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Diet composition of the golden jackal in an area of intensive big game management

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The dynamic spread of the golden jackal (*Canis aureus*) in Hungary results in human–carnivore conflicts. We presumed that in an area of intensive big-game management the jackal's diet would contain an increased proportion of ungulates (or their viscera). We collected and analysed the stomachs of 62 jackals during a period of two years. Viscera and carrion of wild ungulates were found to be the primary food of jackals in every season (wet weight: 55%), and in addition, consumption of adult wild boar and cervids proved remarkable. A deer calf was detected in one stomach. Adult jackals added a higher proportion of big game to their primary diet, while younger animals tended to consume plants and invertebrates to supplement their diet. There was no relevant detectable difference between the sexes. Our study did not find evidence for substantial damage to big-game populations caused by jackals.

Introduction

The golden jackal (*Canis aureus*; hereafter jackal) is one of the most successful medium-sized carnivores (mesopredator) of the 21st century in Hungary and in parts of eastern Europe (Krystufek *et al*. 1997, Heltai *et al*. 2001, Szabó *et al* 2009, Arnold *et al*. 2012). It is native to three continents as its range extends from North and East Africa to southern Europe, and eastwards to Central and South Asia (Macdonald & Sillero-Zubiri 2004). Both its population and its area of occurrence show a rapid invasion-like increase in the Balkans and east-central Europe (Arnold *et al*. 2012). The spread of the jackal, its return to former ranges and its appearance in areas which it has probably never inhabited, has raised questions about the species and generated new research projects in Europe. The first results of these projects were published at the beginning of the 2000s, in Greece (Giannatos *et al*. 2005, 2010), Bulgaria (Spassov & Markov 2004), Serbia (Zachos *et al*. 2009, Ćirović *et al*. 2014), Croatia (Radović & Kovačić 2010, Bošković *et al*. 2013), Slovenia (Krofel & Potočnik 2008), Italy (Lapini *et al*. 2009), Austria (Plass 2007) and Hungary (Heltai *et al*. 2001, Lanszki & Heltai 2002, Szabó *et al*. 2009).

The fast expansion of a mesopredator carries with it a potential for reviving classic human-carnivore conflicts, especially among farmers and wildlife managers (*see* reviews by Macdonald & Sillero-Zubiri 2004, Boitani & Powell 2012). The common belief that jackals consume a substantial number of roe deer and domesticated animals is widespread throughout its distributional range in Europe (e.g. Demeter & Spassov 1993, Szabó *et al*. 2010, Mihelič & Krofel 2012, Bošković *et al*. 2013). According to studies carried out in the Balkan Peninsula, the primary food resource of the species is mostly foods of anthropogenic origin, i.e. carcasses of domestic animals and other sorts of waste (Giannatos *et al*. 2010, Lanszki *et al*. 2010, Ćirović *et al*. 2014); and viscera and carrion left behind by hunters and wildlife managers (Radović & Kovačić 2010, Bošcović *et al*. 2013, Raichev *et al*. 2013). Studies conducted in Hungary to date suggest that small mammals are the primary food resource of jackals all year round in areas of high, small-mammal density and intensive agricultural production (Lanszki *et al*. 2006). However, in areas of particularly high big-game density and intensive big-game management, the diet of jackals is still unknown. Thus, the question arises: does the abundant supply of big-game biomass result in consumption of a higher proportion of big game (i.e. scavenging and/or predation on adults or offspring)? Diet composition analyses usually do not support occasional direct field observations and beliefs of hunters and animal keepers (Szabó *et al*. 2010, Heltai *et al*. 2013) that report on substantial big-game and livestock predation. However, the possibility cannot be excluded (*see* e.g. Yom-Tov *et al*. 1995). The hunting seasons of big game species are designated according to species, sex and age-specific periods within a calendar year (Appendix 1). The patterns of hunting seasons also affect the quantitative and temporal distribution of food biomass available from big game viscera, carrion or wounded animals available for jackals. Based on the length of the Hungarian hunting seasons (Appendix 1) calculated in days, the aforementioned food resources are expected to be available during 41%–100% of the year. However, the greatest availability is between 1 September and the last day of February as this is the main hunting season for all the five big game species in Hungary, namely red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), mouflon (*Ovis aries*) and wild boar (*Sus scrofa*). Consumption identified as big game can reach a high proportion, considering that the majority of shot big game is field-dressed immediately upon harvesting. In the case of red, fallow and roe deer, the removal of the stomach, intestines and oesophagus results in a 20%–25% loss of live weight, while removal of the heart, lung and liver causes an additional loss of 7%–8% (Whitehead 1993). As for white-tailed deer (*Odocoileus virginianus*), a correction of 22% is made when calculating body weight from field-dressed weight (Jensen 2000; Severinghaus 1949 cited in Whitehead 1993). Szunyoghy (1963) added 25% to the field-dressed weight in every case when he estimated the deer's weight at the time of bagging. This means that viscera left behind can reach 25% of the weight of the harvested animals. Assuming that hunting seasons of the big game species (Appendix 1) have an influence on the quantity of available viscera, different proportions of the primary and supplementary food types of the golden jackal in every season of the year can be expected (Lanszki *et al*. 2006, Bošković *et al*. 2013).

Direct observation of the hunting methods of jackal (Kruuk 1972, Lamprecht 1978, Moehlman 1987, Khidas 1990) is especially difficult in Europe, due to their secretive lifestyle and limited visibility in dense vegetation cover. Thus, examination of the diet and feeding habits of jackals is typically carried out indirectly, based on scat- and/or stomach-content analyses. Both methods have their advantages and disadvantages (Witt 1980, Reynolds & Aebischer 1991, Cavallini & Volpi 2005). One of the advantages of stomach content analysis is that, apart from the potential of determining seasonal differences in feeding habits (Kidawa & Kowalczyk 2011, Bošković *et al*. 2013), it enables analysis of the impact of factors which have previously not been examined, such as sex and age group of the jackal.

Based on the known opportunistic feeding strategy of the jackal (Macdonald 1983, Moehlman 1987), our hypothesis was that the intensive big-game management practised in our study area (with an average hunting bag of 10 big-game indiv. km^{-2} annually between 2009 and 2013) would result in substantial consumption of big game (predominantly viscera and carrion) by jackals. The aim of our study was to analyse the season-, sex- and age-dependent diet composition of jackals in an area where the species appeared approximately two decades ago (Heltai *et al*. 2001, Lanszki & Heltai 2002), its presence is continuous since then and the hunting bag (indiv. km^{-2}) increased fourfold over the last five years (2009: 0.06, 2013: 0.24).

Material and methods

Study area

The study area is located in the Pannonian biogeographical region of southwestern Hungary (Lábod region; centre: 46°11´N, 17°30´E; 164.6 km^2). It is basically a flat, lowland area with sand dunes. Forestry, wildlife management and crop cultivation are the region's most important sources of income. The vegetation consists of forests (52.3%), one-third of which is English oak (*Quercus robur*), nearly one-third is willow (*Salix*), alder (*Alnus*) and linden (*Tilia*) species, and the rest is constituted mainly of locusts (*Robinia*). In two-thirds of the forested area, the age of the forests is under 40 years. In the arable areas, row crops and cereals (37.9%) are mainly grown, but pastures (7.5%), fishponds and reeds (1.1%), and human settlements and orchards (1.2%) can also be found. The climate is continental with some sub-Mediterranean features (e.g. moderately wet and relatively mild winter, balancing influences). The mean annual temperature is 10.3 °C; the annual number of days with snow cover is 30–34, with an average snow depth of 6–10 cm and a mean annual precipitation of 740–760 mm (Dövényi 2010). Intensive big-game management, i.e. trophy hunting of fallow deer and red deer, has been practised in the study area, but the population of wild boar is also important. There are supplemental food plots in the area, and additional feeding is also provided.

Study species

Hunting bag data (indiv. km^{-2}) in 2012 (from January to December) and 2013 (from January to November) were as follows: fallow deer 3.09 and 2.53, red deer 0.91 and 0.74, roe deer 0.06 in both years, and wild boar 2.47 and 1.97. Small game species, such as pheasant (*Phasianus colchicus*) and European brown hare (*Lepus europaeus*), were represented by an insignificant number (hunting bag density < 0.1 indiv. km^{-2}).

The data on individual body weights and hunting bag sizes for all the big game species of the area were used to determine the minimum quantity of big-game viscera (some of which is destroyed, but a substantial amount of which remains at the site of harvesting) resulting from hunting. We calculated the loss of viscera being 25% of the full body weight (Szunyoghy 1963, Whitehead 1993). Between January 2012 and December 2013, the number of harvested big game in the study area was 2030 individuals. Of these, 1943 animals were shot during hunting, 1909 heads of which (98.3%) had body weight data (Appendix 2). In addition, 87 individuals of big game were found dead (mortality resulting from wounding, and some non-hunting related mortality, e.g. road kills), and we had body weight data for 25 such animals (28.7%).

The abundance of small mammals was assessed in June 2013 using 200 glass-doored wooden live traps over a four-night period in four terrestrial habitat types (oak forest, *Robinia–Sambucus* shrubbery, cereal and pasture), and the result was 13.0 ± 4.19 indiv. per 100 trap nights. There are two sheep farms in the area. Sheep of the Homokszentgyörgy flock graze outdoors all year round, but are kept in a barn at night. The other flock (in Nagykorpád) is kept outdoors only in summer and in autumn, but as there is no barn they are in the open during the night. One shepherd and a few sheepdogs (smaller sized herding dogs) accompany each flock. The calculated jackal family group density was 0.28 group km^{-2} recorded in March and December 2013 by the stimulated calling method (Giannatos *et al*. 2005). Hunting bag density of the golden jackal in 2012 and 2013 was 0.22 and 0.24 indiv. km^{-2}, while that of the red fox was 0.13 and 0.10 indiv. km^{-2}, respectively. In Hungary for both jackal and fox unlimited hunting is allowed.

Sample analysis

We investigated the feeding habits of jackals by analysing stomach contents of hunted animals (n = 62). The jackals examined were categorised according to sex, age (1 = juvenile, collected in August–October, 2 = adult: ≥ 1 year old from dental features/teeth characters and body size) and season (1 = winter: December–February, 2 = spring and summer together: March–August, 3 = autumn: September–November). We also categorised the feeding periods of the jackals according to when they were collected (1 = dawn, 2 = daytime).

Stomachs were removed and stored at –18 °C prior to analysis. Using standard procedures, we analysed the following features of food items both macroscopically and under a microscope: hair, feather, skin, bone, dentition and chitin shell (for more details *see* Jędrzejewska & Jędrzejewski 1998, Biró *et al*. 2005). Occasionally, in cases of more advanced stages of digestion and numerous prey items, the stomach contents were washed through a 0.5 mm sieve and then all recognisable prey and food remains were separated. To calculate diet composition, we took into account the minimum number of food items which could be identified in the stomachs. We determined the percentage composition of food items in the stomach samples on the basis of both relative frequency of occurrence, O (percentage of the total number of occurrences of all items in the sample), and wet weight (measured to the nearest 0.01 g) of all individual food remains found and separated in the samples, W (proportion of a given food item wet weight in the total wet weight of food remains found in the stomachs; Kidawa & Kowalczyk 2011).

Statistical analysis

The following 13 main food types were used in the comparative analysis of diet compositions:

1. viscera and "other carrion" (waste of wild ungulates, i.e. all remains left by hunters including internal organs with the contents of the digestive organs, remains of skin, end of cervid legs and head of non-trophy females. In addition, old or fresh carcass or remains of carcass, dead before being taken by a jackal, e.g. which can appear with signs of poaching or decomposition);
2. wild boar (adult);
3. deer (red deer or fallow deer; adult);
4. juvenile deer;
5. roe deer (adult);
6. carnivores;
7. small mammals;
8. birds;
9. reptiles;
10. fish;
11. invertebrates;
12. plants (from direct consumption);
13. inorganic materials.

The occurrence of viscera and "other carrion" in stomachs indicates hunting or poaching, and these subcategories were taken together, as it is often difficult to distinguish between them. Adult wild boar and adult cervids were separated, because contrary to the first category, predation could not be excluded in these cases, although there is a low probability of this. Trophic niche breadth (B) was calculated in accordance with Levins (Krebs 1989) on the basis of the above 13 main food categories.

We assessed the effects of sex, age group, season and time of day after logarithmic transformation of the data for stomach content weight with MANCOVA (covariant: body weight; SPSS 10.0). We applied an independent-sample t-test in the adult age group category to examine body weight (after logarithmic transformation of the data) differences between the two sexes. A paired-sample t-test was used to examine stomach weight (after logarithmic data transformation) differences between wild ungulate remains and of other food types. Spearman's correlation was used to test the relationship between quantitative composition based on weight of food remains detected in the stomach (W) and the relative frequency of occurrence data based on the number of food items (O) in the 13 main food types. The statistical relationship between ungulate viscera and carrion availability (estimated biomass, kg km^{-2}) and consumed mass of ungulates (g/jackal stomach) was estimated by a linear regression model. A χ^2-test was used for distribution analysis of the diet composition (13 main food taxa) according to season, sex, age group and times of day.

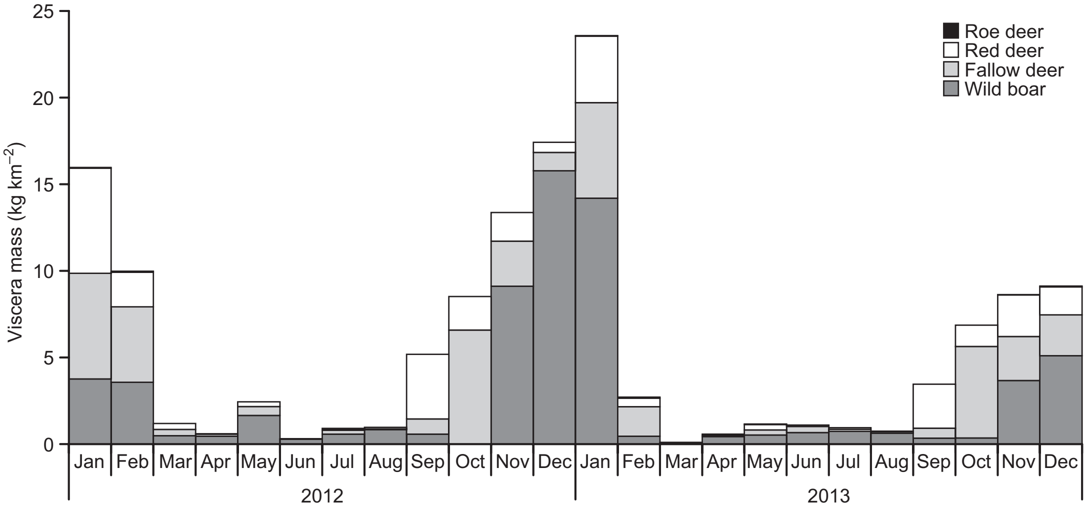

Fig. 1. Estimated quantity of big-game viscera in the study area presented by month. Quantity of big-game viscera was calculated from the size of hunting bags of each big game species (number of individuals) and their individual body weights (kg) with a correction factor of 25% visceral weight (Szunyoghy 1963, Whitehead 1993).

Results

Quantity of available big-game viscera and "other carrion"

The total field-dressed weight of harvested big game during the study period of 24 months was 89 405 kg (or 271.6 kg year^{-1} km^{-2}). Wild boar had the highest share (47.3%), followed by red deer (30.8%) and fallow deer (21.6%), while the proportion of roe deer was low (0.3%). The quantities of venison sold (produced from hunting) along with the quantity of viscera (total weight of viscera: 22 362 kg, or 67.9 kg year^{-1} km^{-2}; Fig. 1) shows a characteristic pattern. As intensive hunting reached its peak between September and January, this was the period when the largest amount of viscera available for jackals. Apart from this, carcasses of wounded and dead animals can also provide a substantial food resource for golden jackals (Fig. 2). The proportion of dead animals in the total sample (n = 2030 harvested big game) was 4.3%, of which the body weight of 25 big-game specimens was known. The total weight of these animals was 1851.5 kg (5.6 kg year^{-1} km^{-2}). Combining this amount with the total number of other dead big game (n = 87), the estimated total weight reaches 6443 kg (19.6 kg year^{-1} km^{-2}), which could have provided an additional food resource during the study period. This amount is 7.2% of the quantity of the harvested game during 24 months.

Diet composition

The mean (± SE) weight of food in the (n = 62) jackal stomachs examined was 137.3 ± 29.21 g (excluding empty stomachs: 152.0 ± 31.73 g). Twenty five percent of the non-empty stomachs contained remains of less than 25 g, and 25% of them contained more than 178 g of food remains; the highest weight was 1559.9 g (15% of the jackal's body weight). The weight of stomach content did not show a significant difference according to sex (MANCOVA: F = 0.19, p = 0.666), age group (F = 0.01, p = 0.930), season (F = 0.50, p = 0.613) and time of day (F = 0.86, p = 0.360). The difference between the weight of wild ungulate remains, and the weight of other food in the jackal's stomachs was non-significant (paired-sample t-test: t_{17} = 1.37, p = 0.188). In the stomachs containing food remains, the mean (± SE) number of food items was 1.8 ± 0.15. The relationship between quantitative composition based on weight of food remains detected in the stomach (W) and the relative frequency of occur-

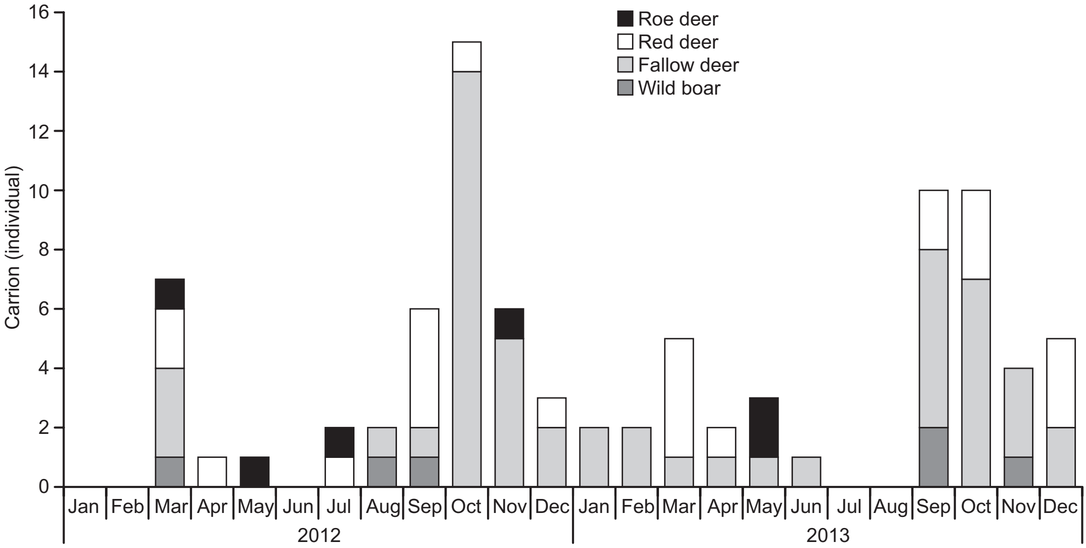

Fig. 2. Number of dead big game (mortality resulting from wounding and reasons other than hunting) in the study area presented by month.

rence data based on the number of food items (*O*) was significant for the 13 main food taxa (Spearman correlation, $r_S = 0.70$, $p < 0.01$).

Table 1. Stomach content of golden jackals (*Canis aureus*) in Hungary (Somogy county, Lábod region). *W* = percentage weight of individual food remains found in the samples, *O* = percentage relative frequency of occurrence.

Food item	*W*	*O*
Viscera of wild ungulates	32.8	24
Other carrion of wild ungulates	22.2	4
Wild boar (*Sus scrofa*) adult	11.6	7
Red deer (*Cervus elaphus*) or fallow deer, *Dama dama*) adult	5.5	4
Deer, juvenile	2.0	1
Roe deer (*Capreolus capreolus*) adult	6.0	4
Domestic dog (*Canis familiaris*)	0.8	2
Badger (*Meles meles*)	6.0	1
Small mammals	0.9	5
Medium-sized birds (Aves)	1.1	2
European green lizard (*Lacerta viridis*)	0.1	1
Fish (Pisces	2.1	5
Locusts (Acridoidea)	0.1	3
Larvae	2.1	8
Other insects	0.4	4
Fruits	6.1	14
Other plants	0.2	10
Inorganic material	0.3	1
Number of samples	62	
Number of food items	100	

According to both methods of calculation (*W*, *O*), the primary food of jackals consisted of viscera and "other carrion" (Table 1). Adult wild boar was the second most important food resource (*W* = 11.6%), which equalled the proportion of adult red, fallow and roe deer. Consumption of juvenile deer was detectable in only one case, in January. Consumption of carnivores was considerable (6.8%), whereas that of small mammal species (*Microtus* sp., Gliridae) proved inconsequential. Among the other vertebrate food taxa, there were occasional medium-sized birds, lizards, spined loach (*Cobitis elongatoides*) and large-sized (> 1 kg) common carp (*Cyprinus carpio*). As for invertebrate species, consumption of locusts and larvae (especially caterpillars of the cotton bollworm, *Helicoverpa armigera*) was considerable, but stomach contents also included scarabs, wasps, wasp nest and dragonflies. We found that jackals ate plants frequently, but in relatively small amounts (Table 1). Among plants, the most important items were fruit, particularly plums (*W* = 5.0%, *O* = 10.5%), grapes, blackthorn and blackberry, and grasses were also frequently eaten (*W* = 0.1%, *O* = 6.0%).

Although viscera and "other carrion" were primary food in every season (Table 2), secondary diet components varied seasonally. Based on quantitative composition, the diet in winter contained a considerable amount of adult big game and, to a lesser degree, carnivores. In spring and summer, plants and roe deer (adult, early spring) were important, while in autumn, invertebrates and fish consumption was considerable. Based on the relative frequency of occurrence, wild boar in winter, and plants and invertebrates from spring to autumn were the most important supplementary food items for jackals. The composition of stomach content showed a significant difference between seasons (χ^2-test: $\chi^2_{24} = 43.39$, $p < 0.01$).

The largest proportion of food consumed by both sexes was made up of viscera and "other carrion" (*W*, male: 63.3%, female: 42.8%). Males supplemented this mainly with adult wild boar (9.0%) and deer (8.9%), while females with adult roe deer (14.8%) and carnivores (14.7%). Mean (± SE) body weight of adult males (n = 27) was 10.8 ± 0.29 kg (min. 8.4 kg, max. 14.0 kg), and that of females (n = 26) 9.6 ± 0.11 kg (min. 8.2 kg, max. 10.5 kg). Despite different body weights (independent samples t-test: t_{51} = 3.93, $p < 0.001$), there was no significant difference between the diet composition of males and females, based on the number of occurrences of food items (χ^2-test: $\chi^2_{12} = 14.64$, $p = 0.262$).

Adult jackals supplemented their primary diet with big game in a greater proportion than juveniles (Appendix 3), which supplemented it with plants (especially plums) and invertebrates (mainly caterpillars) instead. The composition of stomach content was significantly different depending on age group (χ^2-test: $\chi^2_{12} = 25.38$, $p < 0.05$).

According to the time of collection, the jackals examined supplemented their primary food resources of carrion and viscera with wild boar by night and with plants and invertebrates by day (Appendix 4). The composition of stomach content showed a significant difference depending on the time of day (χ^2-test: $\chi^2_{12} = 26.12$, $p < 0.01$).

The trophic niche (*B*) narrowed from winter to autumn (5.34, 5.12 and 4.44, respectively in the three periods), was broader in males than in females (6.01 *vs*. 5.17), in adults than in juveniles (6.32 *vs*. 3.39) and by night than by day (6.58 *vs*. 4.71).

Discussion

The intensity of hunting follows a characteristic annual pattern, and this is also reflected in the quantity of big-game viscera consumed by jackals (Fig. 1). The quantity of venison sold shows an increase from September to January, then in January and February it falls sharply, and from March to August only a very small amount of venison is sold. However, carrion can still be found at this time of the year (Fig. 2). There are several reasons for this extreme pattern that are related to the characteristics of hunting practices.

Table 2. Stomach content of golden jackals according to season. For abbreviations *see* Table 1.

Food item	Winter		Spring and summer		Autumn	
	W	*O*	*W*	*O*	*W*	*O*
Viscera and other carrion	36.2	34.8	49.8	22.7	85.0	30.3
Wild boar (adult)	25.4	17.4	0.6	4.5	0.1	3.0
Deer (adult)	11.8	8.7	0	2.3	0.5	3.0
Deer (juv.)	4.5	4.3	–	–	–	–
Roe deer (adult)	4.8	8.7	16.8	4.5	–	–
Carnivores (badger, dog)	14.8	8.7	0.3	2.3	–	–
Invertebrates			1.8	20.5	6.5	18.2
Plants	< 0.05	4.3	26.3	29.5	0.6	30.3
Other*	2.4	13.0	4.3	13.6	7.4	15.2
Number of samples	20		21		21	–
Number of food items	23		44		33	–
Mean weight of food remains (g)	191.9		97.6		129.7	–

* other items are detailed in Table 1

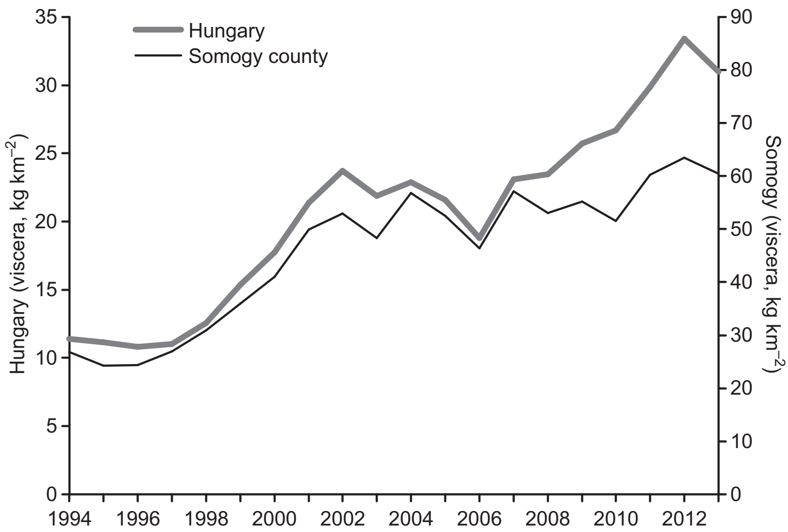

Fig. 3. Estimated annual quantity of big game viscera (kg km^{-2}) in Hungary and in Somogy county between 1994 and 2013. Data estimation was based on the size of hunting bags (individuals) with a calculated visceral loss of 25% from body weight.

In the study area, the big-game hunting season begins with the mating period (rut) of the red deer (1 September), followed by the rut of the fallow deer (1 October), and ends with the driven hunts of wild boar gardens (November–January). The amount and availability of big-game carrion is presumably underestimated in the area. Wild boar can be hunted year-round, and so can roe deer, except in March. Selective hunting of cervids is also permitted all year, which means that wounding and loss of game occurs more frequently in the summer. Furthermore, poaching and road kills, which also take place all year round, provide an food resource (carrion or viscera) for the jackal in the non-hunting season; however amounts, due to the lack of quantifiable data, could only be estimated with great uncertainty.

The relationship between the estimated available biomass of viscera and carrion of wild ungulates and the consumed mass of ungulates by jackals was not statistically significant (Appendix 5). In the study area, big-game populations are intensively managed, and — supporting our hypothesis — the most important food resource of jackals are viscera and carrion, which are available in large amounts. Primary consumption of carrion and viscera in every season demonstrates the ability of jackals to specialise (Lanszki *et al*. 2006) and to base their diet on this easily available food resource. Following the return of golden jackals to Hungary in the beginning of the 1990s (Heltai *et al*. 2001), consumption of big game, principally adult wild boar (carrion), in a proportion almost equal to small mammals, was reported (Lanszki & Heltai 2002) in winter and early spring in an area partially overlapping the present study area. As in our study, considerable consumption of big game (wild boar and cervids) viscera and "other carrion" (waste and carcasses of game animals) was detected in Croatia, especially during the hunting season (Bošković *et al*. 2013). Furthermore, in the forested areas of Bulgaria in winter (Raichev *et al*. 2013), only a small proportion was consumed, mainly through scavenging and predation, which is similar to our finding in Hungary. There are several factors that may be responsible for such high consumption of viscera and carrion.

Based on Hungarian hunting statistics (Sonkoly *et al*. 2013), and using the 25% correction factor, the viscera weight of big game species can be estimated. The statistics from this estimation show that total available big-game viscera weight increased (Fig. 3) from 1061 tonnes to 3099 tonnes between 1994 and 2012. Somogy county, where our study was conducted, has one of the largest big-game populations in the country, and also the highest golden jackal hunting bag (614 individuals in the 2012/2013 season, which is 37% of the national hunting bag). Viscera from field-dressing of the animals shot and carrion of wounded animals all serve as essential and easily available food resources for scavengers, such as the golden jackal.

According to our calculations based on local, regional (county level) and national hunting bag data and the substantial consumption we detected, we conclude that jackals play an important role in sanitation by the removal of waste and carcasses, which has also been observed in other areas (Atánassov 1953, Macdonald 1979, Poché *et al*. 1987, Aiyadurai & Jhala 2006, Giannatos *et al*. 2010, Lanszki *et al*. 2010, Ćirović *et al*. 2014). The large amount of available viscera and carrion (from hunting, poaching, road kills, diseases and natural mortality) is also reflected in the fact that not only jackals, but also the red fox (*Vulpes vulpes*) consumes large amounts of these food resources (e.g. Lanszki & Heltai 2002, Kidawa & Kowalczyk 2011). Our results, based on stomach content analysis, are clearly different from results of a previous Hungarian study using jackal scat analysis in the region of Kétújfalu (Lanszki *et al*. 2006, Lanszki & Heltai 2010). There, jackals consumed mainly small mammals, and did not show any preference for big game species. The low consumption ratio of small mammals in the Lábod region can be explained by the results of a small mammal survey in the summer of 2013, demonstrating that the average abundance of small mammals (indiv. per 100 trap nights) in that location was lower (13.0) than in the aforementioned area in summer (23.8, Lanszki & Heltai 2010), or in another area inhabited by jackals (summer of 2013, Balatoni Nagyberek, 24.4, J. Lanszki unpubl. data). The difference in the data may be due to the less intensive big-game hunting in the previous study: there the hunting bag size was only about one-third of the current study area (average: 3.8 heads km^{-2}, Lanszki *et al*. 2006). This means that because of their opportunistic feeding, jackals are capable of switching to big game viscera and carrion if such big game biomass is readily available, while small mammals constitute their dominant food resource when the latter are in high abundance (Lanszki & Heltai 2010).

We did not find evidence for sheep consumption from jackal stomach samples, although this area is used for sheep grazing and both lambs and carrion were available for jackals. Studies carried out in the Balkans and in the Middle East (e.g. Yom-Tov *et al*. 1995, Giannatos *et al*. 2010, Lanszki *et al*. 2010, Borkowski *et al*. 2011, Raichev *et al*. 2013) reported high consumption ratios of grazing domestic animals kept on pastures. Earlier studies in Hungary also found no (Lanszki & Heltai 2002) or a low ratio (Lanszki *et al*. 2006) of consumption of domestic-animal carrion, and no direct predation on domestic animals was found.

Our findings indicate that the level of big game and domestic animal predation in this area is lower than believed by hunters and animal keepers (Szabó *et al*. 2010, Heltai *et al*. 2013). This means that reports of killing and damage done by jackals are probably exaggerated. We often observed obvious signs of consumption of viscera in the form of pieces of rumen and/or stomach with a large amount of green plants with low nutritional value for jackals. But when jackals feed on whole carrion, beside a few identifiable remains (e.g. hairs, bones), they can obtain a sufficient quantity of easily digestible meat. However, consumption of wild-ungulate carrion may not necessarily be a result of direct predation, since also wounded animals, lost game, road kills and poached animals (e.g. by wire snare: P. Kemenszky, pers. comm.) can be consumed. We have no exact data on the extent of poaching, but we found a piece of a leather glove within a good portion of fallow deer meat in the stomach of one jackal, which indicates illegal bagging, or some other form of manipulation.

The remains of juvenile deer detected in one stomach suggested that predation of (very) young big game (e.g. Lamprecht 1978) does occasionally occur. Due to methodological limitations (Witt 1980, Reynolds & Aebischer 1991), in that case it could not be determined whether carrion (or other remains) or a live animal were eaten. Fully grown deer or wild boar are capable of active self-defence and rapid escape (Lanszki *et al*. 2006) and so predation on healthy adult big game specimens rarely occurs: even the wolf (*Canis lupus*) will hunt wild boar only in packs (Jędrzejewski *et al*. 1992). Jackals are facultative cooperative hunters (Moehlman 1987) and according to observational data, hunting in groups may occur, but it is not very typical of jackal behaviour (Khidas 1990, Demeter &

Spassov 1993). However, hunting in pairs for larger prey seems to be more successful than solitary hunting (Wyman 1967, Eisenberg & Lockhart 1972, Kruuk 1972, Lamprecht 1978, Moehlman 1987). Predation of wounded, injured and weakened adult big game (resulting from hunting, car accidents, fences etc.) is more likely, but in wildlife management this is viewed from a different perspective (e.g. sanitary role). In the jackal stomachs we found remains of adult roe deer prior to the time of fawning (in winter and early spring), and adult red and fallow deer remains also before or after the time of calving (from the end of summer to the end of winter). The annual mean of total consumption of big game species (excluding viscera and other carrion) was 25.1% (*W*). In other Hungarian studies based on scat analysis this figure reached 41.0% (Lanszki & Heltai 2002) and 7.4% (Lanszki *et al*. 2006) in the calculated biomass composition.

As compared with less social canids, it takes jackals a relatively long time to learn to hunt, and parental investment is high (Macdonald 1983, Moehlman 1987). Although the juveniles of late summer — early autumn examined were still part of their family group, the age-dependent difference in their diet was significant, despite the fact that their primary food was identical to that of the adults. The reason for this is that young jackals often supplemented their diet with smaller animals and fruit even at this time of the year and cubs consume these types of food even more frequently (Lanszki *et al*. 2009). Large numbers of cotton bollworm caterpillars, an insect pest which causes severe damage in corn fields, were found in the stomachs of young jackals. The diet composition, which varied depending on the time of day (along with the double-sized diurnal hunting bag) demonstrates the arrhythmic activity of jackals.

In conclusion, successful expansion of the golden jackal in Europe (Arnold *et al*. 2012) is facilitated by its developed social system, cautious and hidden lifestyle, habitat generalism and outstanding adaptability (Macdonald 1979, Moehlman 1987, Fuller *et al*. 1989), combined with a larger body size than its most common competitor, the red fox. Its diverse diet, containing various components (food generalism) is another essential factor aiding in its rapid spread and growth of its local population. In addition, the consumption of a few easily available food resources, such as viscera and other carrion, produced in vast amounts under conditions of intensive big game management and hunting both in our study area and at regional and national levels, is also determining consumption (food "specialisation") and food opportunism. Our study did not provide evidence for substantial damage and considerable losses to big game populations caused by jackals. But from the jackals' point of view the quantity of food available in the form of carrion and viscera of big game shot by hunters during at least six months of the year, is not negligible at all.

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Appendix 1. Hunting seasons of the five big game species in Hungary.

Big game species	Month												No. of open days	Proportion (%) of the year
	Jan	Feb	Mar	Apr	May	VI	VII	VIII	Sep	Oct	Nov	Dec		
Red deer	31	0	0	0	0	0	0	0	30	31	30	31	153	41.9
Fallow deer	31	28	0	0	0	0	0	0	0	31	30	31	151	41.4
Roe deer	31	28	0	15	31	30	31	31	30	31	30	31	319	87.4
Mouflon	31	28	0	0	0	0	0	0	30	31	30	31	181	49.6
Wild boar	31	28	31	30	31	30	31	31	30	31	30	31	365	100.0

Appendix 2. Body weights (without viscera) and number of big game according to age and sex in the Lábod region. All areas were accessible to jackals.

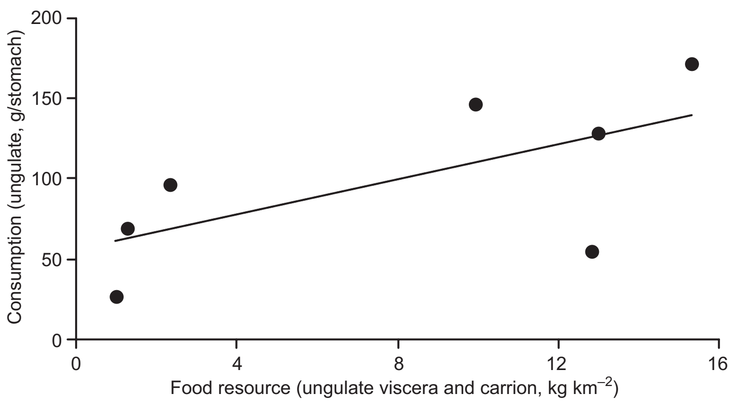
Species	Group	Mean body mass (kg)			Number of specimens			Body mass (mean ± SD)	*n*
		Dead	Enclosure	Open	Dead	Enclosure	Open		
Fallow deer	Buck	45.2		59.2	7		154	58.6 ± 12.2	161
	Fawn			18.0			370	18.0 ± 2.8	370
	Doe	32.5		32.9	2		262	32.9 ± 4.1	264
	Yearling doe	28.0		25.4	1		123	25.4 ± 4.1	124
Red deer	Stag	95.6		134.0	5		47	130.3 ± 33.4	52
	Calf	47.7		45.9	1		129	45.9 ± 11.8	130
	Hind	70.5		84.1	2		65	83.7 ± 16.4	67
	Yearling hind			62.9			26	62.9 ± 12.9	26
Roe deer	Buck	14.3		17.6	3		7	16.6 ± 2.8	10
	Fawn			8.3			4	8.3 ± 1.3	4
	Doe			15.4			9	15.4 ± 1.4	9
Wild boar	Boar	143.0	97.0	76.6	1	86	80	87.5 ± 20.3	167
	Sow	92.0	77.2	77.7	2	57	175	77.7 ± 17.8	234
	Piglet		14.8	15.6		27	24	15.2 ± 3.9	51
	Hogget	35.0	32.4	34.8	1	35	229	34.5 ± 11.5	265
Total		59.2	69.6	44.1	25	205	1704	47.0 ± 30.7	1934

Appendix 3. Stomach content of golden jackals according to age group. For abbreviations *see* Table 1.

Food item	Adult		Juvenile	
	W	*O*	*W*	*O*
Viscera and other carrion	53.8	27.8	66.9	25.9
Wild boar (adult)	12.8	9.7		
Deer (adult)	6.0	4.2	0.1	3.7
Roe deer (adult)	6.6	5.6		
Invertebrates	2.1	6.9	6.9	37.0
Plants	4.4	22.2	24.7	29.6
Others, summary	14.4	23.6	1.5	3.7
Number of samples	53		9	
Number of food items	73		27	
Mean weight of food remains (g)	146.1		85.6	

Appendix 4. Stomach content of golden jackals according to time of day. For abbreviations *see* Table 1.

Food item	Nighttime		Daytime	
	W	*O*	*W*	*O*
Viscera and other carrion	64.8	28	48.0	28.2
Wild boar (adult)	14.8	16	9.8	4.2
Carnivores (badger, dog)	0.2	4	12.2	2.8
Small mammals	1.2	12	0.7	2.8
Fishes	4.4	12	0.4	2.8
Invertebrates			1.9	19.7
Plants	0.1	8	11.2	29.6
Others, summary	14.5	20	15.8	9.9
Number of samples	18		41	
Number of food items	25		71	
Mean weight of food remains (g)	201.3		113.2	



Appendix 5. Relationship between the estimated available biomass of viscera and carrion of ungulates, and the consumed mass of ungulates. Resource estimation is based on the quantity of big game viscera in the study area (Fig. 1). Carrion estimation is based on the number of known dead big game (Fig. 2), measured body mass or in the case of unknown body mass by substitution with average body mass data from Appendix 2. The line indicates a non-significant relationship ($r = 0.654$, $p = 0.111$).