores and small rodents by 23; medium-sized mammals by 50; wild boar by 118; deer by 15; birds by 35; reptiles by 18; fish by 25; insects and molluscs by 5; and fruit, seed, and other plant material by 14 for both mesocarnivores; factors summarized by Jędrzejewska and Jędrzejewski 1998). For wild boar and cervids, we used various coefficients of digestibility as suggested by Jędrzejewski and Jędrzejewska (1992). Wild boars eaten by jackals and foxes were taken from whole carcasses (wounded adults, piglets from predation and (or) mortality), and medium-sized predators consumed mostly meat and less frequently bones or skin with hairs. By contrast, remains of cervids in scats were mainly from the remains (limbs and internal organs) left by hunters, and their availability was similar to wolf kills, where ungulates were used almost completely except for limbs and skin. Therefore, scavengers often ate bones and skin of which the coefficients of digestibility should be lower (Jędrzejewski and Jędrzejewska 1992). The prey species were classified according to mass (Clevenger 1993; for details see Table S2²).

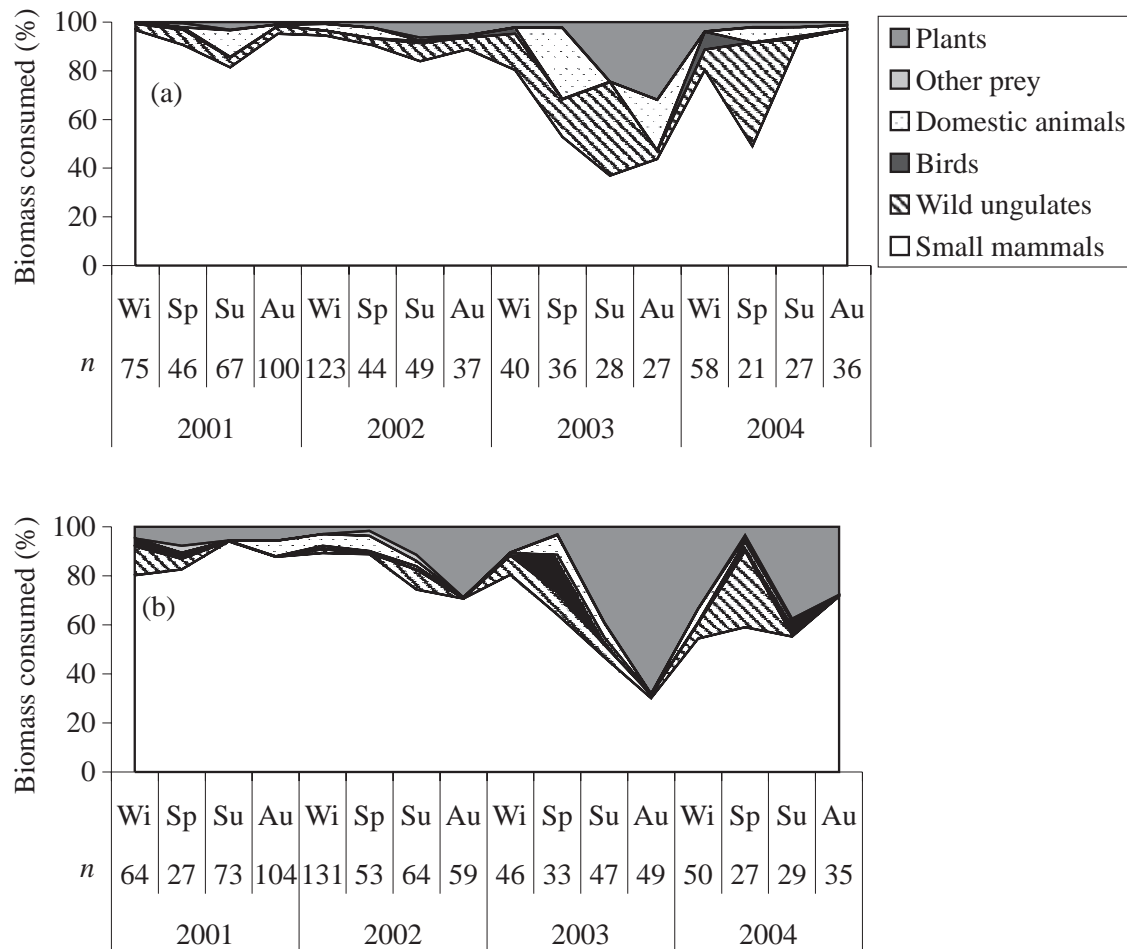
Statistical analysis

General log-linear likelihood tests were used on frequency of occurrence data to test for dietary differences between carnivore species (jackal and fox), seasons (winter: December–February; spring: March–May; summer: June–August; autumn: September–November), and years. The unit of analysis was jackal and fox scats and the response variable was the presence or absence of the food item considered. We fitted the complete models using carnivore species, season, and year as independent variables. Owing to the large number of comparisons (10 dietary categories), we adjusted the level of significance to 0.0064 with a Bonferroni correction (Revilla and Palomares 2002). The consumption of 10 food taxa on the basis of the estimated percent biomass values was also compared between the two predators using paired samples *t* test.

Multivariate analysis of variance (MANOVA, GLM procedure in SPSS[®] version 10.0; SPSS Inc. 1999 with type III sum of squares) was applied to compare canids in consumption of fresh biomass of preys (logarithmic %B data)

² Available on the journal Web site (<http://cjz.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5098. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 2. Seasonal diet composition changes of (a) golden jackals (*Canis aureus*) and (b) red foxes (*Vulpes vulpes*) in the Pannonian ecoregion, Hungary. *n*, the number of scats analyzed; Wi, winter; Sp, spring; Su, summer; Au, autumn.



based on the prey mass as the dependent variable, carnivore species as the fixed factor, and seasons and mass categories as covariates. To test for interspecific difference, the χ^2 test was applied for distribution analysis of the prey consumption (occurrences) based on the prey mass of the predators.

Trophic niche breadth was calculated in accordance with Levins (Krebs 1989): $B = 1/\sum p_i^2$, where p_i is the relative frequency of occurrence of the i th taxon and standardized across food taxa: $B_A = (B - 1)/(n - 1)$, rating from 0 to 1. The following 10 food taxa were used in the calculations related to trophic niche and the comparative analysis of scat composition for predator species: 1, small and medium-sized mammals (insectivores and rodents); 2, brown hare; 3, cervids; 4, wild boar; 5, pheasant; 6, other birds; 7, reptiles and fish; 8, invertebrates; 9, domestic animal carcasses; and 10, fruits, seeds, and other plant matter. Trophic niche overlap was calculated by means of the Renkonen index: $P_{jk} = \sum^n (\text{minimum } p_{ij}, p_{ik}) \times 100$, where P_{jk} is the percent overlap between species j and species k , p_{ij} and p_{ik} are the proportions 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). The food niche breadths and overlap were compared with multivariate analysis of variance (MANOVA, GLM procedure in SPSS®), using standardized trophic niche and trophic overlap values as de-

pendent variables, and season, year, and predator species (only for niche breadth) as fixed factors.

The statistical relationship between percent biomass of small mammals in the scat samples of predators and trophic niche overlap data was estimated by a linear regression model.

Results

Predator diets

Small mammals were generally the most important food of the golden jackal (seasonal mean 70%–90% of consumed biomass; Table S1²), ranging between 37% and 97% in the scat samples (Fig. 2a). The main prey was the common vole (*Microtus arvalis* (Pallas, 1778)), which comprised more than 90% of the taxon *Microtus* (Tables S1, S2).² Important foods were also field mice (species of *Apodemus* Kaup, 1829) and bank voles (*Clethrionomys glareolus* (Schreber, 1780)). European water voles (*Arvicola terrestris* (L., 1758)), muskrats (*Ondatra zibethicus* (L., 1766)), hazel dormice (*Muscardinus avellanarius* (L., 1758)), harvest mice (*Micromys minutus* (Pallas, 1771)), and gleaner mice (*Mus spicilegus* Petenyi, 1882) occurred rarely in the scats of the jackal. Only a small number of shrews (species of *Sorex* L., 1758 and *Crocidura* Wagler, 1832) were found in the sam-

ples. Consumption of smaller carnivores, such as the least weasel and red fox, were very rare. Brown hare was present generally in small amounts (0%–10%) in the scats of jackals. Wild ungulates (0%–43%; Fig. 2a), especially wild boar (mainly piglets in the spring), was the second most important food, whereas there was a low presence of cervids in the scat samples of the jackal (Table S1).² Domestic animals (mainly cattle and pig carcasses, rarely domestic cats) were eaten occasionally and generally in small amounts (0%–29%; Fig. 2a). Other vertebrates, such as birds, snakes, lizards, fish, and invertebrates occurred rarely in the scats. Jackals supplemented their diet with plant material (0.2%–32%; Fig. 2a).

Small mammals were also dominant in the diet of the red fox (seasonal mean 69%–77% of ingested biomass; Table S1²), ranging between 30% and 94% in the scat samples (Fig. 2b). The common vole was the most important prey item (Table S1).² Besides the common vole, field mouse species were also important prey, whereas other small and medium-sized mammals, such as the brown hare (0%–12%), weasel, and marten (*Martes* spp.), occurred rarely in the fox scat samples just like in the jackal scat samples. Scavenging (especially from wild boar carcasses) occurred in all seasons, varying from 0.1% to 31% (Fig. 2b). Domestic animals (mainly cattle and pig carcasses, rarely domestic cats and dogs) were eaten in small amounts (0%–8%; Fig. 2b). Other prey items were generally found in low proportions in the scats. Plants were a secondary important food item in the diet of foxes (2%–68%; Fig. 2b, Table S1²).

Interspecific differences in diets

Main effects of carnivore species (log-linear analysis, Bonferroni test; $\chi^2_{[1]} = 9.86$, $P = 0.0017$), year ($\chi^2_{[3]} = 36.06$, $P < 0.0001$), season ($\chi^2_{[3]} = 26.58$, $P < 0.0001$), and year \times season interaction ($\chi^2_{[9]} = 34.57$, $P < 0.0001$) were significant in consumption of small mammals, but not the species \times year and species \times season interactions. Similarly, main effects of carnivore species ($\chi^2_{[1]} = 13.01$, $P = 0.0003$), year ($\chi^2_{[3]} = 45.72$, $P < 0.0001$), season ($\chi^2_{[3]} = 83.81$, $P < 0.0001$), and interactions were significant ($P < 0.002$, in all cases) in consumption of plants. In the other eight food taxa, main effects of carnivore species were not significant. There were defined differences between the two canids in the consumption rates of the two most important food taxa. Compared with foxes, jackals consumed significantly more small mammals (paired samples t test, jackal 77.2%, fox 68.1%, $P < 0.05$) and less plant matter (jackal 5.6% and fox 18.2%, $P < 0.002$). No statistically or biologically significant differences were found between the canids in terms of consumption of brown hare (1.4% and 2.7%, respectively), wild boar (9.0% and 4.9%, respectively), cervids (2.0% and 1.3%, respectively), pheasant (0.5% and 1.8%, respectively), other birds (0.5% and 0.9%, respectively), reptiles and fish (0.1% and 0.2%, respectively), invertebrates (0.1% and 0.5%, respectively), and domestic animal carcasses (5.1% and 2.7%, respectively).

Seasonal and interyear variation in the predator diets

The diet composition of the golden jackal and the red fox showed occasional significant differences between years and

seasons based on scat analysis (Tables 1, S1²). The occurrence of small mammals (rodents, shrews) in the scats of both predators was higher in winter and autumn and lower in spring and summer. Wild boar was found in higher proportions in jackal scats in spring and in fox scats in winter, and cervids in fox scats in spring. The fox ate more frequently “other” birds (non-pheasant) in spring and summer, whereas plant material was eaten in summer and autumn. Under other food taxa, no considerable season-associated differences were found.

However, the importance of small mammals to both canids decreased during the severe winter of 2003, which was followed by a dry summer (Figs. 1, 2). The difference in small-mammal occurrences in scats between years was only significant in the fox (Table 1). In 2003 and 2004, the jackal complimented its diet primarily with wild boar (piglet and carcass), and in 2003 with domestic animal carcasses and plants, whereas the fox complimented its diet with other birds (non-pheasant) and plants in 2003 more frequently than in other years. Under other food taxa, no significant difference was found in various years (Table 1). Significant interyear and seasonal interactions were only found for foxes, consuming small mammals in low proportions, and for both predators, plants in high proportions in the autumn samples of 2003.

Mass distribution of consumed prey species

Small prey items were the most important food for both canids (between 15 and 50 g; jackal $81.8\% \pm 4.99\%$ (mean \pm SE); fox $83.6\% \pm 4.02\%$) and relatively high presence of prey items larger than 300 g were also found in scat samples ($16.1\% \pm 4.76\%$ and $13.1\% \pm 3.53\%$, respectively). Main effect of carnivore species was not significant in calculating the percentage of consumed biomass data (MANOVA, LSD post hoc test, $P = 0.629$).

Relying on the mass of prey (Table S2),² the distribution of food items in the scat samples was significantly different between the golden jackal and the red fox ($\chi^2_{[4]} = 122.10$, $P < 0.0001$). The most important prey item, between 15 and 50 g, was more frequently eaten by the jackal than by the fox (76.0% and 64.3%, respectively; Fig. 3). Smaller prey (<15 g: 15.9% and 22.9%, respectively) or larger prey (>50 g) occurred more frequently in the scat samples of the red fox (summarized 8.2% and 12.8%, respectively). Generally, both canids characteristically consumed small animals (<300 g).

Trophic niche breadth and trophic niche overlap

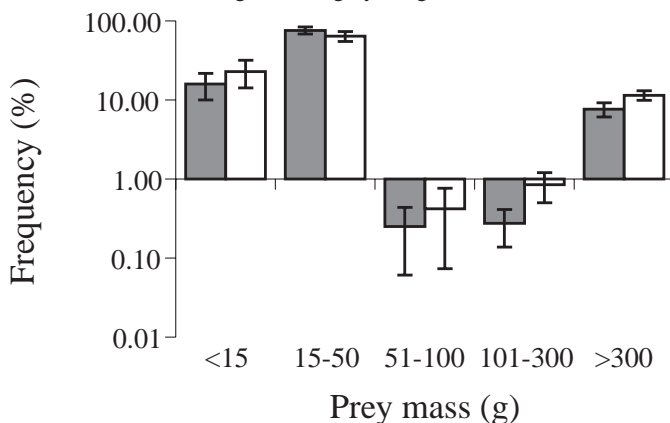
Based on the calculation from the 10 main food categories, the trophic niche breadth of both predators was very narrow, but the golden jackal had a narrower mean value than the red fox (MANOVA, LSD post hoc test $B_A = 0.06 \pm 0.01$ (mean \pm SE) and 0.09 ± 0.01 , respectively, $P < 0.003$). Jackal and fox diets contained 56 and 57 different prey taxa (i.e., taxonomic species or higher classification as in Table S2²), as well as 11 and 16 plant taxa, respectively. The mean trophic niche overlap between jackal and fox was high ($73.2\% \pm 2.71\%$). The trophic niche breadth and overlap values did not vary significantly between seasons ($P > 0.05$ in both cases). Trophic niche breadth values for jackals and foxes significantly increased in 2003,

Table 1. 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 four years (2001–2004) in the Pannonian ecoregion, Hungary, for the effect of years, seasons, and their interaction.

Item	Effect		Golden jackal		Red fox	
		df	χ^2	<i>P</i>	χ^2	<i>P</i>
Small mammals	Year	3	5.1	0.1635	34.1	<0.0001
	Season	3	14.6	0.0021	13.3	0.0040
	Interaction	9	22.2	0.0083	32.4	0.0001
Brown hare	Year	3	9.8	0.0205	13.1	0.0044
	Season	3	0.2	0.9714	4.9	0.1810
	Interaction	9	5.9	0.7494	8.4	0.4972
Cervids	Year	3	4.0	0.2617	6.8	0.0787
	Season	3	6.8	0.0789	17.8	0.0004
	Interaction	9	20.6	0.0147	13.3	0.1483
Wild boar	Year	3	13.7	0.0033	5.0	0.1708
	Season	3	15.5	0.0014	19.2	0.0002
	Interaction	9	14.4	0.1103	13.5	0.1396
Pheasant	Year	3	1.7	0.6274	5.0	0.1687
	Season	3	0.8	0.8385	1.1	0.7873
	Interaction	9	13.7	0.1345	10.9	0.2809
Other birds	Year	3	8.2	0.0429	18.5	0.0003
	Season	3	11.0	0.0118	19.8	<0.0001
	Interaction	9	7.6	0.5707	16.8	0.0519
Reptiles and fish	Year	3	0.2	0.9782	1.0	0.8015
	Season	3	16.0	0.0011	24.7	<0.0001
	Interaction	9	3.4	0.9444	13.5	0.1394
Invertebrates	Year	3	16.2	0.0010	2.8	0.4256
	Season	3	188.1	<0.0001	234.2	<0.0001
	Interaction	9	8.8	0.4542	19.6	0.0207
Domestic animals	Year	3	4.9	0.1816	5.2	0.1546
	Season	3	6.2	0.1022	1.4	0.7037
	Interaction	9	10.0	0.3484	6.2	0.7189
Plants	Year	3	21.9	<0.0001	45.9	<0.0001
	Season	3	48.3	<0.0001	63.5	<0.0001
	Interaction	9	41.3	<0.0001	59.8	<0.0001

Note: *P* values (with Bonferroni corrections) in boldfaced type are significant.

Fig. 3. Distribution frequency of prey in the diet of golden jackals (shaded bars) and red foxes (open bars) on the basis of prey mass, in the Pannonian ecoregion, Hungary. Log scale, mean \pm SE.



and then decreased to the earlier level for jackals and remained at higher values for foxes in 2004 (Table 2). The mean trophic niche overlap values (Table 2) were higher

in the first 2 years (2001–2002) and were significantly lower in the last 2 years (2003–2004) of the study.

No coherent relationship was found between small-mammal consumption by the jackal and food niche overlap values between canids ($r = 0.37$, $P = 0.157$; Fig. 4), whereas the trophic niche overlap increased between the two predators with increasing small-mammal consumption by the fox ($r = 0.83$, $P < 0.0001$; Fig. 4).

Discussion

Interspecific differences

The diet composition of the golden jackal and the red fox showed interspecific differences and marked seasonal and (or) interyear differences as well. The dominant food was small mammals, consumed more by jackals, which was contrary to our expectations (first hypothesis) based on the body masses and social system of the predators. Consumption of ungulates was only occasional, lower than expected from studies in southern areas (Demeter and Spassov 1993). A marked interspecific difference was found in plant-matter consumption; plants did not play an important role in the

Table 2. Standardized trophic niche breadth (B_A) and trophic niche overlap of golden jackals and red foxes in the Pannonian ecoregion, Hungary.

	P											
	Year*	2001	2002	2003	2004	Year	Season	Predator species	Species × year	Species × season	Year × season	Species × year × season
Niche breadth (B_A)												
Golden jackal	0.04±0.014b	0.03±0.006b	0.14±0.018a	0.04±0.013b	0.0001	0.077	0.003	0.004	0.427	0.075	0.044	
Red fox	0.03±0.006b	0.08±0.018b	0.15±0.026a	0.12±0.016a								
Niche overlap												
Golden jackal – red fox	84.4±3.56a	81.2±3.07a	59.8±5.95b	66.4±5.53b	0.003	0.497				0.138		

*Values are given as the mean ± SE. Differences between years marked with different letters are significant (MANOVA, LSD test).

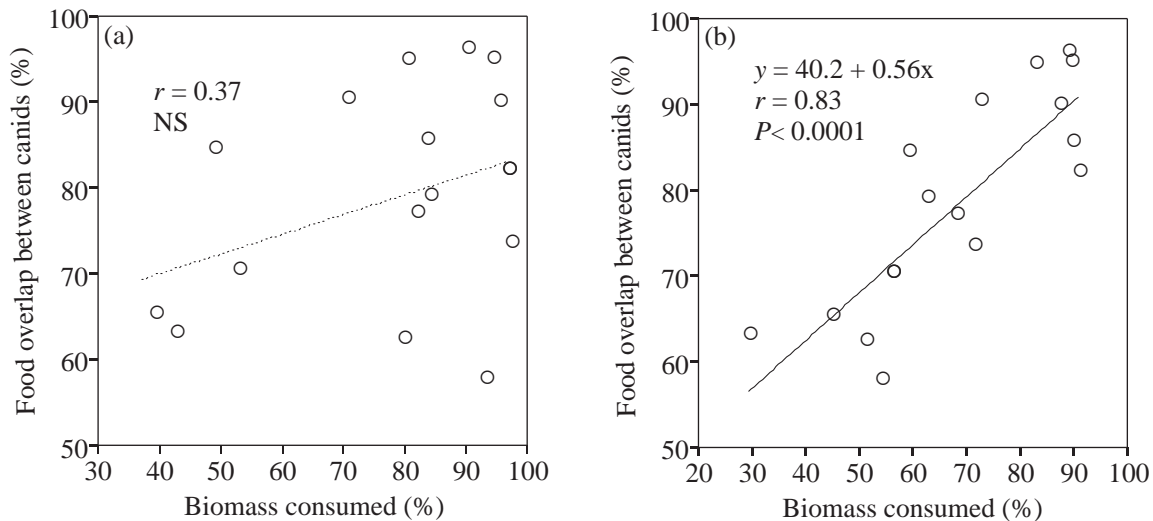
feeding of jackals in our study area compared with the feeding of jackals in southern areas (Balasubramanian and Bole 1993).

Seasonal dominance of small mammals is known in jackal (Taryannikov 1974; Ishunin 1980; Mukherjee et al. 2004) and fox (Hewson 1983; Leckie et al. 1998) diets, which is similar to our findings for the golden jackal in this study and may be common mainly in small mustelids (e.g., McDonald 2002). Because of a lack of small mammals and (or) a long winter, fawns may become prey (Lamprecht 1978) and seasonal scavenging on carcasses of wild and domestic ungulates occurred (Atánassov 1953; Van Lawick and Lawick-Goodall 1970; Macdonald 1979; Poché et al. 1987; Lanszki and Heltai 2002). In contrast to experiences in the Balkans and the Middle East (Demeter and Spassov 1993; Yom-Tov et al. 1995), with the exception of occasional sheep grazing, no depredation on livestock was recorded in this study; because sheep were housed at night in a nearby village and animal husbandry was not extensive, only the scavenging from a dump was confirmed. No garbage consumption was found (Macdonald 1979), as the study area was relatively far from settlements, and there was an abundance of other food items. During rearing and learning of hunting techniques, a large variety (but low quantity) of invertebrates and small passerines, snakes, lizards, and fish occurred in the diets of both canids (Demeter and Spassov 1993; Mukherjee et al. 2004; Lanszki 2005). The low importance of small game (potentially brown hare and pheasant) found in the scat samples may be the result of the inaccessibility of these animals owing to their low densities and fast movements. Jackals living in lower latitudes consumed more fruit than in this study, most likely because of the lower availability of small vertebrates in Asian habitats (Poché et al. 1987; Balasubramanian and Bole 1993; Mukherjee et al. 2004).

Intraspecific differences

The results showed more marked intraspecific (seasonal or interyear) differences for foxes than for jackals. This does not support our first prediction, as the golden jackal does not appear to be more of a food generalist than the red fox. Although both mesopredators showed opportunistic feeding habits, jackals specialized on small mammals more markedly than foxes in the first 2 years of the study. The high presence (both occurrence and consumed biomass) of small rodents in the jackal scat samples, besides the limits of a scat analysis method, indicated a typical searching and hunting strategy. After the severe winter of 2003, small-mammal resources (Fig. 1) may have become a limiting factor (Angelstam et al. 1984). This change necessitated a food-selection shift, which was more intense for the jackal than for the fox (Fig. 2). However, based on changes in food remains in scat samples, the jackal may have used the pursuer hunting strategy more frequently on wild ungulates and scavenging for larger animals than the fox, as seen in Africa (Lamprecht 1978; Demeter and Spassov 1993), whereas the fox might have used the searching strategy more frequently to hunt other small prey (e.g., birds) and ate fruit from bushes or on the ground. Functional response of the jackal to a limited but favoured food item was more rapid than that of the fox. The jackal shifted from small prey to other

Fig. 4. Relationship between the consumption of small mammals by (a) golden jackals or (b) red foxes and trophic niche overlap values in the Pannonian ecoregion, Hungary. Linear regression model.



food items earlier when the availability of small mammals declined, and also returned to rodent hunting earlier than did the fox.

Generally, the jackal and the fox also consumed small prey. Accordingly, both canids should be solitary and searching hunters (Lamprecht 1978; Demeter and Spassov 1993; Admasu et al. 2004). However, in addition to solitary hunting, cooperative hunting and scavenging probably occurred on wild boar piglets or wounded ungulates. What proportion of wild boar or cervids was directly preyed on or scavenged by jackals is unknown. Jackals might remove injured or dead ungulates within a night (J. Lanszki, unpublished observations), but in these cases insect larvae in the scats did not indicate the real scavenging activity. However, considerable small prey in the scat samples indicated that specific pursuer hunting was probably occasional.

Trophic niche breadths and overlap

During the period of heavy use of small-mammal food resource, together with and as a consequence of narrow food niche breadth values, the trophic niche overlap was high. After the winter of 2003, trophic niche breadth values increased and overlap between predators decreased. In 2004, when small mammals were abundant, as in 2001–2002, the jackal returned to small mammal (and seasonally wild boar) consumption (with decreasing food niche breadth), whereas the fox shifted from the favoured small mammals to other food (mainly fruits) items in higher proportion and over a longer period (2003–2004) than did the jackal. The jackal had narrower trophic niche breadth than expected from the body mass differences and appeared to be more of a specialist. The ability to share food resources may contribute to or even help the coexistence of the two canids in the Pannonian ecoregion. However, the food niche of the jackal overlapped with that of the red fox rather than the converse. The results of the regression analysis between small-mammal consumption and trophic niche overlaps suggested that the fox searched for other food items in larger proportions than did the jackal. This finding supported our second hypothesis. However, interspecific relationships between sympatric

golden jackals and red foxes are poorly understood; no evidence of interspecific competition between canids living in the Pannonian ecoregion was reported. The remains of a red fox was found in only one jackal scat, which has been rarely reported (Atánassov 1953); however, it is unknown whether the fox was killed by the jackal or eaten from carrion. Agonistic interactions might be taking place if, for example, foxes are efficient in escaping alive from jackal attacks or if jackals do kill but do not eat foxes. High overlap in food use between carnivores has frequently been associated with competition (Neale and Sacks 2001). In analogous carnivore communities in North America, the larger and more social coyote suppresses the smaller red fox and swift fox (*Vulpes velox* (Say, 1823)) (Gosselink et al. 2003; Kamler et al. 2003; Lavin et al. 2003). The golden jackal may be considered the dominant competitor of the red fox (Giannatos et al. 2005; Scheinin et al. 2006), being double in size and with a highly organized social system and similar space use. Two close relatives can coexist with high trophic niche overlap (Colwell and Futuyma 1971; Schoener 1974; Krebs 1989), as in this study, if the most important resources (e.g., food and microhabitat) are abundant.

In conclusion, the golden jackal appears to be more carnivorous and more specialized than the red fox. The interspecific differences in diets were smaller than expected and the intraspecific differences were more marked for the fox than for the jackal. From a wildlife management point of view, it may be important that our results did not confirm damage (Demeter and Spassov 1993) to ungulates or small game. During a seasonal food shift from their main food (i.e., small mammals), the two mesopredators used different available food resources, reducing the high trophic niche overlap. The results showed that the unique feeding habits of the jackal may have an important role in its recent spread into central Europe.

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