DOCTORAL (PhD) THESIS

NIKOLETT NAGYAPÁTI

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KAPOSVÁR CAMPUS

The Head of Doctorate (Ph.D.) School:

Prof. Dr. András Szabó DSc.

Supervisor:

Prof. Dr. József Lanszki DSc.

Department of Nature Conservation

Institute for Wildlife Management and Nature Conservation

Hungarian University of Agriculture and Life Sciences

EXAMINATION OF TROPHIC INTERACTIONS OF THE GOLDEN JACKAL AND THE RED FOX, AND NEST PREDATION

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Written by:

NIKOLETT NAGYAPÁTI

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List of the most important abbreviations in the dissertation

BC – calculated percentage biomass of food item consumed (in scat analysis)
B_A – standardized trophic niche breadth
DSR – calculated daily survival rate of artificial nests
FO – percentage frequency of occurrence
n – sample number
RFO – percentage relative frequency of occurrence
W – percentage wet weight of individual food remains found in the samples (in stomach content analysis)

1. INTRODUCTION

One of the most common carnivores globally and in Hungary is the red fox (*Vulpes vulpes*). The golden jackal (*Canis aureus*) has a rapidly increasing population in Europe. Due to high or increasing population numbers and known or less explored feeding habits, these mesopredators (mesocanids) are conflict species in the human-carnivore relationship. Knowledge of the trophic ecology, e.g. feeding habits, trophic interactions, and the factors influencing them, is essential for implementing proper carnivore management. In my research, I was planning to gain new knowledge about the trophic ecology of these carnivores.

Many factors, for example changes in the intensity of agricultural production (Gehring and Swihart 2003, Báldi and Faragó 2007), in wild game management (Glen and Dickman 2005), and in food resources (Goszczyński 1986; Hanski et al. 2001, Cagnacci et al. 2003, Raichev et al. 2013), or the appearance of large carnivores (Helldin and Danielsson 2007) have an influence on the feeding habits and population size of medium-sized predators. The socialism collapsed in Hungary in 1989, which resulted that the intensity of agricultural production (e.g. cattle density, fertilizer consumption, and cereal yield) decreased rapidly, and farmland diversity increased. However, from the late 1990s the farmland diversity declined again, because of the increasing land-use intensity (Báldi and Faragó 2007). Biodiversity and related services decline with agricultural intensification (Donald et al. 2001, Kleijn et al. 2009). The food patterns of the predators may follow the change that has occurred, but food switching of medium-sized predators in a changing environment are little known (Panek 2013; Apostolico et al. 2016).

The feeding habits besides prey size or abundance of food resources (e.g. Macdonald 1977, Jędrzejewska and 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.

The range expansion and population increase of some mesopredators (relative position of 'medium-sized' predators within food webs (Prugh et al. 2009) that can adapt to both natural and human-dominated environments have been regionally or globally observed (Prugh et al. 2009, Gehrt et al. 2009, Letnic et al. 2012). The 'mesopredator release effect' – where mesopredators increase when apex predators are removed (Crooks and Soulé 1999) – might be facilitated by the easy access and large amount of anthropogenic food resources available (Bino et al. 2010, Rotem et al. 2011). For these animals directly or indirectly derived food resources (Forsyth et al. 2014) near settlements are mostly livestock, carrion of domestic animals and garbage (Macdonald 1979, Yom-Tov et al. 1995), while farther from settlements these are mostly viscera of big game (wild ungulates) left behind by hunters and wildlife managers on the area (indirectly derived anthropogenic food resource) and carrion of big game from different mortality causes (Cagnacci et al. 2003, Forsyth et al. 2014).

Mesopredators can have a substantial role in sanitation around settlements by the removal of waste and carcasses (Treves and Karanth 2003, Ćirović et al. 2016). Furthermore, by limiting the abundance of smaller predators, mesopredators, e.g. red fox, golden jackal may have an indirect positive effect on biodiversity (Crooks and Soulé 1999, Henke and Bryant 1999) through controlling mammalian pests, e.g common vole *Microtus arvalis* (Glen et al. 2007, Lanszki et al. 2006, Ćirović et al. 2016). Overall, the functional roles of mesopredators in regulating trophic cascades can have a significant impact on the ecosystem (Crooks and Soulé 1999).

While urbanization is spreading, creatin and maintaining urban greenspaces is more important because these public areas are also habitats for many plant and animal species (Tryjanowski et al. 2017). Therefore, more and more emphasis is placed on the research of the ecology of wildlife in towns, parks (Gering and Blair 1999, Thorington and Bowman 2003, Yu and Guo 2014), settlement processes (Rutz 2008) and successfully integrated species (Noske 1999). Birds are important indicators of the aforementioned processes (Fernandez-Juricic and Jokimäki 2001, Weber et al. 2008, Finlayson et al. 2016). Therefore, to see through these processes and the potential consequences, it is crucial not only to understand how birds behave in artificial habitats but also to examine the factors that threaten their existence. Nesting success mostly depends on nest predation (Ricklefs 1969, Martin 1993), which influences the individual numbers (Mason et al. 2018) of the populations and the structure of the bird community (Marini 1997).

In 2010 I joined the dietary study of the golden jackal and red fox as a BSc student, and in 2012 the predation modelling in the Campus Park. Later I participated in my further research topics, and other studies with carnivores in South Transdanubia.

This doctoral dissertation has four topics. 1) I summarized the experience of a dietary study of red foxes in an agricultural area in an area where no golden jackal lived. 2) I evaluated the experiences of the dietary study of coexisting red foxes and golden jackals from an agricultural area in a comparative study. 3) I have discussed the experience of the big game viscera removal experiment in a more forested area under intensive big game management. 4) I analysed the predation on bird population using artificial bird nests in an urban area where the fox lives.

2. LITERATURE REVIEW

2.1 Studied canids

a) The golden jackal

The golden jackal (**Fig. 1**), a developed social system living Eurasian mesocarnivore species, has recently rapidly expanded its range across Europe (Rutkowski et al. 2015, Trouwborst et al. 2015, Hoffmann et al. 2018). In Europe, only isolated populations had survived in the Mediterranean and Black Sea coastal regions until the middle of the 20th century (Trouwborst et al. 2015, Krofel et al. 2017). The species has expanded rapidly from the Balkans in the 1970s-1980s north and west (Kryštufek et al. 1997) and now encompasses western and northern Europe (Stronen et al. 2020, Linnell et al. 2021, **Fig. 2**).

Fig. 1. Golden jackal (photo: Zoltán Horváth)

This native species was extinct in Hungary for few decades (Rakonczay 1990). The last known jackal individual was shot in 1942 (review: Tóth et al. 2009). It is unlikely that hunting led to the extinction of this species; the real reason was probably river regulation and, thus, the destruction of the species' habitat (Spassov 1989, Giannatos 2004, Szabó et al. 2009). After the extinction, the first reproducing jackals appeared in Hungary at the beginning of 1990 in the southern counties and the expansion is still ongoing. During the recolonization, jackal takes back its original areas, which are largely converted. It’s unequivocal that the current population density (Szabó et al. 2009, Tóth et al. 2009, Csányi et al. 2022) is larger than the last few centuries (Tóth et al. 2009).

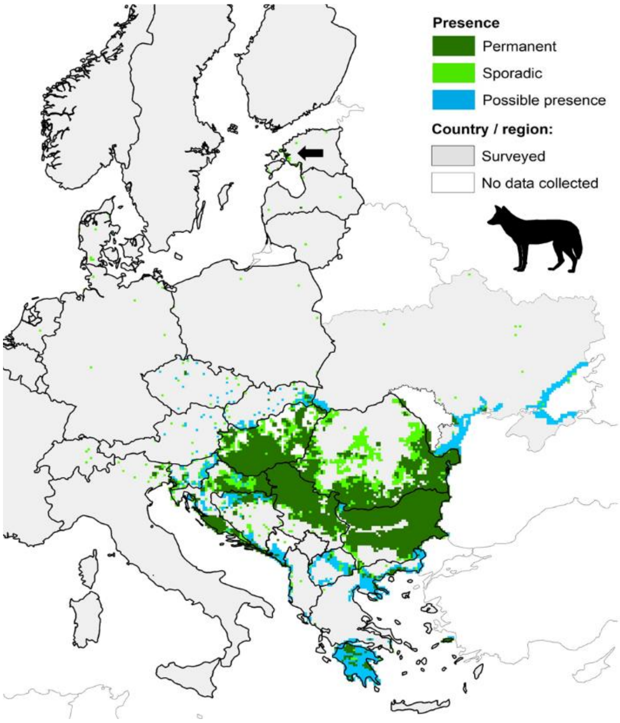

Fig. 2. Distribution of golden jackal (*Canis aureus*) in Europe (https://www.lcie.org/Large-carnivores/Golden-jackal)

The drivers of this range expansion are multifactorial. The population growth and expansion of jackals might be facilitated by several factors, including flexible social behaviour (Macdonald 1983, Moehlman 1987, Rotem et al. 2011), varied dispersal patterns (Kapota et al. 2016, Lanszki et al. 2018), legal protection (e.g. in Bulgaria in ’60s; Markov 2012), the scarcity of larger competitors (Trouwborst et al. 2015, Krofel et al. 2017), poor population control (Markov 2012), abundant food resources (Yom-Tov et al. 1995, Lanszki et al. 2006, 2015, Ćirović et al. 2016), poor sanitation conditions around settlements (Rotem et al. 2011), transformation of habitats (e.g. land use changes, intensification of agricultural production; Gehring and Swihart 2003, Kleijn et al. 2009), global climate change (e.g. range shift, Trouwborst et al. 2015), but there is no consensus of what is driving this rapid range expansion (Trouwborst et al. 2015, Krofel et al. 2017).

In a review (Lanszki et al. 2022) based on 40 dietary studies from Eurasia was found that the main foods of jackals are domestic animals (RFO, mean, 22.9%, mostly from scavenging), small mammals (mainly rodents, 22.7%) and plants (primarily fruits, 21.6%), while wild ungulates (10.2%, mostly from scavenging) and other food types are locally important foods only. The golden jackal feeds on a broad range of smaller sized prey, such as rodents, hares, birds, reptiles and arthropods (Demeter and Spassov 1993, Mukherjee et al. 2004, Lanszki et al. 2006, Jaeger et al. 2007), but also consumes plants (Demeter and Spassov 1993, Mukherjee et al. 2004, Aiyadurai and Jhala 2006, Borkowski et al. 2011), and scavenges on domestic animal remains (Macdonald 1979, 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 and Ćirović 2015), and different kinds of wild ungulate carcasses left by large predators (Aiyadurai and Jhala 2006) or hunters (Lanszki and Heltai 2002, Bošković et al. 2013, Raichev et al. 2013, Lanszki et al. 2015). Considerable calf predation occurs in small enclosed areas in India where golden jackals at high density also kill chital (*Axis axis*) calves and persist on plants (Prerna et al. 2015). In Serbia, jackals consume easily available waste (e.g. domestic animal carrion) from dumps (Ćirović et al. 2016). The group-living jackal successfully preys on medium- and larger-sized wild and domestic ungulates, especially fawns and calves (Demeter and Spassov 1993, Yom-Tov et al. 1995), or injured and weakened adults (Lanszki et al. 2006, 2015). The jackal prefers to prey on smaller animals than 4 kg (Hayward et al. 2017).

The assessment of the jackal is controversial (Urban et al. 2020), it is not an IAS (Invasive Alien Species) in Europe (European Commission 2016), even in areas outside its former (historical) range (Kryštufek et al. 1997, Arnold et al. 2012, Krofel et al. 2017). There are many common beliefs about the jackal, mostly among livestock keepers and hunters, especially regarding its feeding habits (Szabó et al. 2010, Mihelič and Krofel 2012, Bošković et al. 2013, Heltai et al. 2013). Hunters regularly report the damage caused to the big game populations (e.g. Yom-Tov et al. 1995). At the same time, the big game (e.g. red deer *Cervus elaphus*, fallow deer *Cervus dama*, wild boar *Sus scrofa*) populations are increasing in Hungary (Csányi et al. 2022). In pastures, protection solutions against predators are incomplete (e.g. no suitable fence, electric fence, shepherd dog, the shepherd is missing), and the disposal of carcasses and slaughter waste is also often unprofessional. All these lead to a concentrated appearance of predators, which generates conflicts. The backgrounds of such beliefs are often unknown or can be easily misinterpreted because of the lacking knowledge of the real causes of the predation (Szabó et al. 2010, Heltai et al. 2013). Our investigations primarily focus on the ecological role.

b) The red fox

The red fox (**Fig. 3**) is one of the most researched carnivores in the world. Its ecology and behaviour have been written in so many books and studies. (reviewed: e.g. Fox 1975, Lloyd 1980, Harris 1986, Artois and Le Gall 1988, Macdonald and Sillero-Zubiri 2004; in Hungarian: Heltay 1989, Faragó 2006, Heltai et al. 2010, Lanszki 2012).

Fig. 3. Red fox (photo: Péter Lanszki)

The red fox is one of the most widespread and important mesopredators in the Northern Hemisphere (Macdonald and Sillero-Zubiri 2004). It lives in very different habitats, from the subtropical areas to the arctic circle, from different types of forests to large cities, from lowland to high mountains. It is found all over the country (Heltai et al. 2010). Despite of the fact that the fox is a mesopredator, in many areas fox became a top predator, because of the lack of large carnivores.

It's a generalist canid and adapts well to the habitats. The red fox is a solitary hunter, it hunts alone except the cub rearing period. Its breeding takes place between January and March. Cubs (4-5 per litter) are usually born in April. They started to hunt on their own in July-August. Yearling females and males are sexually mature. Fox allows individuals from previous litter to remain and provide alloparental care to future offspring (Whiteside et al. 2011, Baker and Harris 2004, Macdonald 1979). Its home-range size is between 0.1 and 30 km^2 and depends on the abundance of food. Average size is 2-3 km^2 (Voigt and Macdonald 1984, Baker and Harris 2004, Macdonald and Sillero-Zubiri 2004). Fox needs to eat roughly 400-500 grams of food per day (Macdonald 1979, 1983).

There are many data about its feeding habits. Fox is an adaptive and opportunistic forager (Macdonald 1977), the diet composition is varied depending on latitude, habitat characteristics, and seasons (e.g. Kidawa and Kowalczyk 2011, Díaz-Ruiz et al. 2013, Soe et al. 2017). In agricultural areas the fox preys primarily on small mammals or hares, and periodically eats birds, carrion, plants and invertebrates (e.g. Englund 1965, Goszczyński 1977, Macdonald 1977, Jensen and Sequeira 1978, Goszczyński 1986, Jędrzejewska and Jędrzejewski 1998, Leckie et al. 1998, de Marinis and 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 studied competitors such as the jackal. The comparative dietary analyses can also facilitate exploring interspecific interactions (Lanszki et al. 2006). Because of the dramatic decline of large carnivore populations in Europe (Macdonald and Sillero-Zubiri 2004, Chapron et al. 2014), both have become top predators in a majority of the areas they occur in.

c) Golden jackal versus red fox

The differences between the golden jackal and the red fox arise for example from differing body mass (average of sexes, jackal: 9.6-10.8 kg, fox: 5.4-6.3 kg; Heltai et al. 2010, Lanszki et al. 2015), body morphology (jackal: longer legs, stronger dentition; Demeter and 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 habits (Macdonald 1979, 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 1979, 1983). 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 1979, 1983, Demeter and Spassov 1993). Cooperative hunting means competitive advantage compared to the mostly solitary fox (Lloyd 1980) and could be related to habitat (Demeter and 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 vary the hunting techniques, while the smaller red fox preys on relatively smaller animals (<1 kg, Gittleman 1985, 1989). Therefore, the jackal, unlike the fox, can be a pursuer hunter, not only a searcher hunter (Bekoff et al. 1984).

2.2. Trophic niche and diet analysis methods

A thorough understanding of the diet, which broadly defines the ecological niche of a species, is an essential element in determining what limits or promotes populations and is therefore crucial for effective population management and conservation (Kruuk 2006, Trouwborst et al. 2015, Ćirović et al. 2016, Hayward et al. 2017). For carnivores, food is often limited (Macdonald 1983), and diets may vary between regions and seasons (e.g. Jędrzejewski and Jędrzejewska 1992, Kruuk 2006, Lozano et al. 2006, Zhou et al. 2011, Soe et al. 2017, McCain et al. 2018). The preying of the primary or alternative prey can be a source of human-carnivore conflicts (e.g. Kranz 2000, Szabó et al. 2010, Trouwborst et al. 2015). Predators affect directly and indirectly on prey species (e.g. top-down and bottom-up regulations), and links between predators and their prey through trophic systems (competition, cascade mechanisms) are important drivers of evolution (Holt 1977, Abrams and Rowe 1996, Courchamp et al. 1999, Crooks and Soulé 1999, Drossel et al. 2001). The mechanisms are also economically noteworthy. In Serbia jackal population annually removes more than 3700 t of animal waste and 13.2 million crop pest rodents. The researchers also estimated the monetary value of animal waste removal at > 0.5 million € per year (Ćirović et al. 2016).

Research on carnivores' diets (e.g. reviews mentioned above) relies mainly on **traditional methods**, including the analysis of stomach contents and faecal samples. The advantage of the stomach analysis, among others, is the accurate and straightforward species identification (compared to faecal analysis), and several additional information can be attached to it from post mortem analysis. The food remains are only partially digested; therefore, the importance of food items is well quantifiable (e.g. Reynolds and Aebischer 1991, Jędrzejewska and Jędrzejewski 1998, Lanszki et al. 2014, 2018).

In recent decades **new procedures** have become widespread, including DNA metabarcoding, stable isotopic method, fatty acid profile analysis. Traditional morphological dietary studies are limited by their inability to detect rare prey items, difficulties correctly classifying prey from reference skeletons, and the potential to miss soft-bodied organisms, causing predation effort to be often underestimated (Plimpton et al. 2021). DNA barcoding is a methodology that can provide precise and semi-automatable species identification through the design of forward–reverse primer sets for highly conserved regions of mitochondrial (mt) DNA (Hebert et al. 2003). The great perspective of the stable isotopic (C, N) method performed on vibrissae (tactile hair) or hair samples, can provide information on the diet, the food sources for earlier periods (Newsome et al. 2007, Crawford et al. 2008, Tyrrell et al. 2013, Jordaan et al. 2019) and "isotopic niche" of a species (Hette-Tronquart 2019). The method was successfully applied, e.g. in otter species (Jordaan et al. 2019, LaRoche et al. 2021), canids (Roth and Hobson 2000, Kays and Feranec 2011, Webster et al. 2021), cats (McDonald et al. 2020), bears (Merkle et al. 2017), small-sized mustelids (Hammershøj et al. 2004). The overall description of the tissue lipids' fatty acid composition is less applicable for prey identification, because it is influenced by the fatty acid composition of prey (Szabó et al. 2007). However, the method may be suitable for detecting differences in the previous food base.

2.3. Predation experiment on artificial bird nests in a campus park

In artificial bird nest predation tests, we sought the answer to how carnivores prey on bird nests in a campus park. Nesting success mostly depends on nest predation (Ricklefs 1969, Martin 1993), which influences the individual numbers (Mason et al. 2018) of the populations and the structure of bird community (Marini 1997). Tracking the natural clutches comes with disturbances, therefore documenting the predation is possible with artificial nests and clutches (Stuart-Smith and Hayes 2003, Batáry and Báldi 2004, Bateman et al. 2017, Iezekiel et al. 2017) or camera trapping (e.g. Fenske-Crawford and Niemi 1997, Weidinger 2008, Richardson et al. 2009). Studies carried out with artificial clutches can be only indicative because there is no clear evidence that the survival of artificial clutches is consistent with the real nests (e.g. Thompson and Burhans 2004, Purger et al. 2012) or different from them (e.g. Davison and Bollinger 2000, Zanette 2002). Nevertheless, the method is widely used (Stephens et al. 2004, Belthoff 2005, Vetter et al. 2013), because it can help detect the outcome of certain environmental factors. In natural habitats, primarily the predators, but in the anthropogenic environment, the presence and the direct or indirect effects of people (human disturbances) influence the nest success (e. g. Bolduc and Guillemette 2003, Beale and Monaghan 2004, Chace and Walsh 2006, Medeiros et al. 2007). It is barely known (Donnelly and Marzluff 2004, Bocz et al. 2017), to what extent the human impact (e.g. vehicle collision, disturbance, mowing, maintenance of trees and shrubs) are influenced the nest success in shrub- and ground-nesting bird species, however, this information is necessary for the settlement and survival of birds during the creation and maintenance of a park (Paker et al. 2014, Müller et al. 2018).

3. HYPOTHESES AND AIMS OF THE DOCTORAL THESIS

3.1. Long-term changes in the diet of the red fox in an agricultural area

There are a few areas in south-western Hungary, including our study area in Fonó, where the red fox has maintained a stable population as the top predator, considering that in many other areas, the golden jackal took over this role (Szabó et al. 2009, Csányi et al. 2014, Lanszki et al. 2016). We hypothesized that due to changes in the habitat composition and habitat use intensity, the diet composition of the red fox over a longer period (i.e., two decades) would change in an agricultural area.

We aimed to evaluate the intraspecific (period- or survey-dependent and seasonal) differences in diet composition and trophic niche breadth of the fox bas on analysed scat samples in the “first survey” (1992–1997) and “second survey” (2012–2014).

3.2. Diet composition of the golden jackal and the sympatric red fox in an agricultural area

Previous studies performed on agricultural areas in Hungary (periods examined: 1996-1997 and 2000-2004; Lanszki and Heltai 2002, Lanszki et al. 2006, Lanszki and 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 in sympatric jackals, but the 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 jackals with a more varied diet should be more food generalists than foxes. 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.

To better understand the ecology of the golden jackal and interspecific relationships with its main competitor, the red fox, our aims with this three-year study performed in an agricultural area (Vajszló, SW Hungary) 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 studies performed in Hungary.

3.3. Feeding responses of the golden jackal after the reduction of anthropogenic food subsidies

In human-dominated environments, ecosystem dis-services associated with high mesopredator densities are better known, including e.g. as vectors of diseases (Soe et al. 2017), as predators of wild ungulates and of domestic animals in pastoral zones (Yom-Tov et al. 1999, Baker et al. 2008, Prugh et al. 2009). However, the consumption of an animal does not necessarily mean that it came from predation, e.g. in the case of scavenging. Ungulate density directly influences carcass feeding (Cagnacci et al. 2003) and open garbage dumps are attractive to mesopredators and may cause unnaturally large aggregations (Macdonald 1979, Bino et al. 2010, Newsome et al. 2013). The population monitoring and consequent control of certain common generalist carnivores with high population densities may be necessary by non-lethal methods or lethal removal (Treves and Karanth 2003, Baker et al. 2008). One possible method of controlling overabundant carnivores may be a drastic reduction of anthropogenic food sources. It was found (Bino et al. 2010) that removing anthropogenic food increased home range size and decreased the survival of red foxes. Similarly, others (Kapota et al. 2016) found that golden jackal survival under food reduction decreased and was lowest for dispersing individuals. It was experimentally confirmed (Newsome et al. 2014) that human-resource subsidies alter the dietary preferences of dingoes (*Canis lupus dingo*). Medium-sized canids may respond to changing amounts of food by dietary switching (Randa et al. 2009, Lanszki and Heltai 2010, Morehouse and Boyce 2011); jackals use of both prey and directly or indirectly derived anthropogenic food sources. They may also respond with changes in body size (Yom-Tov 2003).

We hypothesise that in an area of intensive big game hunting with high jackal density, reducing the primary food subsidy (e.g. big game viscera; Lanszki et al. 2015) will result in pronounced food switching. To test this hypothesis, we manipulated (reduced) food subsidies at a landscape scale over four years in the first manipulative experimental test of the role of anthropogenic food subsidies on jackal diet (Lábod, SW Hungary). We predicted that this would lead to (1) reduced stomach content weight and body mass of jackals, and (2), an increase in the consumption of food types acquired by depredation by jackals, such as (a) small mammals and/or (b) big game carcasses and/or big games (adult and/or young individuals) as prey.

Furthermore, the consumption of suboptimal food types (with low energy values), such as (c) plants and/or (d) garbage (e.g. leftover food) would also increase. This is because jackals in Hungarian agroecosystems primarily eat small mammals, and wild boar after severe winters (Lanszki et al. 2006).

Our aim was to test whether the dietary composition of jackal stomach contents varied between two 2-year survey periods, the first without big game viscera removal followed by a period with viscera removal.

3.4. Predation experiment on artificial bird nests in a campus park

From a conservation perspective, it would progress to transform city parks (urban habitats) into bird-friendlier habitats. For an effective biodiversity conversation in the urban green spaces of an urban environment, it is crucial to know the relationships between prey (e.g. birds) and predators (Jokimäki and Huhta 2000, Baker et al. 2008, Stracey and Robinson 2012, Kurucz et al. 2021).

The wildlife of the Kaposvár University campus park has been assessed (Kovács-Hajdu et al. 2014), but the interspecific relationships, especially predation impacts were still unknown. Mammalian predators (e.g. red fox, domestic cat (*Felis catus)*, brown rat (*Rattus norvegicus)*, red squirrels (*Sciurus vulgaris*) observed in the area; Kovács-Hajdu et al. 2014) can cause losses in short-cut grass in the campus park.

Furthermore, it is poorly known to what extent the human impact (e.g. vehicles, disturbance, mowing) influences nesting success in shrub- and ground-nesting bird species. This information is necessary for creating parks and maintaining them (Bocz et al. 2017, Müller et al. 2018). During park maintenance (e.g. thinning, pruning the bushes), bird nests can be damaged and become visible to predators; birds (mainly crows) and squirrels can steal eggs and chicks more often. People moving there in their free time can cause losses by trampling too. Our hypothesis is that park management and the presence of predators associated with urban parks significantly impact the survival of bird nests in the campus park (**Appendix 1**).

Our aims of the artificial nest predation tests (predation modelling) performed in the Kaposvár campus park were: 1) to examine the survival rates of clutches of ground- and shrub nesting bird species and 2) to point out the potential predators (e.g. fox) and anthropogenic factors (human influences) threatening the clutches.

4. MATERIAL AND METHODS

4.1. Characteristics in general

The location of the examined areas in south-western Hungary is illustrated in **Fig. 4**, the main habitat characteristics in **Table 1,** and the photos of habitats are in **Appendix 2**.

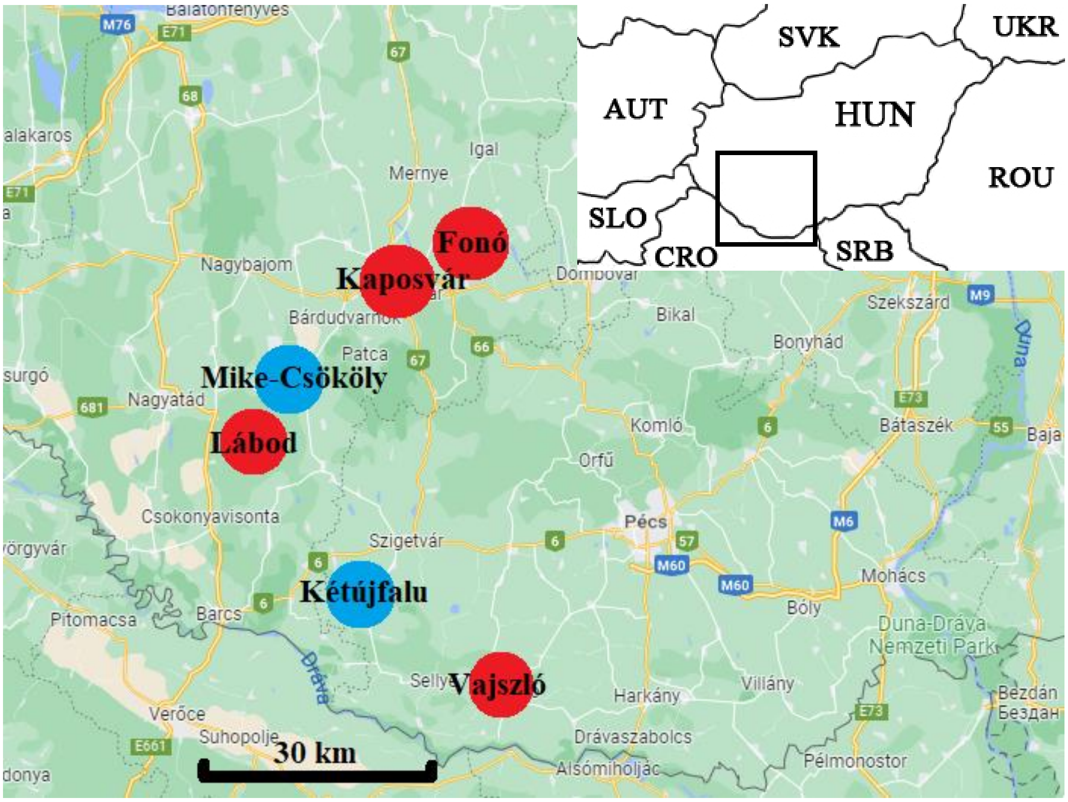

Fig. 4. Location of the study areas in south-western Hungary (displayed on Google Maps). The four main areas are marked in red, and the two areas marked in blue are included in the comparative study.

Table 1. Percentage composition of main habitats of areas studied (further details see Study area sections and Appendices)

Habitat type	Fonó I	Fonó II	Vajszló	Lábod	Kaposvár
Cultivated lands	28	40	59-60	36.7	
Abandoned fields	0-15	0	11-12	0	
Game-field	0-2.4	0	0	0	
Pasture	5	2	0	7.5	
Forests	26-33	26	29	53.5	
Fishpond	0.8-13	13	0	1.1	
Wetlands	19-26	19	0		
Human settlements	0	0	0	1.2	
Urban campus park					100

The study areas lie on the continental climatic region, but there are some sub-Mediterranean features (i.e. moderately warm and wet and relatively mild winter, Dövényi 2010). More details about meteorological data can be found in the primary publications (Lanszki et al. 2016, 2018, 2019, Nagyapáti et al. 2019). Hunting bag data for each area is as follows (**Table 2**):

Table 2. Harvest density (mean, individuals/km^2) of game species in the areas studied.

	Fonó I	Fonó II	Vajszló	Lábod
Red deer	0.04 ± 0.02	0.11 ± 0.01	1.92 ± 0.25	1.10 ± 0.07
Fallow deer	0	0	0	2.12 ± 0.39
Roe deer	0.51 ± 0.09	0.53 ± 0.13	0.80 ± 0.09	0.30 ± 0.03
Wild boar	0.05 ± 0.04	0.75 ± 0.12	3.69 ± 0.33	2.01 ± 0.24
Pheasant	1.63 ± 0.76	0.16 ± 0.07	0.59 ± 0.23	-
Brown hare	0.09 ± 0.05	0.01 ± 0.01	-	-

No specific permissions were required for these studies.

The following calculation methods, which are the most frequently used in traditional dietary studies, were applied by me:

RFO – percentage relative frequency of occurrence

$$\text{RFO}\ (\%) = 100\text{x}\ \frac{\text{number of occurrences of a given food items}}{\text{number of all food items}}$$

FO – percentage frequency of occurrence (proportion of samples containing a given food item)

$$\text{FO}\ (\%) = 100\text{x}\ \frac{\text{number of samples containing a given food item}}{\text{total number of samples}}$$

BC – calculated percentage of biomass consumed. To estimate the fresh mass of food ingested, all dry food remains are weighed separately and the food remains mass data are multiplied by an appropriate conversion factor (summarized from literature data: e.g. Jędrzejewska and Jędrzejewski 1998).

$$\text{BC}\ (\%) =$$

$$= 100\text{x}\ \frac{\text{weight of a given food item remain} \times \text{conversion factor}}{\text{summarised weight of food remains} \times \text{conversion factors in the sample}}$$

W – percentage wet weight of all individual food remains found and separated in the samples

$$\text{W}\ (\%) = 100\text{x}\ \frac{\text{wet weight of a given food item}}{\text{total wet weight of food remains in the sample}}$$

4.2. Long-term changes in the diet of the red fox in an agricultural area

a) Study area

The study area is located near Fonó village (46°22’N 17°55’E, standard route of 4.2 km, 125-160 m a.s.l.). The main land use in this hilly area is intensive arable agricultural cultivation (**Appendix 2**). The determination of proportion of habitat types was based on Land Registry and our systematic field survey data.

b) Study species

The relative abundance of red foxes (individuals per km^2) was calculated on the basis of den density (inhabited den × 2) by own surveys (see methods in Márton et al. 2016) performed in March, 2002–2014. There was sheep grazing within the study area, and fruit growing and animal husbandry (e.g. poultry) are nearby. On the basis of hunting bag data of the local Game Management Unit (**Appendix 3**, Csányi et al. 2014), wild ungulate populations and game management intensity are moderate in the study area (cf. **Table 2**). Golden jackal did not occur in this area.

c) Sample analysis

The diet composition of the fox was investigated by analysis of scat samples. Scats were collected using the same method in the first survey (from December 1992 to November 1997, n = 350 scats) and in the second survey (from December 2012 to May 2014, n = 237 scats), i.e., collected monthly over the same area on a standard route of 4.2 km. The sections of the sample collection route represented the proportions of the habitat types of the area, and there were at least four to six fox territories traversed based on the number of known inhabited fox dens. Scats were analysed using a standard procedure (Jędrzejewska and Jędrzejewski 1998). Dry processing was applied to these samples, therefore Samples collected were frozen stored at –20 °C for months prior analysis. the diet composition from scat samples was expressed on the basis of RFO and FO only. The following 12 food types were used in the calculations related to the comparative analysis of the scat composition and the trophic niche breadth for the two periods: 1 – small mammals (insectivores and rodents), 2 – European brown hare (*Lepus europaeus*), 3 – wild boar (*Sus scrofa*), 4 – cervids, 5 – domestic animals, 6 – carnivores, 7 – pheasant (*Phasianus colchicus*), 8 – other birds and eggs, 9 – reptiles, amphibians, and fish, 10 – invertebrates, 11 – plants (fruits, seeds, and other plant matter), and 12 – inorganic materials (e.g. household waste).

d) Data analysis

To test whether the diet composition differed between the two surveys (1992–1997 vs. 2012–2014), a non-parametric, two-way permutational multivariate analysis of variance (PERMANOVA, 9999 random permutations) was used with period and season as the two independent factors and frequency (RFO or FO) data as dependent factors in the program PAST (version 3.20, Hammer et al. 2001). Similarity percentage (SIMPER) analysis (in PAST) was applied to highlight which food types contributed most to the dissimilarity in diet composition between the two surveys. PERMANOVA and SIMPER results were based on Bray-Curtis dissimilarity matrices (e.g. Sarmento et al. 2015). Chi-square test was applied to examine habitat type distribution differences (hectare data per habitat type) and independent samples *t*-test to examine hunting bag density (individuals / km^2) and red fox density (inhabited den × 2, individuals / km^2) differences between the two periods. 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 of the *i*th food item; and standardised across food items: $B_A = (B - 1) / (n - 1)$, rating from 0 to 1. The seasons were divided into winter

(December-February), spring (March-May), summer (June-August), and autumn (September-November). Seasons with small number of samples were pooled (i.e., summer with spring in 1994, summer with autumn in 1995 and spring with summer in 1996). The seasonal B_A values between the two periods were compared with independent samples t-test. A minimum probability level of $P < 0.05$ was accepted for all the statistics.

4.3. Diet composition of the golden jackal and the sympatric red fox in an agricultural area

a) Study area

Our study area, close to the River Drava is located near Vajszló village (45°51'N 17°56'E, 13.6 km long standard route within a 6.1 km^2 area). Although it is a plain, 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* spp.) and black locust (*Robinia pseudoacacia*), and the 11-12 % of the total area is abandoned grasslands (partially covered by blackthorn (*Prunus spinosa*), common hawthorn (*Crataegus monogyna*), sedge (*Carex* spp.)), common reed (*Phragmites australis*) and oxbow lakes covered by reed, bulrush (*Typha spp.*), willow (*Salix* spp.), alder (*Alnus* sp.) and Canadian goldenrod (*Solidago canadensis*).

b) Study species

On the basis of hunting bag data of the local Game Management Unit (cf. Table 2), in the study area the big game management is less intensive than at some other game management units in SW Hungary (cf. Table 2). 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 acoustic 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. There was no grazing of livestock in the study area.

c) Sample 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 1979) 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, **Appendix 6**). Stray dogs were very rare or not present in the area based on professional hunter's and own observations. Questionable samples (1-2 %) were not collected or were excluded from the analysis.

A total of 373 golden jackal and 268 red fox scats were analysed by means of a standard procedure (Jędrzejewska and Jędrzejewski 1998). Samples collected were frozen stored at –20 °C for months prior analysis. After that scat samples were soaked in water, then washed through a sieve (0.5 mm mesh) and dried. Diet composition of the predators was expressed in two ways: RFO and B (FO data only for main food types were used in the log-linear likelihood tests). To estimate the fresh mass of food ingested (Reynolds and Aebischer 1991), all dry food remains were weighed separately and the food remain mass was multiplied by an appropriate conversion factor, as summarized from literature data by Jędrzejewska and Jędrzejewski (1998). 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, e.g. most small mammals); arboreal (and mainly arboreal but sometimes terrestrial, e.g. passerines); and aquatic (or water-related, e.g. water vole *Arvicola amphibius*, *Anas* sp.). 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 species, 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.

d) 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 were 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 BC 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 BC for both canids as dependent variables, season and year as fixed factors and weighted by food types).

Trophic niche breadth was calculated in accordance with Levins and standardised across food items (Krebs 1989). 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 (FO) and estimated biomass (BC) 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 and Heltai 2002, Lanszki et al. 2006, 2015), including this study. Dendrogram was performed on the basis of arcsin transformed percentage relative frequency (FO) and consumed biomass (BC) data of 10 main food types (same food types as listed above, except 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.

4.4. Feeding responses of the golden jackal after reduction of anthropogenic food subsidies

a) Study area

The 165 km^2 unfenced study area is located in the Lábod region (46°11’N 17°30’E). This is a flat, lowland area with sand-dunes (125-190 m, above sea level). Forestry, wildlife management and crop cultivation are the predominant land use of the region. The vegetation consists of forests (53.5% of all land) of English oak (31.5% of forested areas), willow, as well as alder, linden (*Tilia* sp.) and black locust. The age of the forests is under 40 years. In the arable areas (36.7%), row crops, oilseed rape and cereals dominate, but pastures (7.5%), ponds and wetlands (1.1%), human settlements and orchards (1.2%) also occur (Lanszki et al. 2015). Within the study area or directly around it there are nine small villages, with less than 2,000 inhabitants per settlement. Human population density is 8.2 individuals/km^2.

b) Study species

Intensive big game management via trophy hunting of fallow deer, red deer and wild boar occurs in the study area (482 km^2 hunting area of the Lábod district; SEFAG Co.), while roe deer (*Capreolus capreolus*) is a less important hunted species (**Table 2**, **Appendix 9**). The legal hunting season of the fallow deer is between October and February, the for red deer between September and January, in case of the wild boar it is year-round, and for the roe deer it is year-round except March and first half of April. We estimated the viscera monthly. Small game species, such as pheasant (*Phasianus colchicus*) and European brown hare (*Lepus europaeus*), were rarely hunted (hunting bag < 0.1 individuals/km^2). There is supplementary feeding in the area for wild ungulates. There are no accurate population estimates for these species.

Data on individual body mass data 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 human hunting activity. We calculated the viscera (stomach, intestines, oesophagus, heart, lung and liver) weight with a constant factor of 25% compared to full body mass (Whitehead 1993) in both survey occasions from the weight of field-dressed animals (i.e., with viscera and blood removed). In the second survey period, viscera were collected and deposited by professional hunters in a properly fenced location inaccessible to jackals.

Between January 2012 and November 2013 (the first survey period when there was no viscera removal, Lanszki et al. 2015), and between December 2013 and October 2015 (the second survey period when food subsidies were experimentally manipulated via viscera removal), the number of harvested big game was 1903 and 1526 individuals in the study area, respectively. Of these, 1821 and 1408 animals were shot during hunting activities, 1789 and

1341 individuals (98.2% and 95.2%) of which had body mass data collected in each survey period, respectively. In addition, 82 and 88 game individuals were found as carrion (mortality resulting from wounding and the loss of the individual, poaching, and some non-hunting related mortality, e.g. road casualties, diseases), and we had body mass data for 23 and 18 of these (28.0% and 20.4%) in the two surveys periods (these were not removed from the area). Estimation of this carrion was based on the number of registered individuals and known average body mass data by species, sex and age group separately as detailed elsewhere (Lanszki et al. 2015).

There are two sheep (merino) farms in the area (separated by 17-18 km). Sheep of the Homokszentgyörgy flock graze outdoors all year round, but are kept in a barn overnight. The Nagykorpád flock is kept outdoors in summer and autumn, but there is no barn and they are in the open during the night. One shepherd and a few sheepdogs (smaller sized herding dogs) accompany each flock. Domestic ungulates are registered and marked individually, and dead animals are compulsorily dispatched and disposed. Live animals are sold, therefore slaughtering can occur very infrequently, whereupon viscera are available for scavengers.

The mean (± *SE*) jackal density of the area was 0.27 ± 0.02 groups/km^2 plus 0.05 ± 0.01 individuals/km^2, (0.31 ± 0.01 groups/km^2 plus 0.04 ± 0.03 individuals/km^2 and 0.25 ± 0.04 groups/km^2 plus 0.07 ± 0.02 individuals/km^2 for the two 2-yearl long survey periods, respectively) calculated from records of seven surveys between March 2013 and November 2015 by the stimulated calling method (Giannatos et al. 2005). Jackal groups and individuals (when a call response from a single jackal occurred) were treated separately. The mean (± *SE*) annual hunting bag density of the jackal was 0.19 ± 0.04 individuals/km^2, while that of the red fox was 0.11 ± 0.01 individuals/km^2. In Hungary, unlimited hunting is allowed for both jackal and fox. There are no grey wolves (*Canis lupus*) in the area.

c) Sample analysis

We investigated the feeding habits of jackals by analysing stomach contents from samples provided through legal hunting with sample sizes of n = 62 and 138 in the first and second survey intervals, respectively. We measured the full body mass of jackals to within 0.1 kg, then stomach samples of jackals were removed and stored at -18 °C prior to analysis.

After weighing the stomach content separately for each food type, food items were analysed both macroscopically and by microscope on the basis of hair, feather, skin, bone, dentition and chitin shell characteristics using standard procedures (Jędrzejewska and Jędrzejewski 1998). Occasionally, in cases of more advanced stages of digestion and when small food items were difficult to count and identify, 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 that could be identified in the stomachs. We determined the percentage composition of food items in the stomach samples on the basis of RFO, FO and W. The following 16 major food types (supplemented by three categories used by Lanszki et al. (2015) were used in the comparative analysis of diet compositions: 1 – viscera and 'other carrion' of wild ungulates (i.e. all remains left by hunters including internal organs with the contents of the digestive system, skin remains, ends of cervid legs and heads 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 – adult wild boar, 3 – juvenile wild boar (piglets and young wild boar, based e.g. on hooves, bones and hair characteristics), 4 – adult deer (red deer or fallow deer), 5 – juvenile deer, 6 – adult roe deer, 7 – carnivores (wild), 8 – small mammals, 9 – European brown hare, 10 – domestic animals, 11 – birds (wild), 12 – reptiles and amphibians, 13 – fish, 14 – invertebrates, 15 – plants (from direct consumption), 16 – inorganic materials. The occurrence of viscera and 'other carrion' in stomachs indicated human hunting or poaching, and these subcategories were taken together, as it is often difficult to distinguish between them. Fly larvae or pupa in the stomach content indicated feeding on carrion, but jackals might have been feeding on injured or dead ungulates overnight (Lanszki et al. 2006), and, in these cases, larvae could not be found. Adult wild boar and adult cervids were separated from the viscera and 'other carrion' category, because contrary to the first category, predation could not be excluded in these cases, although, in the case of healthy individuals, there is a low probability of this (Lanszki et al. 2015). In these cases, predation and scavenging are also possible. As with sheep, no cow or poultry losses reported were attributed to jackals, therefore consumption of these domestic animals mostly means scavenging.

We categorised the jackals examined according to sex and season, i.e., 1 – December-April (winter and early spring, mating and gestation period of jackals, and gestation period of cervids), 2 – May-July (spring end and early summer; pupping of jackals, calving of cervids and early parental care period), 3 – August-November (teaching young jackals for hunting, and intensive trophy hunting of cervids) (Demeter and Spassov 1993, Reinken 1987).

d) Data analysis

Analysis of covariance (ANCOVA, GLM procedure, SPSS 11.5) was used to compare the estimated total mass of detected mortality from human hunting and other mortality causes (as dependent variable; kg/km^2) found during the two 2-yearl long survey period (as fixed factors) depending on season (as covariate; three seasons). Three-way ANOVA (with Bonferroni post hoc test) was applied in the adult age group category of jackals to examine body mass (after logarithmic transformation of the data) differences between the survey periods, seasons and sexes.

The chi-square (χ^2) test was used for distribution analysis of the empty and non-empty stomachs between the two-survey periods. For non-empty stomachs, we assessed the effects of food subsidy manipulation (survey period), season and sex after logarithmic transformation of the data for stomach content weight with ANCOVA (with body mass as covariate).

Because, relationships between basic data of the three calculation methods (RFO, FO and W) were significant according to the 16 main food taxa (Spearman's rank correlation, four years, n = 96, RFO–FO: $r_S = 0.992$, $P < 0.001$, RFO–W: $r_S = 0.891$, $P < 0.001$ and FO–W: $r_S = 0.902$, $P < 0.001$), subsequent statistical analyses were performed mainly on FO and W values. General log-linear analysis was used on FO data to test for dietary differences between survey periods, seasons and sexes. The unit of analysis was jackal stomach and the response variables were the presence/absence of the food items considered. The model was fitted using survey period, season and sex as categories. Owing to the large number of comparisons (16 food categories), we adjusted the level of significance to 0.0031 with a Bonferroni correction. MANCOVA was applied to test differences in quantitative composition of the diet (arcsin transformed %W values as dependent variables, survey period and season as fixed factors and sex as a covariate). 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.

Trophic niche breadth from RFO data was calculated in accordance with standardized Levins index (B_A, rating from 0 to 1; Krebs 1989). The B_A values between the two survey periods (and taking into account the seasons) were compared with a paired samples t-test. The difference between the numbers of food items per stomach between survey occasions was compared with an independent samples t-test. A minimum probability level of $P < 0.05$ was accepted in all statistical tests, except log-linear analysis.

4.5. Predation experiment on artificial bird nests in a campus park

a) Study area

The study area is the campus park of Kaposvár University (46°23’N 17°49’E) is located on the area of 5 hectares. The campus is surrounded by agricultural lands, tree alleys and forest patches (**Appendix 1**). About 60% is covered by trees, 35% of the area is lawn, and the remaining 5% are sidewalks and parking area (Kovács-Hajdu et al. 2014). Most of the planted trees are native deciduous species or alien coniferous trees; however, there are also some invasive plant species (e.g. black locust). The grassland is mown regularly; therefore, mostly disturbance- and treading-tolerant species were included (Kovács-Hajdu et al. 2014).

b) Nest predation experiment

The survival chances of ground- and shrub-nesting bird species were tested in 2012 and 2014 with artificial nests and clutches. Ground nests were formed by creating a depression in the soil using our heel. The artificial bush nests were cup-shaped (15 cm in diameter and 5 cm deep) made from wire mesh, attached to the foliage using wires at a height of 1-2 m and lined with grass litter (Bayne and Hobson 1999). Both years we placed 21 ground nests and 21 shrub nests alternately, 20 m apart: hence nests of the same type were 40 m apart (**Appendix 10**). In total 42 nests were placed per year. Both year one quail egg and one plasticine egg of similar size were placed in each artificial nest. Both types of eggs were stored outdoors for 1-2 weeks prior to the test to eliminate unnatural odors (Bayne and Hobson 1999). The plasticine eggs were attached using green wires to the nearest plant on the ground or to the shrub nest to prevent the egg from being removed from the nest by the predator (Purger et al. 2004).

c) Data collection and analysis

In both years the study was started on 10th May (second clutch period for many bird species, Ludwig et al. 2012) and nest content was checked on the first (11th May), third (13th May), sixth (16th May) and thirteenth days (23th May) after placement, between 07.00 and 08.00 A.M. each time. During the last check, the remaining eggs and attaching materials were removed. Artificial nests were considered to be predated if the quail egg had disappeared or had been damaged in some way (Bayne and Hobson 1999). In these cases, egg wasn't replaced and we collected the nest. Nest predators were identified from the tooth or beak marks left by them on the plasticine eggs (Niehaus et al. 2003).

Daily survival rates (DSR) of quail eggs were calculated with the Mayfield method (Mayfield 1975) and compared using the test proposed by Johnson (1979).

$$\mathrm{DSR} = \frac{\text{total number of damaged quial or plasticine eggs or nests}}{\text{number of observed days (when the egg or the nest was intact)}}$$

For comparison, the freeware "J-test" developed by K. Halupka (http://zeb.uni.wroc.pl/halupka/) was used. For the predation events of plasticine eggs, Chi-square test with Yates correction for continuity was applied (Zar 1999). A minimum probability level of $P < 0.05$ was accepted for all the statistics.

5. RESULTS AND DISCUSSION

5.1. Long-term changes in the diet of the red fox in an agricultural area

Red fox diet

Based on the analysis from the 12 main food types, there were significant differences in diet composition of foxes between the first survey (1992–1997) and the second survey (2012–2014) for both RFO and FO data (two-way PERMANOVA; RFO, $F_1 = 2.08$, $P = 0.0022$; FO, $F_1 = 1.99$, $P = 0.0027$). There were also significant differences in the diet of the fox among seasons (RFO, $F_3 = 1.09$, $P = 0.0095$; FO, $F_3 = 1.01$, $P = 0.0159$). The survey × season interaction was not significant (RFO, $F_3 = 2.15$, $P = 0.5920$; FO, $F_3 = 2.21$, $P = 0.7276$). The four most important food types of the fox, i.e., small mammals, plants, invertebrates, and wild boar, together comprised > 70% of the difference between diet composition from the two surveys (SIMPER, contribution, RFO, 23.8%, 22.7%, 15.4%, and 9.9%, respectively; FO, 23.2%, 23.2%, 15.2%, and 9.3%, respectively).

In both surveys, small mammals (mainly *Microtus* voles and *Apodemus* mice) were the primary food type for the fox in the scat samples (**Table 3, Appendix 6**). Small mammals were consumed more frequently in the first survey (seasonal value ranged between 15.8% and 55.4%) compared to the second one (range: 14.1–37.1%), most frequently in winter and least in summer (**Fig. 4**). Plants (mainly fruits), the second most important food of the fox, were consumed most frequently in summer and autumn, but, in the second survey, these were frequently eaten throughout the year. Foxes consumed invertebrates (mainly beetles), the third most important food types, more frequently in the second survey, and mostly in spring and summer.

Table 3. Diet composition of the red fox (*Vulpes vulpes*) in the first and second survey periods (17 seasons in 1992–1997 and six seasons in 2012–2014; Fonó, SW Hungary)

Food types	Survey period							
	First		Second		First		Second	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Relative frequency of occurrence (%)				Frequency of occurrence (%)			
Small mammals	39.2	12.0	26.8	8.8	75.4	15.8	53.4	16.9
European brown hare	1.3	2.8	0.4	0.9	2.7	6.1	0.8	2.0
Wild boar	0.9	1.9	7.5	7.4	1.7	3.7	13.5	15.8
Cervids	6.2	8.1	4.7	2.4	11.8	15.2	10.3	5.8
Domestic animals	8.5	6.3	5.1	2.6	15.6	12.1	10.3	4.0
Carnivores	2.8	3.8	0.4	0.7	5.6	7.4	1.0	1.6
Pheasant	2.5	4.3	1.6	2.3	4.6	7.7	3.1	4.1
Other birds	6.0	3.8	6.3	2.7	11.5	10.3	11.5	4.1
Other vertebrates	1.7	3.3	5.2	4.9	3.2	5.9	10.6	10.2
Invertebrates	11.0	13.2	15.0	10.2	21.2	26.6	30.9	22.3
Plants	19.0	11.9	26.7	13.1	31.8	21.9	50.2	28.8
Inorganic materials	1.0	1.5	0.2	0.4	2.5	5.0	0.5	0.8

Depending on season (**Fig. 4**) foxes supplemented their diet in the first survey mainly with domestic animals and cervids (carcasses; mainly in winter), other birds (mainly in spring and summer), while in the second survey mainly with wild boar (including piglets; mainly in winter and spring) and other birds (mainly in winter and spring). Other food types, such as brown hare, pheasant, mustelids, other vertebrates, and inorganic materials (piece of plastic) were consumed occasionally (**Fig. 4, Appendix 4**).

Based on the calculation from the 12 main food types, the standardised trophic niche breadth (B_A) had narrower mean value in the first than in the second survey (mean ± *SD*, 0.25 ± 0.07 and 0.34 ± 0.09, respectively, independent samples t-test, $t_{21} = 2.33$, $P = 0.030$). Fox scat samples contained 42 and 31 different animal taxa over the two periods and the number of plant taxa was constant at 12.

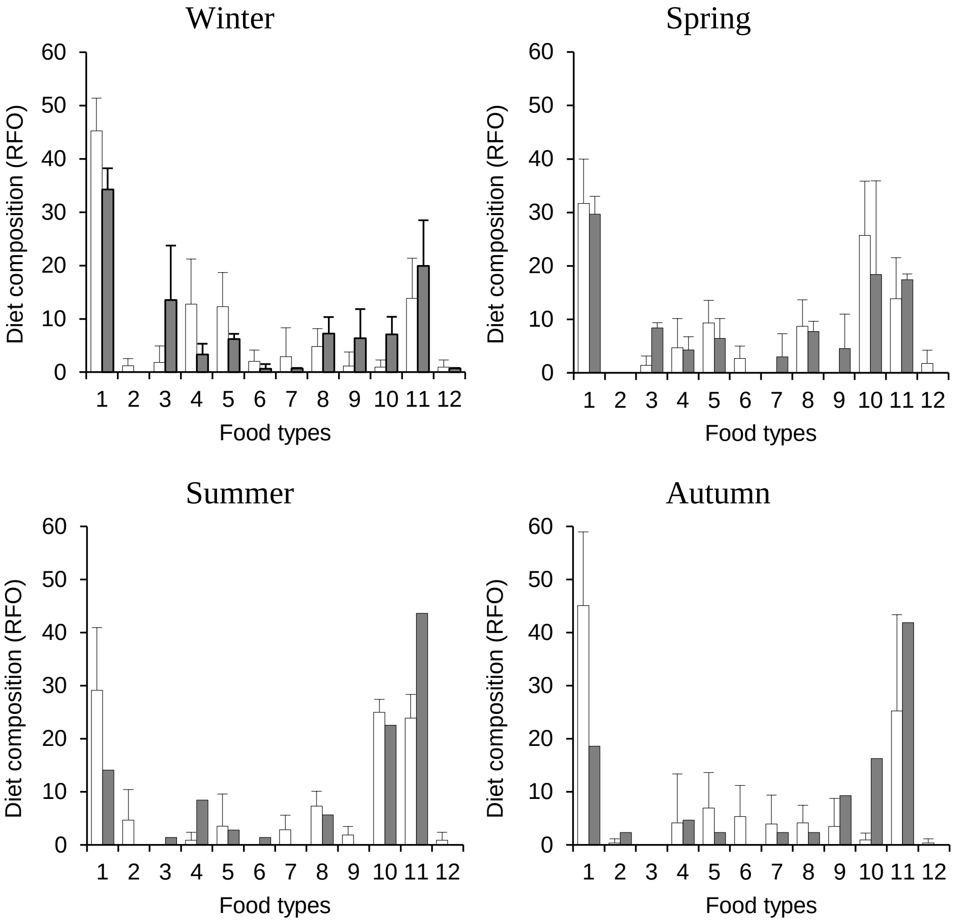

Fig. 4. Seasonal diet composition of the red fox (*Vulpes vulpes*) during the first (1991–1997, white columns) and the second (2012–2014, grey columns) survey periods (Fonó, SW Hungary).

1 – small mammals (insectivores and rodents), 2 – European brown hare, 3 – wild boar, 4 – cervids, 5 – domestic animals, 6 – carnivores, 7 – pheasant, 8 – other birds and eggs, 9 – reptiles, amphibians, and fish, 10 – invertebrates, 11 – plants (fruits, seeds, and other plant matter), and 12 – inorganic materials. RFO – Percentage relative frequency of occurrence data; mean ± *SD*.

During the two decades the proportion of cultivated areas has increased and the coverage of near natural habitat types have decreased (**Appendix 2**). The period-dependent difference between the distribution of habitat types was significant (Chi-square test, $\chi^2_6 = 14.74$, $P = 0.022$). The fox population density (individuals / km^2) did not differ significantly between the two survey periods (**Appendix 2**, independent samples *t*-test, $t_{10} = 1.78$, $P = 0.102$). In terms of major game species, hunting bag density of wild boar was higher (independent samples *t*-test, $t_4 = 9.30$, $P = 0.001$), while density of pheasant ($t_4 = 3.33$, $P = 0.029$) and mallard (*Anas platyrhynchos*, $t_4 = 2.79$, $P = 0.049$) were lower during the second survey period compared with the first one (**Appendix 3**).

Discussion

The diet composition and trophic niche breadth of red foxes in the study area have changed over the two decades. This is expressed mainly in the case of four main food types of the fox, i.e., in decreasing small mammal consumption and increasing plant, invertebrate and wild boar consumption, and in widening trophic niche. However, the diet varied as well seasonally, which confirms the flexibility of the fox feeding habits and adaptation to a changing environment.

The dietary pattern of the fox in the first survey (Lanszki et al. 1999) showed more similarities to results of central European areas, where in addition to the primarily important small mammals, consumption of other food types (i.e., lagomorphs, birds, domestic animals, insects, or plants) was also considerable throughout the year (e.g. Goszczyński 1986, Jędrzejewska and Jędrzejewski 1998, Soe et al. 2017). In the second survey, the dietary pattern of the fox is more similar to experiences in southern areas of Europe (Díaz-Ruiz et al. 2013, Soe et al. 2017). There the importance of small mammals is often only secondary to plants (especially fruits) and arthropods, which are available in large quantities throughout the year. Both dietary patterns differed greatly from experiences in the northern areas of Europe, where the fox diet is dominated by small mammals throughout the year, birds (mainly Tetraoninae), and lagomorphs, as alternative food types were temporarily important (Lindström and Hörnfeldt 1994, Soe et al. 2017).

The decrease in the consumption of small mammals in the second survey is presumably (Kleijn et al. 2009) related to decreasing habitat diversity and the intensification of agricultural production (**Appendix 2**). According to the first survey, the consumption of small mammals in our study area (annual mean, RFO: 39.2%) was similarly frequent as in other, less intensively cultivated areas in SW Hungary (Kétújfalu, 49.2%: Lanszki et al. 2006; Vajszló, 41.9%: Lanszki et al. 2016). In the second survey, consumption of suboptimal foods (plants, small-sized invertebrates) compared to mammalian prey (with high protein level) became more frequent. Temporary food switching of the fox from small mammals to plant consumption under limited food sources are known in other agricultural areas of SW Hungary (Lanszki et al. 2006). Fleshy fruits with high levels of carbohydrate and vitamins, but low protein contents (Jordano 2000); almost all year round, they are available in gardens, abandoned orchards, and in the wild. Most of the fibrous plant debris (finely chopped plant parts) found might originate from the stomach or rumen content of big game, mainly as a result of eating viscera (Hartová-Nentvichová et al. 2010, Lanszki et al. 2015), which indicates increasing importance of wild ungulates as foods.

More frequent wild boar consumption in the second survey most likely relates to the increase in the wild boar population in the area (**Appendix 3**), which has also been experienced for decades on a nationwide scale (Csányi et al. 2014) and elsewhere in Europe (Massei et al. 2015). We also detected piglet and young wild boar consumption; their consumption frequency increased especially at the end of winter and in spring. Adult wild boars, due to their tusks and active defence, are difficult to prey upon even for wolves (Jędrzejewska and Jędrzejewski 1998). Piglet and young wild boar consumption relate more to carrion eating (e.g. mortality caused by cold weather) than active predation (Cagnacci et al. 2003, Prigioni et al. 2008), but the occurrence of predation could not be excluded. The frequent consumption of wild boar found in the study area was uncommon in studies performed in other areas of Hungary (2.2–3.7%), even with the presence of golden jackal, because this consumption pattern is more typical of the bigger body sized competitor, the jackal (Lanszki et al. 2006, 2015, 2016). The consumption of cervids (probably eating viscera or carrion; Lanszki et al. 2015) was subordinate; when comparing the second survey to the first, its role declined in winter and increased in summer, with an overall slight decrease in consumption. Although the removal of carcasses (ecosystem services of scavengers) may be important (Cagnacci et al. 2003, Raichev et al. 2013, Lanszki et al. 2015, Ćirović et al. 2016). In Estonia Süld et al. (2014) found that when medium-sized carnivores gather to wild boar feeding sites or wild boar carcasses, diseases and parasites spread among the carnivores. These could be topics of future studies.

Among the less importance food types, in the second survey, compared to the first one, the fox consumed less frequently brown hare, pheasants, domestic animals, and carnivores, but consumed other vertebrates more frequently. In the first survey hare was consumed more frequently in summer (reproduction period), while in the second survey it was more eaten in autumn (official hunting season). Pheasant occurred in the samples more often throughout the year (except spring) during the first survey, however, in the second survey its consumption was frequent only in spring (reproduction period) and autumn (official hunting season). The consumption frequency of other birds did not change, but there was a slight shift between the two surveys, from the more frequent spring-summer consumption (nesting period) to the more frequent winter-spring consumption. Hunting bag of small game species declined (e.g. pheasant) or stagnated (brown hare) (**Appendix 3**). This indicates the potential impact on terrestrial prey species

(Panek 2013, Massei et al. 2015), to which habitat transformation and other factors may have contributed. The fox in agricultural areas of SW Hungary, where it coexists with the jackal (Lanszki et al. 2006, 2016), has eaten hare more often (0.7–1.3%) and birds with similar frequency (4.3–8.3%), as compared to our study area. For the fox, fish were available mainly in autumn and winter in fishponds, while access to domestic animals (carcasses, offal) near the village was continuous. The dietary patterns of urban foxes differed greatly from our findings, with anthropogenic foods (household waste, pet food) more important to them (Doncaster et al. 1990).

5.2. Diet composition of the golden jackal and the sympatric red fox in an agricultural area

Golden jackal diet

Small mammals were dominant in the diet of the golden jackal (annual mean, RFO: 65.1 %, BC: 72.0 %, **Table 4**). Proportion of small mammal consumption ranged between 28.6 % and 79.7 % (RFO) or 36.1 % and 95.8 % (BC) among seasons and years (**Fig. 6**) 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 (*Myodes glareolus*) and European water vole (*Arvicola amphibius*). Carnivores (Eurasian badger *Meles meles*, domestic cat) occurred rarely in the diet; European brown hare (*Lepus europaeus*) was eaten in small amounts. Wild ungulates were the second most important (BC) or third food type (RFO, **Table 4**). 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. 6**). The presence of cervids in the samples was low. Other vertebrates, such as birds, lizards, snakes, frogs, and invertebrates (mainly beetles) were consumed in low proportions. Depending on season jackals supplemented their diet mainly with wild fruits and corn. Inorganic materials occurred very rarely (plastic, rag, gravel, paper in 1-1 case) in the analysed samples.

Table 4. Seasonal and annual relative frequency of occurrence and biomass percentage of food items in scats of golden jackals (*Canis aureus*) in Vajszló, Hungary.

Food items	Spring		Summer		Autumn		Winter		Annual	
	RFO	BC	RFO	BC	RFO	BC	RFO	BC	RFO	BC
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 sp.)	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 (*Phaseanus 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

Scat samples collected between July 2010 and May 2013, RFO – relative frequency of occurrence, BC – percentage of consumed biomass, + – biomass under 0.05 %, B_A – standardized trophic niche breadth value.

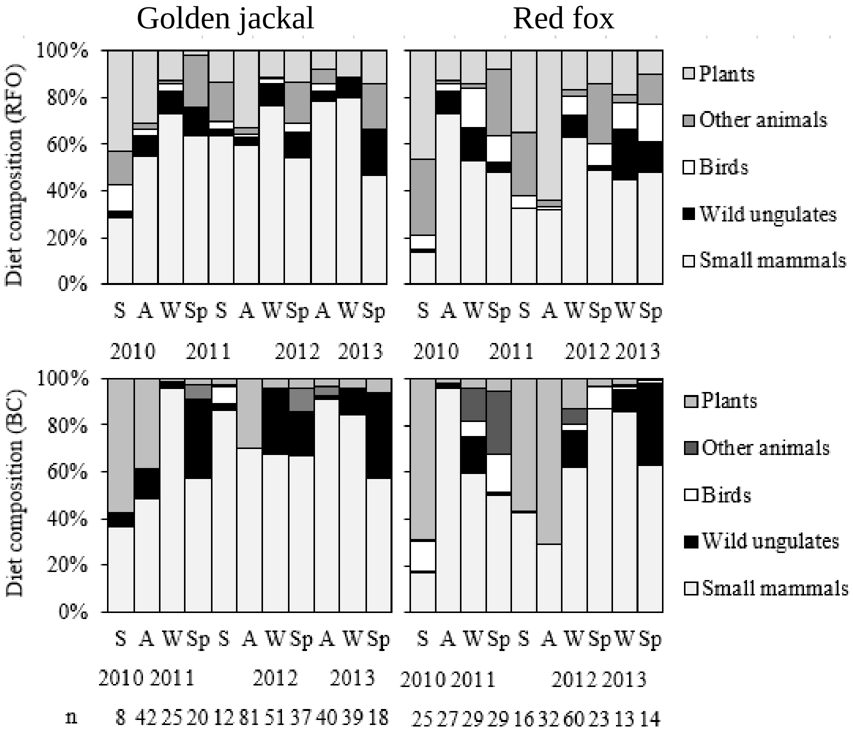

Fig. 4. Seasonal diet composition changes of golden jackals (*Canis aureus*) and red foxes (*Vulpes vulpes*) in Vajszló (Hungary).

n – the number of scats analysed, W – winter, Sp – spring, S – summer, A – autumn.

RFO – relative frequency of occurrence, BC – percentage of biomass consumed.

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 5**), while season × year interactions were significant in all food types.

No significant differences were found in consumption ratios depending on season (MANOVA, $F_3 = 0.30$, $P = 0.825$), year ($F_2 = 0.20$, $P = 0.817$) or these interactions ($F_5 = 0.32$, $P = 0.901$). In the jackal diet, the role of small mammals was determinant in all seasons, their consumption increasing from spring RFO: 55.1 %, BC: 61.9 %) or summer RFO: 44.6 %, BC: 63.0 %) to winter RFO: 77.2 %, BC: 78.2 %). The ungulates and the plants switched places with each other in the diet along this interval. The jackal consumed ungulates in spring and winter, while plants in summer and autumn in higher proportions.

Table 5. Results of log-linear models for the frequencies of occurrence of food types in the scats of golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) during three years (2010-2013) in the four different seasons in Vajszló, Hungary, for the effect of years, seasons, and their interaction.

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, amphibians and fish	Year	2	1.29	0.5249	0.88	0.6438
	Season	3	11.77	0.0082	6.04	0.1098
	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**

P values (with Bonferroni corrections) in boldfaced type are significant. In case of pheasant (for fox) and wild carnivores there were not enough data to perform the calculation.

Red fox diet

Small mammals were also the primary food type of the red fox (annual mean, RFO: 41.9 %, BC: 50.3 %, **Table 6**) in the scat samples. Their consumption fluctuated between 13.4 % and 73.0 % RFO) or 16.9 % and 87.1 % (BC) among seasons and years (**Fig. 6**). The 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. 6**). 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 6**). The consumption of plants showed great inter-year differences and varied over a wide range (**Fig. 6**). The third most important diet items of the fox were ungulates; the most important species was the wild boar (mainly piglets). The wild boar consumption largely fluctuated during the study period (**Fig. 6**), while cervids were eaten in small amounts. The bird (mainly medium-sized species) consumption was considerable in spring and summer (**Fig. 6**). Other vertebrates, such as carnivores, lizards, snakes, snake eggs, and invertebrates were consumed in small amounts. The analysed scat samples contained inorganic materials very rarely (pieces of plastic, gravel, textile and cigarette butts 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 5**), the difference among years were 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 (BC) 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 determinant (RFO: 48.4-57.3 %, BC: 63.1-64.9 %), and their consumption dropped in summer (RFO: 20.2 %, BC:

23.8 %) and autumn (BC: 32.8 %, RFO: 32.4 %), while consumption of plants increased (RFO: 42.3-57.4 %, BC: 65.7-66.8 %).

Table 6. Seasonal and annual relative frequency of occurrence and biomass percentage of food items in scats of red fox (*Vulpes vulpes*) in Vajszló, Hungary.

Food items	Spring		Summer		Autumn		Winter		Annual	
	RFO	BC	RFO	BC	RFO	BC	RFO	BC	RFO	BC
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 (*Phaseanus 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	

Scat samples collected between July 2010 and May 2013, RFO – relative frequency of occurrence, BC – percentage of consumed biomass, + – biomass under 0.05 %, BA – standardized trophic niche breadth value.

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; $\chi^2_1 = 9.52$, $P = 0.0020$) or summarized data of birds (all birds, including pheasant; $\chi^2_1 = 8.17$, $P = 0.0043$). Compared with jackal, the fox consumed more frequently birds. Main effects of season were significant in the consumption of small mammals ($\chi^2_3 = 18.28$, $P = 0.0004$) and summarized data of reptiles and amphibians ($\chi^2_3 = 16.67$, $P = 0.0008$), and main effect of year was significant only in the consumption of wild boar ($\chi^2_2 = 12.53$, $P = 0.0019$), interactions were not significant. Compared with jackal, the fox consumed significantly higher proportions (BC) 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. taxonomic species or higher classification), as well as 13-13 plant taxa, respectively. The standardized trophic niche (B_A, **Table 4** and **6**) of both predators was equally very 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 (**Appendix 5**). Significant interspecific differences were found (**Appendix 5**) in consumption of 301-1000 g prey category (for RFO 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 of arboreal species than fox.

Area specific differences in diet compositions

On the basis of Euclidean distances (E_d) from the hierarchical cluster analysis (**Fig. 7**), the mean dissimilarity among overall diet compositions of jackal and fox from different studies from Hungary was 32.9 (RFO data) and 41.1 (BC data).

Mean E_d among all group pairs ranged between 9.9 and 58.1 (RFO data) or between 13.2 and 80.5 (BC data). Independently of variable (RFO or BC) jackal and fox from Vajszló and Kétújfalu, as they mainly consumed small mammals (**Fig. 7**) 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 food, so they fell into the third cluster for BC data, while foxes, due to frequent bird consumption fell into a separated group for RFO 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, because 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. That means, ungulates were one of the important food types, but only in a specific part of the year. Larger jackal consumed more ungulates than smaller fox.

The seasonal and inter-year variation of the diet composition was high in this study like in the Balkans (Radović and Kovačić 2010, Markov and Lanszki 2012, Bošković et al. 2013, Penezić and 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).

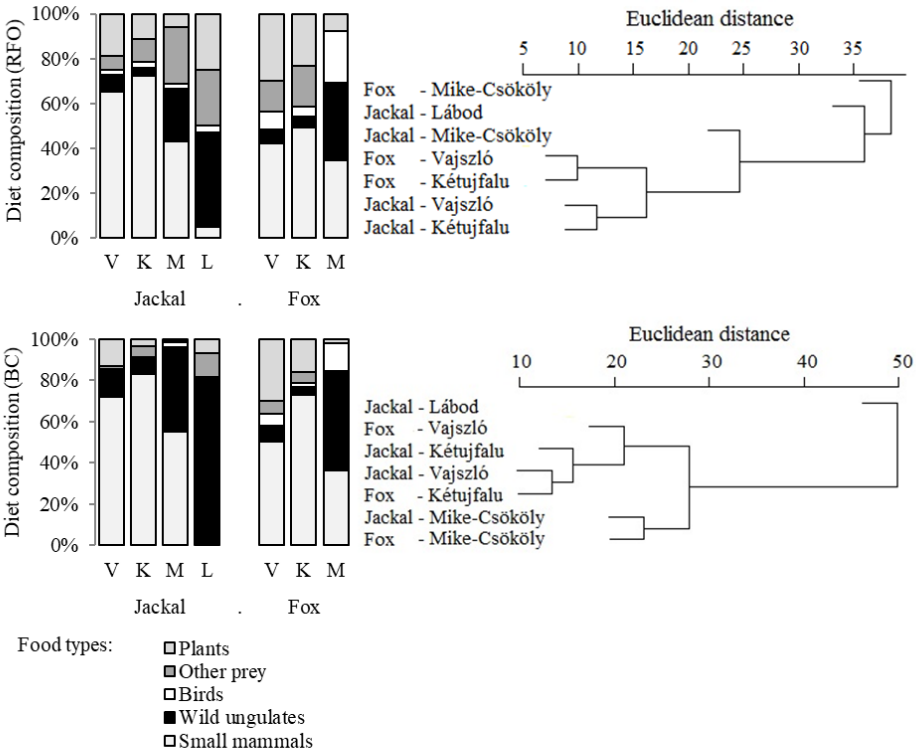

Fig. 7. Distribution of food types in the diet and similarity dendrogram of the Euclidean distances among general diet compositions of golden jackal and red fox from different areas of Hungary.

V – Vajszló (present study), L – Lábod (present study), K – Kétújfalu (Lanszki et al. 2006), M - Mike-Csököly (Lanszki and Heltai 2002). RFO – relative frequency of occurrence, BC – percentage of consumed biomass. For details see methods.

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 diet 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 and Sequeira 1978, Goszczyński 1986, Lanszki et al. 1999, Goldyn et al. 2003), seasonal and inter-year differences in fox diets were found to be larger.

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 (RFO) calculation. Small mammal dominated diet is known mainly from agricultural areas where both the jackal (Khan and Beg 1986, Lanszki et al. 2006, Jaeger et al. 2007) and the fox occur (Englund 1965, Jensen and Sequeira 1978, Lanszki et al. 1999), however exceptions in the case of the fox 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 and Spassov 1993, Radović and Kovačić 2010, Bošković et al. 2013) and in intensively managed big game areas (Lanszki et al. 2015), or according to 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 consumption of cervids was occasional. In studies where, considerable ungulate consumption was found, golden jackal (Aiyadurai and Jhala 2006) or similar, medium-sized *Canis* species (Moehlman 1987), consumed prey remains of larger predators or ate carrion, which were usually remains left from official hunting or poaching (Lanszki and Heltai 2002, Radović and Kovačić 2010, Bošković et al. 2013, Lanszki et al. 2015, Penezić and 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 in open grass lands.

Regarding golden jackal, in addition to solitary hunting and scavenging (Macdonald 1983, Demeter and Spassov 1993), co-operative hunting probably also occurred on wild boar piglets or wounded ungulates. Due to limitations of the applied methodology (Reynolds and 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 and Traviani 2000, Baltrūnaitė 2002, Lanszki and 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, that was lower than others experienced in warmer climate areas (Mukherjee et al. 2004, Aiyadurai and 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 that also can indicate competitive disadvantages, as in the case of the sympatric fox and jackal have been 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 and Spassov 1993, Lanszki et al. 2009, red fox: Lever 1959, Kolb and Hewson 1980, Goldyn et al. 2003, Lanszki et al. 2007). The bird consumption of the fox was substantially higher during nesting period. The differences found in bird consumption also indicate interspecific separation between the species.

Consumption of other food items was occasional. No predation on livestock, only consumption of domestic cat and dog were detected from 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 1979, Yom-Tov et al. 1995, Lanszki et al. 2009, Giannatos et al. 2010, Lanszki et al. 2010, Radović and Kovačić 2010, Bošković et al. 2013, Penezić and Ćirović 2015), but in these cases the carrion eating was dominant, as in the case of the fox in other studies (Englund 1965, Jensen and 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, arthropods 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, much like generalist species, e.g. the badger (Kruuk 1989, Jędrzejewska and Jędrzejewski 1998), the diet of both canids was diverse, and feeding habits were flexible (Macdonald 1979, Demeter and Spassov 1993, de Marinis and 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 and 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 resources 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). Although, 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 jackal and red fox 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 and 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).

5.3. Feeding responses of the golden jackal after reduction of anthropogenic food subsidies

Quantity of big game viscera and available carrion

The total field-dressed mass of harvested big game was 271.6 kg year/km^2 in the first survey period and 198.6 kg year/km^2 in the second one. According to hunting bag data, wild boar was the most harvested species (47.3% and 44.2%, respectively) in both survey periods, followed by red deer (30.8% and 23.0%) and fallow deer (21.6% and 32.5%), while the proportion of roe deer was low (0.3% in both periods). The quantity of viscera (total weight of viscera: 67.9 kg year/km^2 and 49.6 kg year/km^2, respectively in the two-surveys) showed a characteristic pattern, influenced by the hunting seasons (**Fig. 8**).

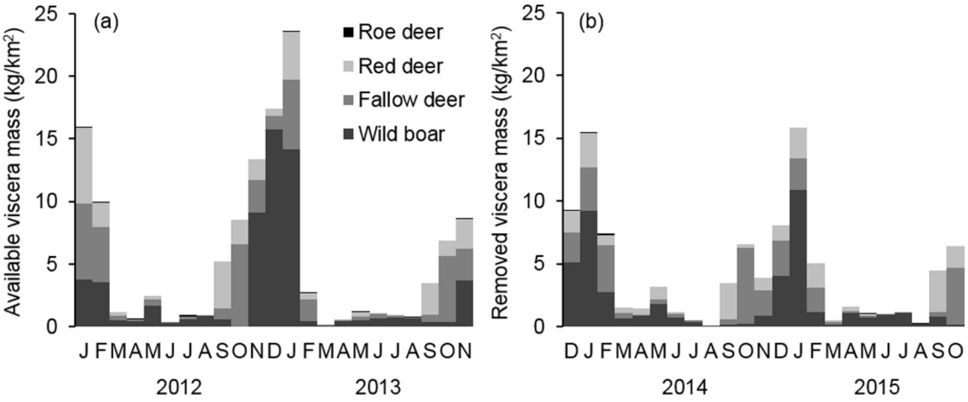

Fig. 8. Estimated quantity of big game viscera in the study area presented by months. Left figure (a) shows available big game viscera mass for jackals in the first period, while right figure (b) shows removed viscera mass (non-available for jackals) in the second period. For calculation, see methodology.

Most of the viscera arose between September and February in the first period, but this was absent in the second survey due to our experimental removal from the available food supply. Nonetheless, big game carrions from other detected mortality causes still provide a substantial food resource for jackals in both survey periods (**Fig. 9**). The proportion of these carrions (from other detected mortality) in the total sample (n = 1903 and 1408 harvested big game) for each survey occasion was 4.3% and 8.4%, respectively. The estimated total mass of dead big game from other mortalities than hunting did not differ significantly between the first and second survey (16.8 kg year/km^2 *vs.* 16.2 kg year/km^2, ANCOVA, $F_{1,9} = 0.005$, $P = 0.943$) and among seasons ($F_{1,9} = 0.235$, $P = 0.639$).

Fig. 9. Number of detected dead big game (mortality resulting from wounding and other non-hunting related mortality) in the study area presented by months.

Body mass

The body mass of adult jackals did not differ between the surveys (3-way ANOVA, $F_{1,152} = 0.429$, $P = 0.513$), but differed depending on sex ($F_{1,152} = 23.208$, $P < 0.001$) and season ($F_{2,152} = 5.348$, $P = 0.006$). Mean (± *SE*) body mass of males was 11.10 ± 0.17 kg (min. 8.2 kg, max. 14.8 kg, n = 80), and that of females 9.44 ± 0.11 kg, (min. 6.9 kg, max. 12.9 kg, n = 84). Jackals were heavier between December and April (10.68 ± 0.17 kg) than between

May and July (9.87 ± 0.22 kg) or August and November (9.94 ± 0.21 kg). The survey period × sex interaction was significant ($F_{1,152} = 4.705$, $P = 0.032$); males were heavier (10.84 ± 0.29 kg *vs*. 11.23 ± 0.20 kg) and females lighter (9.59 ± 0.11 kg *vs*. 9.38 ± 0.15 kg) in the second survey than the first.

Feeding responses

The proportion of empty stomachs (9.7% *vs*. 13.0%) did not differ significantly between the two surveys (Chi-square test, $\chi^2_1 = 0.459$, $P = 0.498$). The mean (± *SE*) weight of food in the jackal stomachs examined (n = 62 and 138) was 137.3 ± 29.2 g and 129.1 ± 16.7 g (excluding empty stomachs: 152.0 ± 31.7 g and 147.8 ± 18.5 g) in the two surveys, respectively. The highest stomach content weight values were 1559.9 g (15% of jackal body mass; first survey period, September) and 1589.6 g (12.5% of the jackal's body mass; second survey period, March). The weight of different food items in jackal stomachs was not significantly different between surveys (ANCOVA, $F_{1,163} = 0.074$, $P = 0.786$), season ($F_{2,163} = 0.092$, $P = 0.912$) or sex ($F_{1,163} = 0.431$, $P = 0.512$). The survey occasion × season interaction was significant for the December-April period ($F_{2,163} = 5.164$, $P = 0.007$) as jackals had lower stomach content weights during the second survey compared to the first.

In the first survey period, when food subsidies were present, the primary food of jackals was viscera and carrion (55% of the diet; **Table 7**). Adult wild boar was the second most important dietary component and cervids the third. In the second survey period, with viscera removal, the primary animal food types of jackals were also viscera and other carrion of wild ungulates, which formed nearly one-third of the diet (**Table 7**).

Based on weight, adult cervids were the second most important and juvenile wild boars the third most important foods. Juvenile cervids (fallow deer fawns), small mammals, domestic animals (dog, poultry feather, tallow of ungulate) and plants (mainly fruits) were of similar importance (W: 6-8%); however, plants were the most frequently eaten foods (FO: 38.4%). Other food types were consumed occasionally or in small amounts (**Table 7**). Big game consumption did not increase significantly ($R^2 = 0.209$, $P = 0.158$) with the increase in the amounts of available viscera and carrion (**Fig. 10**).

Table 7. Annual stomach content of golden jackals (*Canis aureus*) in SW Hungary (Lábod region). First survey occasion: from January 2012 to November 2013; second survey occasion: from December 2013 to October 2015.

Food categories	First survey occasion (Food subsidies present)			Second survey occasion (Food subsidies removed)		
	RFO	FO	W	RFO	FO	W
Viscera and other carrion	28.0	45.2	55.0	13.8	30.4	28.9
Wild boar, *Sus scrofa*, adult	7.0	11.3	11.6	4.0	8.7	1.3
Wild boar, *Sus scrofa*, juvenile				1.7	3.6	11.8
Deer*, adult	4.0	6.5	5.5	7.6	16.7	18.5
Deer*, juvenile	1.0	1.6	2.0	1.3	2.9	6.2
Roe deer, *Capreolus capreolus,* adult	4.0	6.5	6.0	0.7	1.4	1.5
Badger, *Meles meles*	1.0	1.6	6.0	0.3	0.7	0.1
Small mammals	5.0	8.1	0.9	14.5	13.8	7.2
Brown hare, *Lepus europaeus*				0.7	1.4	0.3
Domestic animals	2.0	3.2	0.8	1.6	3.6	6.2
Birds	2.0	3.2	1.1	4.0	8.7	1.4
Reptiles and amphibians	1.0	1.6	0.1	0.7	1.4	0.1
Fish	5.0	8.1	2.1	3.6	8.0	4.2
Invertebrates	15.0	16.1	2.6	17.5	21.0	4.1
Plants	24.0	29.0	6.3	25.4	38.4	7.9
Others (inorganic materials)	1.0	1.6	0.3	2.6	5.8	0.3
Number of samples (n)	62			138		
Empty from this (-n)	6			18		
Number of food items (N)	100			303		
Total weight of food remains (g)			8514			17690

RFO – percentage relative frequency of occurrence, FO – percentage frequency of occurrence, W – percentage weight of individual food remains found in the samples. *Fallow deer (*Cervus dama*) or red deer (*Cervus elaphus*).

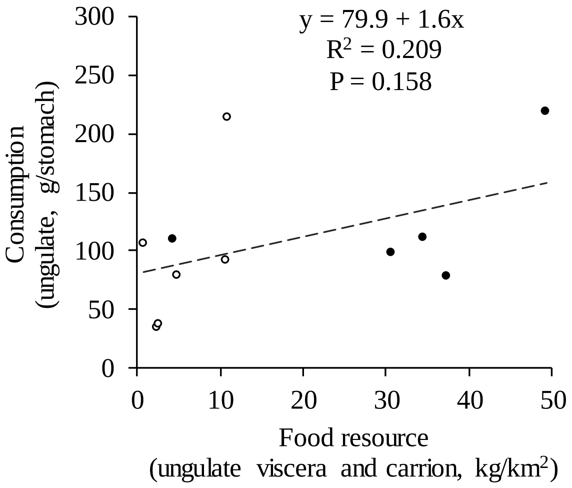

Fig. 10. Weak relationship between the estimated available biomass of viscera and carrion of ungulates, and the consumed mass of ungulates.

Resource estimation is based on the quantity of big game viscera in the study area (**Fig. 8**). Carrion estimation is based on the number of known dead big game (**Fig. 9**). Full circle – food subsidies present, empty circle – food subsidies removed (but carrions are available). The dashed line indicates a non-significant linear relationship.

In log-linear analysis the survey period was not a significant predictor of the consumption of any food types (**Table 8**). Compared to December-April, jackals consumed significantly more small mammals in May-July, and invertebrates and plants in May-November (**Fig. 11**). Compared to males, females consumed more plants (FO, 5.6% *vs.* 15.4%).

Table 8. Results of log-linear models for the frequencies of occurrence of food types in the stomachs of golden jackals in SW Hungary (Lábod region), for the effect of survey period (food subsidies present and food subsidies removed), seasons (December – April, May – July, August - November), sex and their interaction.

Item	Effect	df	χ^2	P
Viscera and other carrion	Survey	1	2.40	0.1215
	Season	2	0.64	0.7257
	Sex	1	1.49	0.2229
	Survey × season	2	6.21	0.0448
	Survey × sex	1	2.75	0.0975
	Season × sex	2	0.09	0.9543
Wild boar, adult	Survey	1	0.88	0.3472
	Season	2	3.34	0.1887
	Sex	1	2.75	0.0973
	Survey × season	2	2.54	0.2813
	Survey × sex	1	0.14	0.7097
	Season × sex	2	0.47	0.7906
Wild boar, juvenile	Survey	1	0.06	0.8089
	Season	2	1.16	0.5593
	Sex	1	0.23	0.6309
	Survey × season	2	1.14	0.5644
	Survey × sex	1	0.03	0.8699
	Season × sex	2	1.44	0.4880
Deer*, adult	Survey	1	3.37	0.0665
	Season	2	5.79	0.0552
	Sex	1	2.04	0.1530
	Survey × season	2	1.55	0.4617
	Survey × sex	1	1.24	0.2660
	Season × sex	2	5.13	0.0770
Deer*, juvenile	Survey	1	0.95	0.3303
	Season	2	7.28	0.0262
	Sex	1	0.18	0.6713
	Survey × season	2	0.16	0.9212
	Survey × sex	1	0.51	0.4756
	Season × sex	2	0.64	0.7275
Roe deer, adult	Survey	1	3.76	0.0526
	Season	2	5.66	0.0591
	Sex	1	1.45	0.2279
	Survey × season	2	0.52	0.7727
	Survey × sex	1	0.94	0.3324
	Season × sex	2	1.16	0.5609
Brown hare	Survey	1	0.38	0.5351
	Season	2	2.26	0.3224
	Sex	1	1.02	0.3128
	Survey × season	2	0.40	0.8197
	Survey × sex	1	0.33	0.5633
	Season × sex	2	0.38	0.8264
Domestic animals	Survey	1	0.30	0.5860
	Season	2	0.41	0.8153
	Sex	1	1.10	0.2932
	Survey × season	2	4.48	0.1067
	Survey × sex	1	0.01	0.9421
	Season × sex	2	0.95	0.6222
Birds	Survey	1	0.18	0.6705
	Season	2	3.00	0.2236
	Sex	1	1.18	0.2767
	Survey × season	2	0.61	0.7383
	Survey × sex	1	0.10	0.7546
	Season × sex	2	0.10	0.9535
Reptiles and amphibians	Survey	1	0.99	0.3186
	Season	2	1.59	0.4520
	Sex	1	0.00	0.9458
	Survey × season	2	0.19	0.9107
	Survey × sex	1	0.35	0.5563
	Season × sex	2	0.04	0.9805
Fish	Survey	1	0.05	0.8286
	Season	2	1.50	0.4716
	Sex	1	0.15	0.6984
	Survey × season	2	3.21	0.2008
	Survey × sex	1	0.00	0.9915
	Season × sex	2	0.12	0.9405
Invertebrates	Survey	1	5.56	0.0184
	Season	2	20.20	*0.0000*
	Sex	1	0.15	0.7021
	Survey × season	2	2.26	0.3224
	Survey × sex	1	0.03	0.8741
	Season × sex	2	5.04	0.0806

Continuation of Table 8

Item	Effect	df	χ^2	P	Item	Effect	df	χ^2	P
Carnivores	Survey n	1	1.31	0.2518	Plants	Survey	1	1.24	0.2653
	Season	2	0.28	0.8698		Season	2	24.79	*0.0000*
	Sex	1	0.34	0.5615		Sex	1	8.46	0.0036
	Survey × season	2	1.38	0.5018		Survey × season	2	2.95	0.2287
	Survey × sex	1	0.00	0.9605		Survey × sex	1	0.00	0.9644
	Season × sex	2	0.44	0.8023		Season × sex	2	1.38	0.5024
Small mammals	Survey	1	0.08	0.7754	Others	Survey	1	0.38	0.5385
	Season	2	12.60	*0.0018*		Season	2	1.81	0.4043
	Sex	1	2.52	0.1123		Sex	1	0.64	0.4251
	Survey × season	2	0.12	0.9406		Survey × season	2	3.54	0.1700
	Survey × sex	1	0.05	0.8265		Survey × sex	1	0.02	0.9007

*Fallow deer (*Cervus dama*) or red deer (*Cervus elaphus*). Survey – survey period. Numbers in italics indicate significant values (*P* < 0.0031, Bonferroni correction).

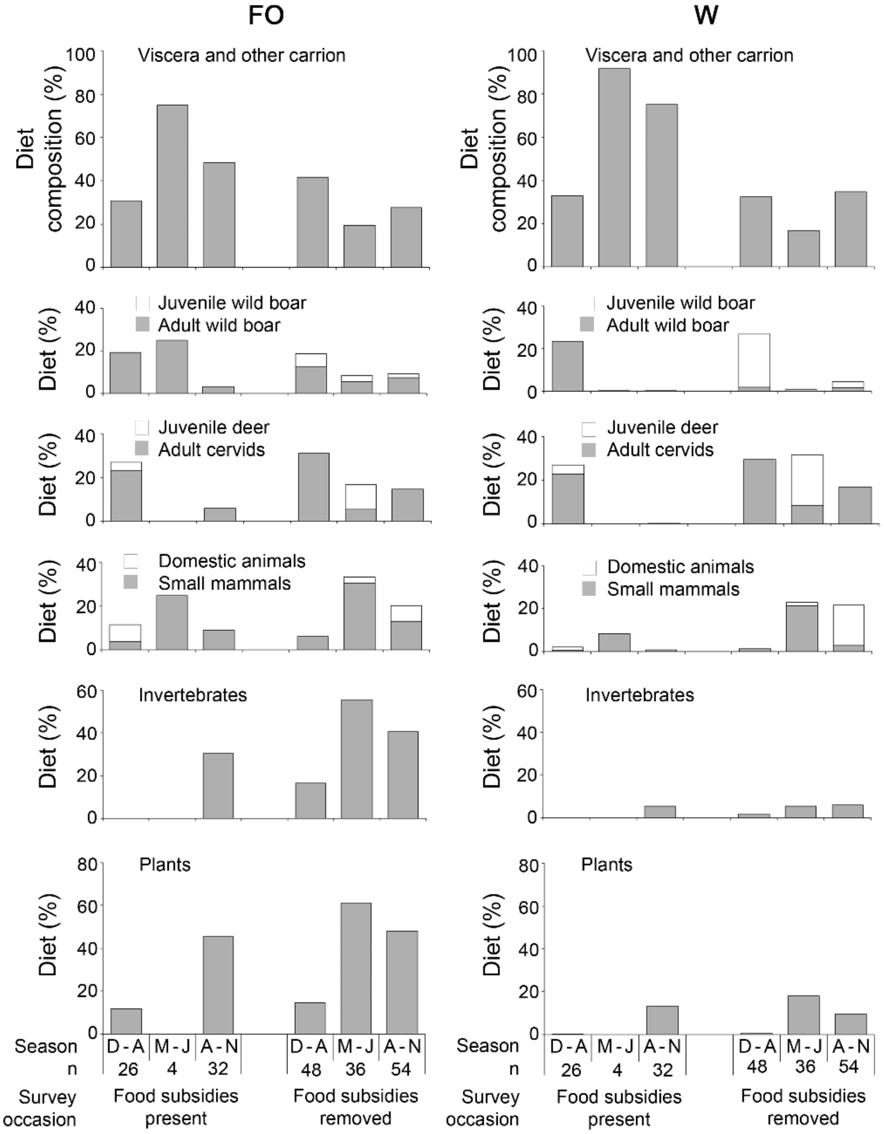

Fig. 11. Seasonal stomach content composition of golden jackal in Hungary (Lábod region) depending on survey period (food subsidies present and food subsidies removed).

FO – percentage frequency of occurrence, W – percentage weight of individual food remains found in the samples. n – number of samples.

In MANCOVA there was no significant difference in viscera and other carrion consumption either in the main effects (survey period, season, sex) or survey period × season interaction (**Table 9**). In the first survey, jackals consumed a higher proportion of adult wild boar (W: 11.6% *vs*. 1.3%), while during the second survey occasion, juvenile wild boars (0 *vs*. 11.8%), domestic animals (0.8% *vs*. 6.2%) and invertebrates (2.6% *vs*. 4.1%) were more eaten (**Fig. 11**). Compared to other seasons, in December-April jackals consumed adult wild boar while in a significantly higher proportion while in August-November they consumed more domestic animals, invertebrates and plants. The survey occasion × season interaction was significant in some cases (**Fig. 11**). Significantly more adult wild boar consumption occurred in the first survey period in December-April, while more domestic animal consumption occurred in the second survey occasion in August-November, and invertebrates were not detected during the first survey period in December-July (**Fig. 11**).

Trophic niche and number of food items

The standardized trophic niche did not significantly differ between survey occasions for either RFO data (B_A, mean ± *SE*, 0.25 ± 0.09 *vs*. 0.32 ± 0.05, paired samples t-test, $t_2 = 1.577$, $P = 0.256$) and W data (0.10 ± 0.08 *vs*. 0.26 ± 0.03, $t_2 = 1.492$, $P = 0.274$). Compared to the first survey, the stomachs in the second survey contained significantly more food items (mean ± *SE*, 1.79 ± 0.15 and 2.55 ± 0.15, independent samples t-test, $t_{174} = 3.119$, $P = 0.002$).

Table 9. Results of MANCOVA for the wet weight of food types in the stomachs of golden jackals in SW Hungary (Lábod region), for the effect of survey period (food subsidies present and food subsidies removed), seasons (December - April, May - July, August - November), sex and survey period × season interaction.

Effect	Food categories	df	F	P	Effect	Food categories	df	F	P
Survey occasion	Viscera and carrion	1	3.89	0.106	Sex	Viscera and carrion	1	0.12	0.747
	Wild boar, adult	1	99.56	*0.000*		Wild boar, adult	1	0.28	0.618
	Wild boar, juvenile	1	10.81	*0.022*		Wild boar, juvenile	1	0.00	0.962
	Deer*, adult	1	2.92	0.148		Deer*, adult	1	0.53	0.500
	Deer*, juvenile	1	0.19	0.680		Deer*, juvenile	1	0.19	0.680
	Roe deer, adult	1	0.35	0.579		Roe deer, adult	1	0.40	0.556
	Carnivores	1	0.97	0.371		Carnivores	1	1.05	0.353
	Small mammals	1	0.09	0.773		Small mammals	1	2.27	0.192
	Brown hare	1	2.50	0.175		Brown hare	1	2.50	0.175
	Domestic animals	1	11.27	*0.020*		Domestic animals	1	4.98	0.076
	Birds	1	3.77	0.110		Birds	1	1.54	0.270
	Reptiles, amphibians	1	0.03	0.868		Reptiles, amphibians	1	0.09	0.775
	Fish	1	1.17	0.328		Fish	1	1.74	0.244
	Invertebrates	1	38.19	*0.002*		Invertebrates	1	2.91	0.149
	Plants	1	0.71	0.438		Plants	1	7.70	*0.039*
	Others	1	1.29	0.308		Others	1	1.46	0.281
Season	Viscera and carrion	2	0.57	0.599	Survey occasion × season	Viscera and carrion	2	0.77	0.513
	Wild boar, adult	2	389.97	*0.000*		Wild boar, adult	2	308.12	*0.000*
	Wild boar, juvenile	2	2.40	0.186		Wild boar, juvenile	2	2.40	0.186
	Deer*, adult	2	0.80	0.501		Deer*, adult	2	0.00	0.998
	Deer*, juvenile	2	0.53	0.619		Deer*, juvenile	2	1.20	0.375
	Roe deer, adult	2	1.49	0.311		Roe deer, adult	2	0.35	0.719
	Carnivores	2	0.99	0.435		Carnivores	2	1.03	0.422
	Small mammals	2	3.27	0.124		Small mammals	2	0.00	0.997
	Brown hare	2	0.63	0.572		Brown hare	2	0.63	0.572
	Domestic animals	2	6.43	*0.042*		Domestic animals	2	12.16	*0.012*
	Birds	2	0.94	0.450		Birds	2	5.53	0.054
	Reptiles, amphibians	2	1.56	0.298		Reptiles, amphibians	2	0.08	0.928
	Fish	2	3.13	0.131		Fish	2	0.29	0.760
	Invertebrates	2	43.83	*0.001*		Invertebrates	2	14.11	*0.009*
	Plants	2	9.84	*0.018*		Plants	2	2.64	0.165
	Others	2	1.24	0.366		Others	2	1.49	0.311

*Fallow deer or red deer. Numbers in italics indicate significant values ($P < 0.05$).

Discussion

Changes in food sources resulting from big game management

The removal of viscera did not result in a statistically significant decrease in its consumption. Despite the lack of statistical significance, the difference was biologically considerable, their consumption was nearly halved (frequency of occurrence: 45% *vs*. 30%; wet weight: 55% *vs*. 29%, respectively). There could be several explanations for this. Firstly, the annual pattern of viscera and carrion left during intensive big game management is related to the characteristics of hunting practices, e.g. to legal hunting seasons (Bošković et al. 2013, Ćirović et al. 2016), and there are injured ungulates and carcasses from other mortality causes in this area. Although there were differences between surveys in viscera availability, these anthropogenic food subsidies are available in the highest quantities for scavengers (including the jackal) in autumn and winter (**Figs. 8** and **9**). In these otherwise critical periods, the scattered and easily available food with high energy values help animals to survive. For example, fat deposited in autumn can help overwintering medium-sized canids, e.g. foxes (Kolb and Hewson 1980) or coyotes (Poulle et al. 1995). During the winter, the amount of available food is relatively scarce (Lanszki et al. 2006, Bartoń and Zalewski 2007) without anthropogenic food subsidies (**Appendix 7**). With these, as in our study area, jackals were the heaviest in the December-April period, which is also the mating season of the jackal (Demeter and Spassov 1993), which is associated with more intense daily and territorial activity (Lanszki et al. 2015, Kapota et al. 2016, Lanszki et al. 2018) and therefore greater energy requirements. Although the amount of the big game viscera drastically declined in spring and summer (period of pupping or calving and early parental care), carcasses were still available in large numbers during this period (it was impossible to remove them all). So, in spring and summer the importance of viscera reduction is small.

Secondly, the professional hunters could not remove all viscera from the area. Outside the study area viscera was accessible and we cannot rule out that some of the 44 jackal groups we recorded in our study area (see Material and methods) might have immigrated from beyond the area where viscera were not removed. The extent of the study area (besides the relatively high jackal density) was enough big to reduce the occurrence of examining animals from outer areas. Poaching with snares and guns is common in the region (Faragó and László 2014, Lanszki et al. 2015). Besides large quantities of fresh deer meat, a piece of a leather glove (Lanszki et al. 2015) and a bullet from an illegally used gun were found within jackal stomachs, indicating presence of poaching. Therefore, wounded individuals and remains of ungulates still occurred in the area despite our efforts to remove them. In these cases, the cleaning role of jackals (Ćirović et al. 2016) is more decisive. Wounding (from hunting and poaching) and vehicle collisions leave big game carcasses throughout the year (Csányi et al. 2016), and some of these are not found (unregistered). Therefore, the amount of big game carrion is presumably underestimated in the area.

Thirdly, golden jackals are socially flexible and neighbouring groups are able to reduce their normal territorial antagonism and share locally abundant food sources (Macdonald 1979, Lanszki et al. 2006). The big game carcasses contribute to the increased need for food during the pup rearing period (Macdonald 1983, Moehlman 1987). There was no significant difference between survey periods in the quantity of registered carcasses.

Fourthly, a part of the consumed viscera may have been derived from carcasses. In intensive big game management areas, where ungulates are available from many sources, they are very important food resources for jackals (Raichev et al. 2013, Lanszki et al. 2015), alongside domestic animals and garbage (Giannatos et al. 2010, Borkowski et al. 2011). Throughout the year (not just during calving), jackals can find a large variety of big game species.

Changes in stomach content weight and body mass

Contrary to our first prediction, food removal did not significantly increase the proportion of empty stomachs and did not significantly reduce stomach weight. The low percentage (10-13%) of empty stomachs was similar (14-15%, Bošković et al. 2013, Ćirović et al. 2013) or smaller (20-24%, Csányi et al. 2016, Stoyanov 2012) than in other studies. This indicates that the availability of food sources was high, although stomach content weight was lower than others (Ćirović et al. 2016) found in winter (190 g). Because we found that stomach content weight in December-April of the second survey was significantly lower than in the first, it seems that during the critical winter-early spring period (Bartoń and Zalewski 2007), a decrease in food intake can occur. Overall, the food supply has remained favourable for jackals despite the reduction in anthropogenic food subsidies.

The body mass analysis only partially supported the first prediction that big game viscera removal results in reduced body mass. We observed significant effects only in the survey occasion × sex interaction. The different effect on each sex may be explained by the burden associated with pregnancy and lactation in females compared to males (Macdonald 1983, Moehlman 1987). Therefore, the negative effect associated with viscera removal is likely to affect females more, so it could lower the body mass. In addition, females consume a higher proportion of less nutritious plants (Atkinson et al. 2002), which may also have contributed to their lower body mass.

Intraspecific differences in diet

Contrary to our hypothesis, the primary food of the jackals remained viscera and carrion of big game despite their reduced availability. This is related to the changes in food sources resulting from big game management. The regression analysis showed no strong (and non-significant) relationship between the consumption of big game and the availability of viscera and carrion. That is, with low big game viscera and carcass availability, consumption of big game can still be considerable. We collected data from acoustic surveys to explore the numerical responses of the jackal population to big game viscera removal, but observed only a low decrease in family group density and an increase in lonely jackal density. Furthermore, in the second survey, reproduction among one-year old females was also observed. Presumably, food reduction in less productive areas (Bino et al. 2010, Kapota et al. 2016) compared to areas of high ungulate density can result in greater impacts of decreasing population density and survival, and increasing home range size of medium-sized canids. To better understand the ecology of the jackal, parallel with feeding habits, for example population size, reproduction and habitat use, should be analysed in relation to food abundance (or: amount of food available) during a long-term period.

Overall, even the seemingly small amount of anthropogenic food subsidies in our high ungulate density area is sufficient to sustain the jackal population, as well as other species that rely on scavenging, such as wild boar, common raven (*Corvus corax*) and white-tailed eagle (*Haliaeetus albicilla*). Similarly, no relationship was found between small mammal availability and small mammal consumption by the jackal and the red fox in Hungarian agroecosystems (Lanszki et al. 2010). Therefore, in addition to rodent control, our study illustrates the sanitary or cleaning role of jackal (Lanszki et al. 2015, Ćirović et al. 2016) instead of ungulate population regulation (i.e. the top-down regulation is not proved). In addition to the above-mentioned problematic issues of viscera removal and access to carcasses (e.g. changes in quantity within the year, poaching, wounding and vehicle collision), data collection (hunting bag data, carrion registration; Imperio et al. 2010) and investigation methodological constraints (Reynolds et al. 1991) could have contributed. From stomach analysis, it is often impossible to separate viscera consumption and eating from carrion (Lanszki et al. 2015, Bošković et al. 2013). Because there was only viscera removal, but no carrion removal (it was not feasible), the use of the combined food category (viscera and other carrion) may mask a part of the actual impact of the food manipulation.

The feeding responses of the jackal to the source reduction were less pronounced than expected in the case of other food types. Contrary to our second prediction, we did not find significant differences between treatment periods by log-linear analysis of any of the main food types. However, with MANCOVA, we found treatment period differences in consumption of some food types, but, many other (presumed) food types (e.g. small mammals, young cervids), had no statistically significant increase in consumption ratios. However, less adult wild boar was consumed in the second survey occasion. The consumption of adult wild boar by a mesocarnivore is more likely to be caused by scavenging, than predation (Bošković et al. 2013, Ćirović et al. 2013), although the predation e.g. on wounded, sick individuals cannot be excluded. Wild boar population densities depend on the severity of winter (Melis et al. 2006), however our study site experienced no major differences in weather conditions (**Appendix 8**) and wild boar population (**Appendix 9**) between the study periods. Increased consumption of young wild boars indicates food shift, which supported our prediction. Wild boar young are close to the 4-5 kg preferred weight category of the golden jackal (Hayward et al. 2017) for hunting. Food switching by mesocarnivores from scavenging to predation on young of wild ungulates has been observed in the case of high scavenger or predator abundance (Yom-Tov et al. 1995, Moehlman 1987, Prerna et al. 2015, Kamler et al. 2010). As we have assumed, due to the removal of viscera, jackals consumed more food from garbage or dumps (indicated by inorganic materials and domestic animals, **Table 7**), however we detected lower consumption rates from garbage than in southern Europe (Giannatos et al. 2010, Bošković et al. 2013, Ćirović et al. 2013, Ćirović et al. 2016). This, alongside the high wild ungulate abundances, can be related to the low human population density in the study area (Rotem et al. 2011, Lanszki et al. 2018).

5.4. Predation experiment on artificial bird nests in a campus park

In the artificial nest predation tests performed in the Kaposvár university campus park (**Appendix 10**) 21 ground nests and 21 shrub nests were used per year. In the first year of the study, one quail egg disappeared from the ground nest, three quail eggs disappeared from shrub nests, while in three cases eggs were broken by birds. Accordingly, the daily survival rate of quail eggs in ground nests (0.996) was significantly higher (Z = 1.964, P = 0.049) than that in shrub nests (0.976) (**Fig. 12**).

Our results support the statements by Söderström et al. (1998) that nest predation risk was significantly higher for shrub than for ground nests at various distances from the forest edge. There are forests close to the campus park (Kovács-Hajdu et al. 2014), thus the layout of our ground and shrub nests were somewhat similar to the layout of the study by Söderström et al. (1998). Our observation during field work suggested that human disturbance reduced the activity of larger-sized birds on the ground level in comparison to the shrub or tree canopy level. The missing quail eggs were most likely taken away by the common Eurasian jay (*Garrulus glandarius*) or Eurasian magpie (*Pica pica*), both of them being well-known nest predators (Newson et al. 2010, Wegge et al. 2012) in the area. Different corvid species tend to rob nests at different distances from the forest edge, while jays rob nests closest to edges (Söderström et al. 1998).

During the repeated study in 2014, 19 quail eggs disappeared or were taken away from the ground nests and 15 from the shrub nests. The daily survival rate of quail eggs in the shrub nests was higher (0.912), than that in the ground nests (0.833), but the difference was not significant ($Z = 1.907$, $P = 0.056$), or had only marginal significance. Our studies were performed in the middle of May, which is the second clutch period for many bird species (Ludwig et al. 2012). Our results suggested that in the late breeding season nest predation was higher on ground nests than on elevated nests, which is in accordance with the results of Ludwig et al. (2012).

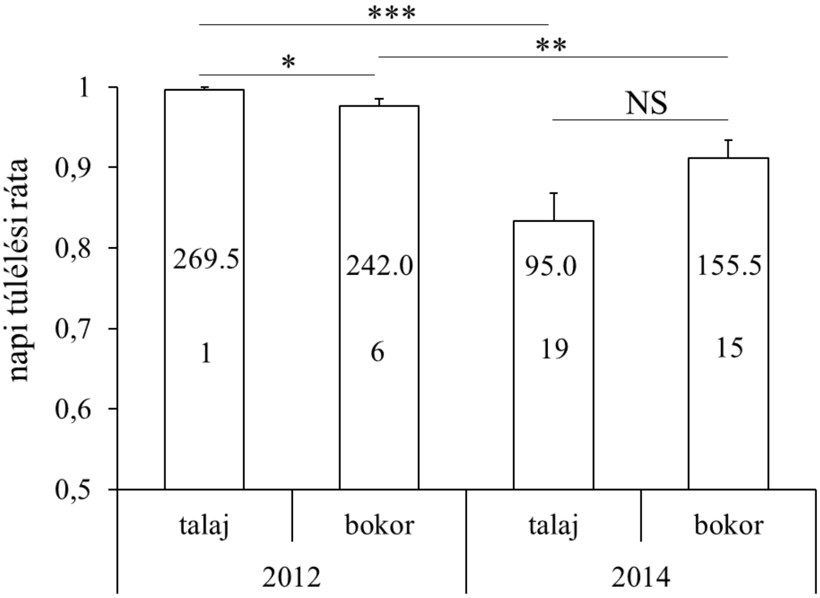

Fig. 12. Daily survival rates of quail eggs (+*SE*) in artificial ground and shrub nests.

The upper numbers within columns indicate the total number of exposure days, while the lower figures show egg losses. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS – non-significant.

However, the results of our first study showed an opposite pattern of predation, probably due to a much lower predator activity. This is reflected also in the significantly lower daily survival rate of quail eggs on the ground ($Z = 4.643$, $P < 0.0001$) and in the shrub nests ($Z = 2.686$, $P = 0.007$) in the second study year in comparison with the first one. In the second year of our study, predators e.g. the red squirrel and the brown rat were observed more often. Domestic cats were living in the park and according to our observation they were fed regularly by residents of the campus, which caused a steady increase in their population. No predation by foxes occurring in the park could be detected.

Results of the analysis of plasticine eggs showed that in the first year of the study the damage to one of the injured plasticine eggs in the ground nests was caused by some mechanical cause (pressure), the other one contained bite marks of a medium-sized mammalian predator. On the plasticine eggs in the shrub nests only beak and tooth marks of small-sized birds and mammals were visible (**Fig. 13**). In the second year of the study, based on the imprints in plasticine eggs, at least in seven cases ground nests were depredated by medium-sized mammals, while depredation of elevated nests was mostly related to birds (**Fig. 13**).

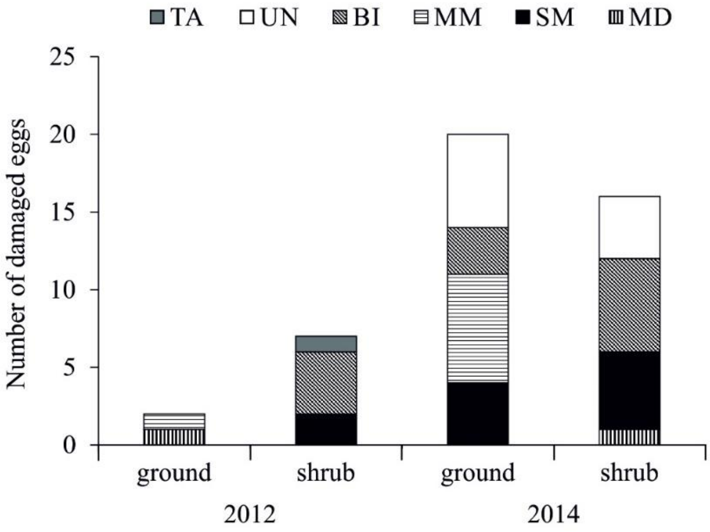

Fig. 13. Identification of predators by using plasticine eggs in ground- and shrub artificial nests.

Causes of damage: TA – taken away, UN – unknown, BI – birds, MM – medium-sized mammals, SM – small mammals, MD – mechanical damage.

Mechanical damage by trampling on plasticine eggs was found only in two cases (**Fig. 13**). Based on the marks left on plasticine eggs there was a significant difference in the depredation of the two nest types according to the predators' distributions ($\chi^2 = 12.486$, $df = 5$, $P = 0.029$).

In the second year the role of mammalian predators was considerable in the depredation of the ground nests, while in the case of shrub nests the birds' role was dominant (**Fig 13**). There was a clear separation of predators between shrub and ground nests as identified from marks in plasticine eggs. Mammals mainly depredated ground nests, whereas birds (mainly corvids) accounted for almost all predation on shrub nests (Söderström et al. 1998, Ludwig et al. 2012, Purger et al. 2015, Arbeiter and Franke 2018). Based on the tooth marks on the plasticine eggs, predation caused by small mammals was frequent in both nest types.

In the studied campus park, mostly small-sized bird nests on the ground and in the shrubs (Kovács-Hajdú et al. 2014) and their thin egg shell is easily broken by small predators (Maier and DeGraaf 2001). This can be one reason why there are only few ground nesting bird species in the parks (Jokimäki 1999). There are several mammal species in the campus (Kovács-Hajdu et al. 2014, Arbeiter and Franke 2018) which are common or casual nest predators, like brown rat, red squirrel, domestic cat, stone marten (*Martes foina*) and red fox (Arbeiter and Franke 2018). Jokimäki and Huhta (2000) suggested that in the town center most nests are destroyed by birds, while in the area of detached houses mostly mammals are the predators. The number and occurrence frequency of dogs and cats depend on humans; therefore, relationship can be found between the activity of these potential nest predators and urbanization (Jokimäki et al. 2005, Bocz et al. 2017, Woinarski et al. 2017).

The role of green surfaces in urban environments in preserving biodiversity can largely be interpreted with the knowledge of predation. Parks provide shelter and favourable conditions for the breeding of many bird species, but in the case of high abundance of predators, these habitats can operate as ecological traps (Rodewald et al. 2009, Shipley et al. 2013).

6. CONCLUSIONS AND RECOMMENDATIONS

6.1. Long-term changes in the diet of the red fox in an agricultural area

The diet composition of the red fox as a top predator in the studied agricultural area has changed together with its habitat in a long period

Based on the analysis from the 12 main food types, there were significant differences in the diet composition of red foxes between the survey periods for both RFO and FO data. This supports the fact that the change in the habitat (e.g. the transformation of the structure of cultivation branches) affects the predator's diet, which can measure through the change in the food composition. Consumption of small mammals decreased, while consumption of plants, invertebrates and wild boar increased. There were also significant differences in the diet of the fox among seasons. The trophic niche has widened. These detected changes also indicate a change in the intensity of plant cultivation. For example, more intensive production can be associated with fewer accessible rodents, but at the same time, omnivorous predators have easier access to plant food, and at the same time, their food becomes more balanced, which is also indicated by the widening of the trophic niche. During the two decades, the proportion of cultivated areas has increased and the coverage of near natural habitat types has decreased. Regarding major game species, wild boar hunting bag density was higher during the second survey period than the first one. The results of the diet composition analysis indicate the growth of the wild boar population in the area. That is, the fox diet shifted, and the wild boar (a wild ungulate) consumption is increased without the presence of a larger predator (e.g. golden jackal).

In conclusion, mesopredators' dietary patterns and shifts in feeding habits, like the red fox, over a long-term period, should be analysed further in areas where larger-scale habitat conversion is expected, parallel with undisturbed areas, and where the golden jackal has not yet been settled. This could also help to gain a better understanding of the effects of change in the intensity of agricultural production on trophic relationships/structures and the ecological role of larger, currently spreading carnivores. Furthermore, the latest analyses could contribute to understanding the ecological role of the globally most common carnivore, the red fox. For example, this could reduce the number of illegal poisoning cases in agricultural areas.

6.2. Diet composition of the golden jackal and the sympatric red fox in an agricultural area

Dietary similarities and opportunism

The results of parallel studies can be interesting from both a theoretical and a practical point of view because they provide information on sympatric species' current (time-same) trophic interactions. These interactions also extend to the relationships between predator-prey and between predators.

The diet compositions of the two canids were similar, with the dominance of small mammals. The consumption of small mammals in high proportions is in line with the results of the study carried out earlier in another agricultural area (in the vicinity of Kétújfalu) (Lanszki et al. 2006). The jackal consumed wild ungulates (mainly wild boar *Sus scrofa*, including piglets) in higher proportions in winter and spring and plants (mainly wild fruits) in summer and autumn. This experience confirms the jackal's relatively common choice of wild boar and, in comparison, the rare choice of cervids. The red fox consumed plants in high proportions in summer and autumn, and birds in spring and summer. That is, both canids use, but with partial differences, periodically abundant food sources. Compared with the jackal, the fox consumed more frequently birds. This is also important for wildlife management and nature conservation and points to the dietary separation of these species. Small-sized, terrestrial, open field living or habitat generalist and wild living animals were the most important food for both predators. In general, jackals consumed higher ratios of forest-living and lower ratios of arboreal species than foxes. The analysis of the characteristics of the prey species detected in the scat samples is essential not only for the exploration of the trophic interactions between these two canids but also for the further trophic interactions that make up the carnivora community, for example, with mustelids and felids (e.g. for comparative studies). Trophic interactions may indicate competition between species.

The trophic niche of both canids was similarly very narrow, and due to dietary similarities, the trophic niche overlap was high. The trophic niche patterns were obtained by their coexistence. All of this indicates the high ecological flexibility of both canids. Both carnivore species utilise many resources to varying degrees at the same time. In addition, to the abundant resources, the competition could have been moderate because we did not detect a similar change in diet patterns, unlike in the Kétújfalu agroecosystem, where the forced conditions (harsh winter) led to changes in diet.

Dietary differences depend more on area (management) than on species

The diet composition of the golden jackal and the red fox based on studies performed in Hungary differed greatly depending on the area (habitat type and/or wildlife management) than on the carnivore species.

In conclusion, better knowledge of the ecological role of sympatric mesocarnivores may facilitate the choice of appropriate management approaches. Further field studies must explore community-level and area-specific trophic interactions, especially in human-dominated habitats. Furthermore, the comparative studies should also include other habitat types (e.g. forests, wetlands) previously or newly inhabited by jackals. Moreover, it would be worthwhile to include several carnivore species (native, non-native, or species belonging to different body sizes and ecological guilds) in the comparative studies to reveal the extent of the effect of coexistence on population size. The high feeding flexibility 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.

6.3. Feeding responses of the golden jackal after reduction of anthropogenic food subsidies

The feeding responses of the golden jackal to the reduction of food subsidies were less pronounced than we expected

The ungulate viscera removal did not result in a statistically significant decrease in its consumption. Even after the reduction of food subsidies, the primary food of jackals was viscera and carrion from wild ungulates, and scavenging was not affected by season or sex. Frequency data revealed no significant differences between surveys in consumption of either food type. Wet weight data revealed that in the first period with food subsidies, jackals consumed a higher proportion of adult wild boar (from predation or scavenging). In contrast, juvenile wild boar (from predation or scavenging), domestic animals (mostly from scavenging) and invertebrates increased in the second period. The stomachs in the second survey occasion contained more varied food items, but the trophic niche was not significantly wider.

Moderate effects on stomach content weight and body mass

Food removal did not significantly increase the proportion of empty stomachs and did not significantly reduce stomach weight. The food supply has remained favourable for jackals despite the reduction in anthropogenic food subsidies. We observed significant effects only in the survey occasion

× sex interaction. The negative effect associated with viscera removal is likely to affect females more, so it could lower the body mass. In addition, females consume a higher proportion of less nutritious plants, which may also have contributed to their lower body mass.

In conclusion, the feeding responses of jackals to the reduction of food subsidies were less pronounced than expected despite 50 kg of viscera removed per km per year. Because in high big game density areas, wild ungulate carrions from different mortality causes are available in high quantities throughout the year, predator populations can be maintained despite the high amount of viscera removal.

To better understand the ecology of the jackal, parallel with feeding habits, for example population size, reproduction and habitat use, should be analysed in relation to food abundance during a long-term period. This should cover areas with a higher jackal population density, historical (e.g. Asian) and European regions populated by jackals decades ago, and newly populated areas with lower jackal population densities.

Management implications

In the absence of large carnivores (top-down regulation), the abundance of mesopredators is usually limited by available food resources (Courchamp et al. 2003, Beschta and Ripple 2009), and bottom-up regulation prevails. Food abundance has an influence on coyote (*Canis latrans*) numbers, reproductive rates, survival, dispersal and space-use patterns (Bekoff and Gese 2003), and this has also been demonstrated experimentally on red fox (Bino et al. 2010) and golden jackal (Kapota et al. 2016). Leaving big game viscera or of domestic animal carcasses and garbage (Bošković et al. 2013, Raichev et al. 2013, Ćirović et al. 2016) can maintain the population of scavengers (Yom-Tov et al. 1995, Bino et al. 2010, Morehouse and Boyce 2011, Cozzi et al. 2015, Kapota et al. 2016). For these reasons (e.g. illegal hunting, illegal garbage deposition), a resource reduction by experts can cause moderate changes. A greater impact can be achieved with the removal of food subsidies on a larger area, as it was experienced in the case of sanitation (i.e. removal of domestic animal carcasses around farms) in Israel (Bino et al. 2010, Kapota et al. 2016).

6.4. Predation experiment on artificial bird nests in a campus park

In artificial bird nest predation tests, we sought the answer to how carnivores prey on bird nests in a campus park. In the first year of the study, the daily survival rate of ground-nesting birds was significantly higher than that of shrub-nesting birds. Corvids, well-known nest predators, most likely took away the missing quail eggs. In the second study year, the daily survival rate of quail eggs in the shrub nests was higher than in the ground nests, only with a marginal significance. In the second year of the study, the significant reduction in daily survival rates of both nest types can be explained by the increasing number of predators. The red squirrel and the brown rat were observed more and more often. Stray cats were living in the park and they were fed regularly, which caused a slow increase in their population (our observation). The daily survival rates were high overall, which did not support the high bird nest loss expected (hypothesised) in the park.

There was a clear separation of predator faunas between shrub and ground nests, as identified from marks in plasticine eggs. Mammals mainly depredated ground nests, whereas birds, mainly corvids accounted for almost all predation on shrub nests. Based on the tooth marks on the plasticine eggs, predation caused by small mammals was frequent in both nest types. The number and occurrence frequency of dogs and cats depend on humans. The park maintenance had a small direct impact on the nest survival during both surveys. There was only one case of nest loss due to park management. Fox has been shown to reduce the nesting success of ground-nesting birds in many towns (Gilbert 1989), but we could not identify the red fox as a predator.

Park management implications

Shwartz et al. (2008) studied different management regimes of the parts of a large park may contribute the diversity, number of individuals and structure in a bird population. Have to strengthen the collaboration between gardeners, ecologists, zoologists and botanists (Paker et al. 2014), thus it would facilitate the maintenance alignment in space and time, e.g. bigger works should be done outside of nesting and rearing periods. Autochthon species should be preferred instead of ornamental trees and shrubs (Paker et al. 2014) (especially fall crops species for the winter bird guests). Should create undisturbed areas where no maintenance works can be tested (Shwartz et al. 2008), and these spaces should be impassable for dogs, cats or humans (Paker et al. 2014). Should create small lakes that increase the diversity and individual numbers of insects and water-bound or shyer birds (Solimini et al. 2003).

Parks provide shelter and favourable conditions for the breeding of many bird species. Still in the case of a high abundance of predators (mammals and birds), these habitats can operate as ecological traps.

7. NEW SCIENTIFIC RESULTS

1. According to the study carried out in South-West Hungary (Fonó), the diet composition of the red fox (*Vulpes vulpes*) has changed in connection with the growing intensity of crop cultivation over the last 20 years, decreased the small mammal consumption, while that of plants, invertebrates, and increasing population wild boar's (adult and piglet) consumption increased.

2. In the investigated agricultural area (Vajszló, SW Hungary) the diet composition of the golden jackal (*Canis aureus*) and the sympatric red fox showed great similarity. Small mammals dominated their diet; the fox consumed a larger proportion of birds.

3. Based on studies performed in Hungary, the diet composition of the golden jackal and the sympatric red fox was determined more by the characteristics of the area (habitat type and/or the intensity of game management) than by the species of the carnivore species.

4. In an area with intensive big game management (Lábod, SW Hungary) in the first ungulate viscera removal experiment in Europe, we demonstrated moderate food shift. However, the feeding responses of the golden jackal to the reduction of food subsidies were less pronounced than was expected. Since jackals could access viscera and carcasses due to different mortality causes in the whole year, we did not find significant differences in the consumption of any food type based on frequency data between the two survey periods (viscera removal or leaving out). Based on the wet weight data, when the viscera were left, the jackals consumed a higher proportion of adult wild boar, while the consumption of juvenile wild boar,

domestic animals and invertebrates increased when the viscera were removed; jackals switched to a diet with more variety in food items, but the trophic niche did not become significantly wider.

5. In the examined campus park, damage by small and medium-sized mammals and crows affected bird nestling survival differently depending on the year. Although foxes appear in the area, we did not experience any predation due to foxes, and the direct loss resulting from park maintenance was lower than expected.

8. SUMMARY

The red fox (*Vulpes vulpes*) is one of the world's most distributed and studied carnivores. Due to its widespread, it is one of the most important mammalian predators. The golden jackal (*Canis aureus*) has a rapidly increasing population in Europe. Due to high or increasing population numbers and known or less explored feeding habits, these mesopredators (mesocanids) are conflict species in the human-carnivore relationship. Knowledge of the trophic ecology, e.g. feeding habits, trophic interactions, and the factors influencing them, is essential for implementing proper carnivore management. In my research, I was planning to gain new knowledge about the trophic ecology of these carnivores.

Long-term changes in the diet of the red fox in an agricultural area

In a changing environment, dietary patterns of mammalian predators are influenced by many factors. In an agricultural area in south-western Hungary, where the red fox is the top predator and has a stable population, we aimed to analyse how the diet composition based on scat samples changed over a longer period (first survey period: 1992–1997, n = 350; second survey period: 2012–2014, n = 237). Based on the analysis from 12 main food types, a shift was found in the dietary pattern of the fox. When comparing the results from the second survey with those of the first survey, small mammals were consumed less frequently (relative frequency of occurrence, 39.2% vs. 26.8%, respectively), while plants (mainly fruits; 19.0% vs. 26.7%), invertebrates (11.0% vs. 15.0%), and wild boar (0.9% vs. 7.5%; including piglets in the second survey) were consumed more frequently. These four main food types together comprised > 70% of the difference between diet composition from the two surveys. The trophic niche breadth had a narrower mean value in the first than in the second survey. The dietary shift can be related to the intensification of agricultural production and increased occurrence of wild boar in the area.

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

To better understand the ecology of the golden jackal and interspecific relationships among carnivores, we studied its dietary pattern and the diet of its main competitor, the red fox, over three years. 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 (BC, mean biomass consumed: 72%). The secondary food sources were wild ungulates (in winter and spring; mainly wild boar, including piglets) and plants (in summer and autumn; mainly wild fruits). The fox also primarily consumed small mammals (BC: 50.3%), but their consumption dropped in summer and autumn, because that time, two-thirds of the 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 the 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.

Feeding responses of the golden jackal after reduction of anthropogenic food subsidies

Little is known of the resources that limit or promote the rapidly expanding golden jackal population in Europe. We hypothesised that in an area of intensive big game hunting, a reduction of the main food resource (human subsidised big game viscera) would result in dietary switching. We used multivariate analyses to test whether the dietary composition of 200 jackal stomachs varied between two 2-year-long survey periods, the first without big game viscera removal (availability of 68 kg viscera/year/km^2) followed by a period with viscera removal (minimum of 50 kg of viscera/year/km^2 removed). Even after the reduction of food subsidies, the primary food of jackal was viscera and carrion from wild ungulates (FO, frequency of occurrence: 45% vs. 30%; W, wet weight: 55% vs. 29%, respectively), but scavenging was not affected by season or sex. In the first period with food subsidies jackals consumed a higher proportion (W) of adult wild boar (11.6% vs. 1.3%; from predation or scavenging), while juvenile wild boar (0% vs. 11.8%; from predation or scavenging), domestic animals (0.8% vs. 6.2%; mostly from scavenging) and invertebrates (2.6% vs. 4.1%) increased in the second period. The stomachs in the second survey contained more varied food items, but the trophic niche was not significantly wider.

Predation experiment on artificial bird nests in a campus park

With the spreading of urbanization, understanding biological processes in the modified environment becomes more important. In this study, we paid particular attention to the nesting success of birds in urban environments. We aimed to detect the effects of predation and human disturbances on the potential nesting success of birds. We tested the survival of quail and plasticine eggs in artificial ground and shrub nests in the campus park of Kaposvár University. The results of the first survey in 2012 showed that the daily survival rate (DSR) of quail eggs in ground nests was significantly higher than in shrub nests (DSR = 0.996 and 0.976, respectively). Imprints left on the plasticine eggs suggested bird and mammalian predators. The daily survival rates of both nest types were significantly lower in the repeated survey in 2014, but the DSR of the two nest types was the other way around compared to the first study year. The daily survival rate of quail eggs in the ground nests was lower than in the shrub nests (0.833 and 0.912, respectively) because of the higher predation activity of small- and medium-sized mammals and birds. The results of our survey suggested that park maintenance had a low impact on nest survival. On the other hand, the nesting of birds can be safer in the campus area if undisturbed fragments of habitats are created by excluding mammalian predators (e.g. dogs and cats).

In conclusion, we have shown that the habitat changes with the growing intensity of crop cultivation and increasing wild boar population in the agricultural area have a marked effect on the red foxes' diet. We found that the diet composition of the golden jackal and the sympatric red fox in an agricultural area were similar, with the dominance of small mammal food. The diets of these canids were determined more by the characteristics of the area than by the species. The feeding responses of the golden jackal to the reduction of food subsidies were less pronounced than expected. Viscera and carrions from different mortality causes (e.g. poaching, road-kills) are available throughout the year and are easily accessible for the carnivores. That’s why the predator populations can be maintained despite the high amount of viscera removal. Although foxes appear in the examined university campus park, we did not experience any predation due to foxes. Furthermore, the direct loss resulting from park maintenance was lower than expected.

ÖSSZEFOGLALÁS

A vörös róka (*Vulpes vulpes*) a világ egyik legelterjedtebb és leginkább tanulmányozott ragadozója. Elterjedtsége miatt az egyik legjelentősebb emlős predátor. Az aranysakál (*Canis aureus*) állománya gyorsan nő Európában. A magas vagy növekvő populációlétszám és az ismert, vagy kevésbé feltárt táplálkozási szokások miatt ezek a mezopredátorok (közepes testméretű kutyafélék) konfliktusos fajok az ember-ragadozó viszonylatban. A táplálkozási szokások és interakciók, az azokat befolyásoló tényezők ismerete elengedhetetlen a ragadozókkal való ésszerű gazdálkodáshoz. Kutatásom során ezen ragadozók táplálkozás-ökológiájáról igyekeztem új ismereteket szerezni.

A vörös róka táplálkozásának hosszú távú változása mezőgazdasági területen

Változó környezetben a ragadozó emlősök táplálkozási szokásait számos tényező befolyásolja. Egy délnyugat-magyarországi mezőgazdasági területen, ahol a vörös róka a csúcsragadozó és stabil populációval rendelkezik, célunk az volt, hogy ürülékminták alapján megvizsgáljuk, hogy változik hosszabb időn keresztül a táplálék összetétele (első felmért időszak: 1992–1997, n = 350; második felmért időszak: 2012–2014, n = 237). Tizenkét fő tápláléktípusra alapozott elemzéssel, a róka táplálék mintázatában változást találtunk. A második időszakban, az elsőhöz képest ritkábban fogyasztottak kisemlősöket (relatív előfordulási gyakoriság, 39,2% *vs*. 26,8%), míg gyakrabban fogyasztottak növényeket (főleg gyümölcsöt; 19,0% vs. 26,7%), gerincteleneket (11,0% *vs*. 15,0%) és vaddisznót (0,9% vs. 7,5%; a második időszakban a malacokat is beleértve). Ez a négy fő táplálék típus a két időszak táplálék-összetétele közötti különbségnek összesen több, mint 70%-át tette ki. A táplálkozási niche az első időszakban szűkebb volt, mint a második időszakban. A táplálék-összetétel eltolódása az intenzívebbé váló mezőgazdasági termeléssel és a vaddisznó területen való gyakoribbá válásával hozható összefüggésbe.

Az aranysakál és a vele együtt előforduló vörös róka táplálék-összetétele magyarországi mezőgazdasági területen

Az aranysakál ökológiájának és a ragadozók interspecifikus kapcsolatainak jobb megértése érdekében, három éven keresztül vizsgáltuk a sakál és a fő versenytársának számító vörös róka táplálkozási mintázatait. A vizsgálatot egy délnyugat-magyarországi mezőgazdasági területen, ürülékminták elemzésével (sakál n = 373, róka n = 268) végeztük. A sakál elsődlegesen fontos táplálékát minden évszakban kisemlősök alkották (átlagos fogyasztott biomassza részesedés, BC: 72%). A másodlagos táplálékai nagyvadfajok (télen és tavasszal; főként vaddisznó, beleértve a malacot is) és növények (nyáron és ősszel; főleg vadon termő gyümölcsök) voltak. A róka is elsődlegesen kisemlősöket fogyasztott (BC: 50,3%), de fogyasztásuk nyáron és ősszel visszaesett, mert akkor a táplálék kétharmadát növények alkották, míg a madarak fogyasztása tavasszal és nyáron volt magasabb. A két ragadozó táplálék-összetétele hasonló volt. A sakálhoz képest azonban a róka lényegesen nagyobb arányban fogyasztott madarakat. Mindkettő standardizált táplálkozási niche-szélessége (B_A) nagyon szűk volt (0,09), és a táplálék-összetételeik nagymértékben átfedtek (69,8%). A vizsgálat a táplálékforrások részleges felosztását és mindkét kutyaféle opportunista táplálkozását megerősítette.

Az aranysakál antropogén eredetű táplálékforrás elvonásra adott táplálkozási válasza

Kevéssé ismert, hogy mely források korlátozzák a dinamikusan terjeszkedő aranysakál populációit Európában. Feltételeztük, hogy egy intenzív nagyvadgazdálkodás alatt álló területen a fő táplálékforrás (ember által nyújtott nagyvad zsiger) mennyiségének csökkentése táplálékváltást eredményez. Ennek tesztelése érdekében, két kétéves időszakban, zsiger kint hagyás (1. időszak, min. 68 kg zsiger/km^2/év), majd ezt követő zsigerelvonás mellett (2. időszak, min. 50 kg zsiger/km^2/év) többváltozós elemzéssel hasonlítottuk össze 200 db sakál gyomortartalom összetételét. A zsigerelvonást követően is zsiger és nagyvad tetem volt a sakálok elsődleges tápláléka (FO, előfordulási gyakoriság: 45% vs. 30%; W, nyers súly: 55% *vs*. 29%, az időszakok sorrendjében), a dögevés nem függött évszaktól és ivartól sem. A sakálok az első időszakban nagyobb részesedési arányban fogyasztottak kifejlett vaddisznót (W, 11.6% *vs*. 1.3%; predációból vagy dögevésből), míg a második időszakban vadmalacot (0 *vs*. 11.8%; predációból vagy dögevésből), háziállatot (0.8% *vs*. 6.2%; főként dögevésből) és gerincteleneket (2.6% *vs*. 4.1%). Az elsőhöz képest a második időszakban több táplálékelemet (1.79 *vs*. 2.55) tartalmaztak a gyomrok, de a táplálkozási niche nem vált szignifikánsan szélesebbé.

Madárfészkekre nehezedő predációs nyomás egy campus parkban

Az urbanizáció terjedésével egyre fontosabbá válik a megváltozott környezetben zajló biológiai folyamatok megértése. Tanulmányunkban kiemelt figyelmet fordítottunk a madarak városi környezetben való fészkelési sikerességére. Célunk az volt, hogy mesterséges fészek tesztben megbecsüljük a ragadozók és az emberi zavarások madárfészkekre nehezedő hatását. A Kaposvári Egyetem campusának parkjában, mesterséges talaj- és bozótfészkekben teszteltük a fürj- és gyurmatojások „túlélését”. Az első évi felmérés (2012) eredményei azt mutatták, hogy a fürjtojások napi túlélési aránya (DSR) a talaj fészkekben szignifikánsan magasabb volt, mint a bozótfészkekben (DSR = 0,996, ill. 0,976). A gyurma tojásokon hátra hagyott nyomok madarakra (elsősorban varjúfélék) és emlős predátorokra utaltak. A megismételt felmérésben (2014), az első vizsgálati évhez képest, mindkét fészektípus napi túlélési aránya szignifikánsan alacsonyabb volt, de a két fészektípus DSR aránya megfordult. A fürjtojások napi túlélési aránya a kisés közepes emlősök és madarak nagyobb predációs aktivitása miatt a talaj fészkekben alacsonyabb volt, mint a bozótfészkekben (0,833, ill. 0,912). Felmérésünk eredményei arra utalnak, hogy a parkfenntartás csekély hatással volt a fészkek túlélésére. Másrészt a madarak fészkelése biztonságosabb lehet az egyetem területén, ha az emlős ragadozók (pl. kutyák és macskák) távol tartásával zavartalan élőhelyfoltok jönnek létre.

Összegzésképpen, kimutattuk, hogy a mezőgazdasági területeken bekövetkező élőhelyváltozás a növénytermesztés intenzitásának fokozódásával és a vaddisznóállomány növekedése befolyásolja a vörös róka táplálkozását. Megállapítottuk, hogy mezőgazdasági területen az aranysakál és a szimpatikus vörös róka táplálék-összetétele hasonló, kisemlősök dominanciájával. E kutyafélék táplálkozását inkább a terület adottságai, mint a faj határozták meg. A sakálnak a forrás elvonására adott táplálkozási válaszai a várttól elmaradtak. Ennek oka, hogy vadzsiger és állattetemek különböző elhullási okokból egész évben rendelkezésre állnak és nagy mértékben szabadon hozzáférhetők a ragadozók számára. Bár az egyetemi kampusz parkban megjelennek, de nem tapasztaltunk rókára visszavezethető predációt. A park gondozásból eredő közvetlen veszteség elmaradt a várttól.

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11. PUBLICATION ON THE TOPIC OF DISSERTATION

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13. SHORT PROFESSIONAL BIOGRAPHY

Between 2009 and 2012 Nikolett Nagyapáti studied as a nature conservation engineer BSc student at Kaposvár University. From the beginning she was most interested in the ecology of carnivores. In 2013 she started her nature conservation MSc studies at Pannon University and graduated in 2015. During this time she also worked as a volunteer at Danube-Drava National Park. Between 2015 and 2018, she was a PhD Student at Doctoral School in Animal Science at Kaposvár University. She has been the supervisor of two students. In 2020 she did mid terms succesfully.

She worked as an animal keeper for a few months between 2012 and 2015 in Belgium on a goat farm. In 2014 for a few months, she worked as an administrator at Trigo, Ltd. (measuring house) in Mélykút. From 2018 till 2019 she was a credit controller at Diageo plc in Budapest. Since 2020 she has been working as a financial manager at Danube-Ipoly National Park Directorate.

She has an intermediate level exam in English and a basic exam in German.

APPENDICES

Appendix 1: Images about the study areas in SW Hungary.

Fonó, Somogy county

Vajszló, Baranya county

Lábod, Somogy county

Kaposvár, university campus, Somogy county

(Photos: József Lanszki)

Appendix 2. Habitat and climatic characteristics of the Fonó study area and the estimated density of the red fox (*Vulpes vulpes*) population

Characteristics		First survey (1992–1997)	Second survey (2012–2014)
Habitat	Cultivated lands (mainly cereals and rape *Brassica napus*)	28%	40%
	Abandoned fields	0–15%	0%
	Game-field (mainly maize *Zea mays*)	0–2.4%	0%
	Wood pasture (with silver birch *Betula pendula*, black locust *Robinia pseudo-acacia*)	5%	2%
	Forests (Austrian oak *Quercus cerris*) (approx. 65 years old in 1992)	26–33%	26%
	Fishpond	0.8–13%	13%
	Wetlands (grey willow *Salix cinerea*, sedge *Carex,* common reed *Phragmites australis*)	19–26%	19%
Climate	Mean annual temperature	10.8°C	11.2°C
	Mean winter temperature	1.5°C	2.4°C
	Mean summer temperature	20.4°C	21.0°C
	Annual number of days with snow cover	no data	20 days
	Mean annual precipitation	637 mm	670 mm
Red fox	Population density in March (mean ± *SD*), individuals per km^2	2.26 ± 0.78[a]	3.09 ± 0.19

Source of climate data: Hungarian Meteorological Service (https://www.met.hu, Accessed 11 May 2017). The relative abundance of red foxes (individuals per km^2) was calculated on the basis of den density (inhabited den × 2) by own surveys performed in March.

[a] 2002–2014.

Appendix 3. Mean harvest density (individuals/km^2) of game species in Fonó study area

Period		Red deer	Roe deer	Wild boar	Hare	Pheasant	Mallard	Red fox
		Hunting bag (individuals/km^2)						
1997–1999	Mean	0.04	0.51	0.05	0.09	1.63	0.46	0.24
	SD	0.02	0.09	0.04	0.05	0.76	0.15	0.15
2012–2014	Mean	0.11	0.53	0.75	0.01	0.16	0.20	0.26
	SD	0.01	0.13	0.12	0.01	0.07	0.05	0.08

Source: Hungarian Game Management Database (Csányi et al. 2014)

Appendix 4. Number of items in each taxon in scats of red foxes (*Vulpes vulpes*) in the first and second survey periods (1992–1997 and 2012–2014; Fonó)

Food items	1992-1997	2012-2014
Common vole (*Microtus arvalis*)	145	15
Field vole (*Microtus agrestis*)	1	
Microtus sp.	21	63
Bank vole (*Myodes glareolus*)	48	11
Muskrat (*Ondatra zibethicus)*	3	
Water vole (*Arvicola amphibius*)		1
Red squirrel *(Sciurus vulgaris*)	1	
Fat dormouse (*Glis glis*)	1	
Common dormouse (*Muscardinus avellanarius*)	4	
Apodemus sp.	48	58
Harvest mouse (*Micromys minutus*)	2	1
Brown rat (*Rattus norvegicus*)	2	1
Other small rodents (Rodentia)	10	
Sorex sp.		1
European brown hare (*Lepus europaeus*)	4	1
Small mustelids (Mustelidae)	2	3
European badger (*Meles meles*)	9	
Wild boar (*Sus scrofa*) adult	9	30
Wild boar (*Sus scrofa*) juv.		21
Roe deer (*Capreolus capreolus*)	58	19
Undetermined cervids (Cervidae)	1	2
Domestic dog and cat	8	
Domestic rabbit	14	
Domestic ungulates	20	18
Poultry	29	6
Poultry egg	1	3
Pheasant (*Phasianus colchicus*)	16	5
Other medium sized birds		24
Small birds (Passeriformes)	41	7
Bird egg		2
Grass snake (*Natrix natrix*)	4	
Anurans (Anura)	1	
Cyprinids (Cyprinidae)		6
Bullhead (*Ameiurus* sp.)		5
Undetermined fish	4	13
Carabid beetles (*Carabus* sp.)	20	36
Melolontha sp.	15	4
Stag beetle (*Lucanus cervus*)	4	1
Other beetles (Coleoptera)	6	12
Orthopterans (Orthoptera)	9	4
Other insects (Insecta)	14	13
Grape fruit (*Vitis vinifera*)	9	4
Cherry (*Cerasus avium*)	11	10
Apple (*Malus* sp.) and pear (*Pyrus* sp.)		13
Plum (*Prunus domestica*)	6	15
Blackthorn (*Prunus spinosa*)	16	1
Other fruits	8	10
Grass	18	15
Corn (*Zea mays*)	28	14
Common sunflower (*Helianthus annus*)	12	6
Plant debris	8	35
Inorganic materials	8	2

Source of earlier data: Lanszki et al. (1999)

Appendix 5. Distribution of animal food types in the diet of golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) on the basis of weight, zonation, habitat type and environment association of animal prey species in Vajszló study area.

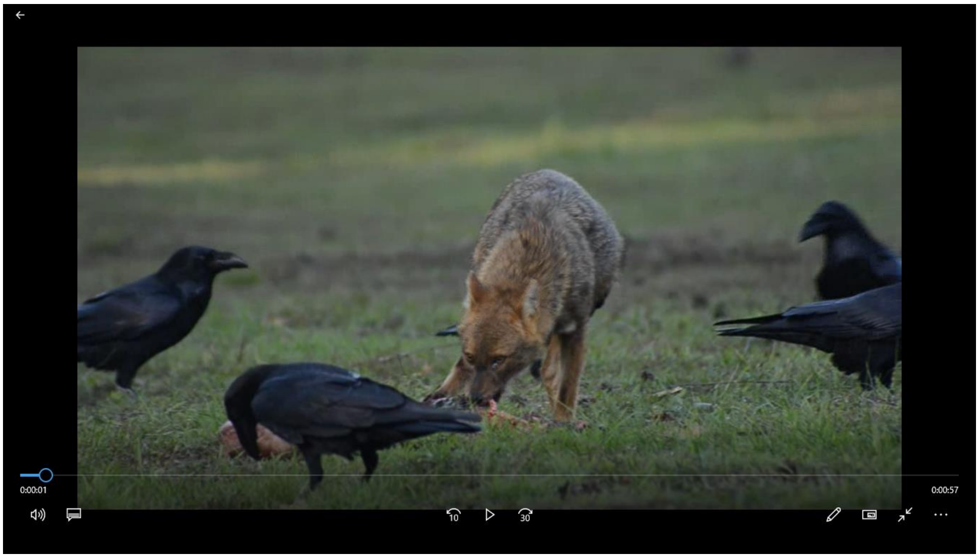
Prey		RFO					BC				
characteristic		Jackal	Fox	G	df	P	Jackal	Fox	G	df	P
Weight (g)	<15	10,8	19,7	2,66	1	NS	3,3	3,9	0,04	1	NS
	15-50	71,1	52,1	2,95	1	NS	70,5	53,4	2,37	1	NS
	51-100	1,1	1,8	0,18	1	NS	0,8	0,9	0,01	1	NS
	101-300	5,5	9,7	1,19	1	NS	8,2	14,7	1,87	1	NS
	301-1000	1,1	6,1	3,72	1	NS	0,2	11,8	14,46	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	Wild	92,2	72,1	2,47	1	NS	98,1	85,8	0,83	1	NS
association	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

RFO – relative frequency of occurrence, BC – percentage of consumed biomass. Significance was tested by G-test.

Appendix 6. Scat samples of carnivores.

1 – Eurasian otter (*Lutra lutra*), 2 – stoat (*Mustela erminea*), 3 – stone marten (*Martes foina*), 4 – pine marten (*Martes martes*), 5 – badger (*Meles meles*), 6 – red fox (*Vulpes vulpes*), 7 – golden jackal (*Canis aureus*). (Lanszki 2002)

Appendix 7. Wild-living adult golden jackal (*Canis aureus*) eating the viscera of big game.



Jackals eat considerable amounts of meat quickly, in relatively large chunks. The 58-second film was made by Zoltán Horváth (Danube-Drava National Park Directorate) in daylight, ca. 15 kilometres away from our study area. https://doi.org/10.1371/journal.pone.0208727.s004

Appendix 8. Meteorological data of the Lábod study.

Year	Number of frost days	Number of days with snow cover	Average snow depth (cm)	Mean temperature (°C)			Annual precipitation (mm)
				Winter	Summer	Annual	
2011	115	18	0.8	0.0	20.2	10.3	456
2012	85	13	3.0	0.3	21.4	11.3	526
2013	82	35	2.5	1.2	20.3	10.8	876
2014	53	3	2.0	3.3	19.4	11.6	1011
2015	73	14	1.5	2.4	21.4	11.5	693

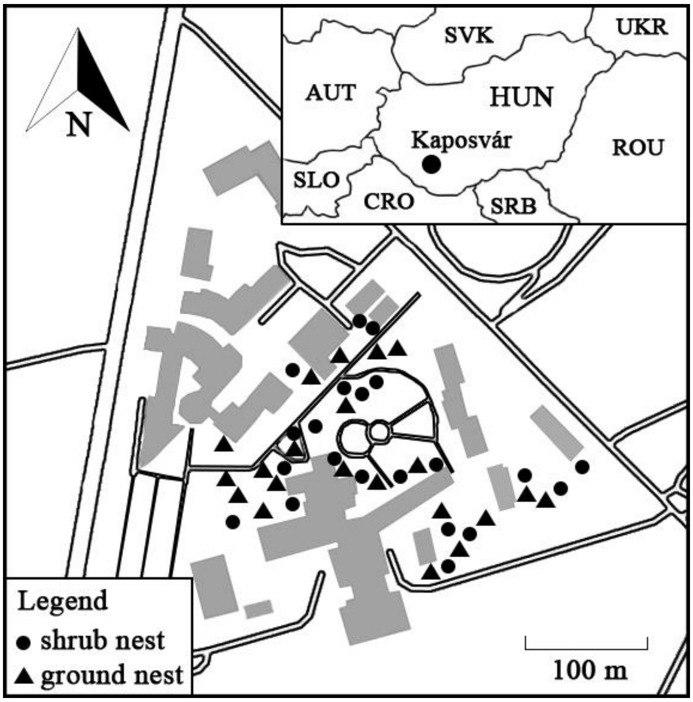
Source of climate data: Hungarian Meteorological Service.

Appendix 9. Harvest density (individuals/km^2) of game species in Lábod region.

Year	Red deer	Fallow deer	Roe deer	Wild boar	Golden jackal	Red fox
	Hunting bag (individuals/km^2)					
2010/2011	1.31	3.36	0.38	1.18	0.05	0.12
2011/2012	1.30	3.24	0.38	1.64	0.13	0.11
2012/2013	1.04	1.88	0.32	2.83	0.20	0.11
2013/2014	1.02	1.67	0.30	1.82	0.20	0.12
2014/2015	0.90	1.34	0.18	2.21	0.29	0.10
2015/2016	1.02	1.20	0.22	2.39	0.27	0.10
Mean	1.10	2.12	0.30	2.01	0.19	0.11
± SE	0.07	0.39	0.03	0.24	0.04	0.01

Source: Hungarian Game Management Database (http://ova.info.hu).

Appendix 10. Design of the artificial nest predation experiment performed in the Campus of Kaposvár University.



Locations of 21 ground (▲) and 21 shrub (●) artificial nests. Grey surface – buildings.