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

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1. BACKGROUND OF RESEARCH, HYPOTHESES AND OBJECTIVES

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.

This doctoral dissertation has four topics. First, I summarized the experience of a dietary study of red foxes in an agricultural area in an area where no golden jackal lived. Second, I summarized the experiences of the dietary study of coexisting red foxes and golden jackals also from an agricultural area in a comparative study. Third, I have summarized the experience of the big game viscera removal experiment in a more forested area under intensive big game management. Fourth, I modeled the predation of bird population in urban area.

Hypotheses and aims

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 top predator, considering that in many other areas the golden jackal took over this role. We hypothesized that due to changes in the habitat, the diet composition of the red fox over a longer period (i.e., two decades) will change in an agricultural area (Fonó, SW Hungary).

Our aim was to evaluate the intraspecific (period- or surveydependent and seasonal) differences in diet composition and trophic niche breadth of the fox on the basis of analysed scat samples in the "first survey" (1992–1997) and "second survey" (2012–2014).

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) showed similarity in diet composition and small mammal preference, trophic niche of both canids was narrow, but there were detectable characteristic differences as well. Assuming, that the larger body massed, social predator takes larger prey more often than the smaller, solitary hunter, the first prediction was, there should be considerable intraspecific differences in feeding habits, that is, the golden jackal should consume wild ungulates, meanwhile the red fox should consume small mammals in greater proportion. The second prediction was that the more varied diet jackal should be more food generalist than the fox. Based on the resource partitioning hypothesis, 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 Hungarian studies.

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

We hypothesise that in an area of intensive big game hunting with high jackal density (Lábod, SW Hungary), reducing the primary food subsidy (big game viscera) will result in pronounced food switching. To test this hypothesis, we manipulated 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. Our predictions were 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.

To test our hypothesis, we manipulated food subsidies at a landscape scale over four years. We used multivariate analyses to test whether the dietary composition of 200 jackal stomachs varied between two 2-yearly survey occasions, the first without big game viscera removal followed by a period with viscera removal.

How Successful Bird Nesting Can be in a Campus Park?

From a conservation perspective it would be a progress to transform city parks (urban habitats) into bird-friendlier habitats. For an effective biodiversity conversation, it is important to know the relationships between preys and predators. 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, however, such information is necessary for creating bird-friendlier parks and maintening them. The wildlife of the Kaposvár University campus park has been assessed, but the interspecific relationships, especially predation effects were still unknown.

Our aims of the predation experiment performed in the 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 and anthropogenic factors threatening the clutches.

2. MATERIAL AND METHODS

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

Study area and species

The study area is located near Fonó village. The main land use in this hilly area is intensive arable agricultural cultivation. 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, 2002–2014. During these years golden jackal did not occur in this area.

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, 1992–1997, n = 350 and in the second survey, 2012–2014, n = 237): monthly over the same area on a standard route of 4.2 km. Scats were analysed using a standard procedure. The diet composition from scat samples was expressed on the basis of RFO and FO (The calculation method can be found at the end of the subsection).

Data analysis

To test whether the diet composition differed between the two periods, PERMANOVA was used with period and season. 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. 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. The seasonal B_A (standardized trophic niche) values between the two periods were compared with paired samples t-test.

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

Study area and species

The study area, close to the River Drava is located near Vajszló village. 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, forests and abandoned grasslands. 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. There was no grazing in the study area.

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 between November 2010 and March 2013 (jackal n = 373, fox n = 268 samples). Scat samples 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.

Scats were analyzed by means of a standard procedure. Diet composition of the predators was expressed in two ways: RFO and BC. To estimate the fresh mass of food ingested, all dry food remains were weighed separately and the food remain mass was multiplied by an appropriate conversion factor. Recorded animal food types were classified according to body mass and behavioural or ecological variables. Firstly, prey species were classified on the basis of their mass (< 15 g, 15-50 g, 51-100 g, 101-300 g, 301-1000 g, and > 1000 g). The second classification was based on the “zonations” (behavioural feature) such as: terrestrial (and mainly terrestrial but sometimes arboreal); arboreal (and mainly arboreal but sometimes terrestrial); and aquatic (or water-related). Thirdly, they were classified on the basis of their

typical habitat associations (or vegetation). Classes were: open field species (e.g. common vole *Microtus arvalis*); forest species or species living in dense shrubbery (e.g. bank vole *Myodes glareolus*); and habitat generalist species which may live both in open fields and in forests (e.g. *Apodemus* mice, European brown hare *Lepus europaeus*, wild ungulates). Fourthly, animal food species were classified on the basis of their typical environmental associations, such as: human-linked, wild, and mixed (which may live both near settlements and in the wild).

Data analysis

General log-linear likelihood tests were used on frequency of occurrence data to test for interspecific (between jackal and fox) and intraspecific differences. 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 comparisons, 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. MANOVAwas applied to explore intraspecific differences in consumption of fresh biomass of preys.

Trophic niche breadth was calculated in accordance with Levins. The trophic niche overlap was calculated by the Renkonen index. 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 (RFO) and estimated biomass (BC) values were compared using G-test.

Hierarchical cluster analysis was applied to compare diet composition among golden jackal and red fox.

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

Study area and species

The study area is located in the Lábod region. This is a flat, sand area. Forestry, wildlife management and crop cultivation are the predominant land use of the region. We calculated the viscera (stomach, intestines, oesophagus, heart, lung and liver) weight with a constant factor of 25% compared to full body mass. In the second survey occasion, viscera were collected and deposited by professional hunters in a properly fenced location inaccessible to jackals. Estimation of the carrion was based on the number of registered individuals and known average body mass data by species, sex and age group separately. The jackal density of the area was calculated from records of seven surveys.

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 occasions, respectively. We measured the 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.

We determined the percentage composition of food items in the stomach samples on the basis of RFO, FO and W. We categorised the jackals examined according to sex and season.

Data analysis

ANCOVA was used to compare the estimated total mass of detected mortality (as dependent variable; kg/km^2) between the two 2-yearly survey occasions (as fixed factors) depending on season (as covariate; three seasons). MANOVA was applied in the adult age group category of jackals

to examine body mass (after logarithmic transformation of the data) differences between the survey occasion, season and sex.

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

Relationships between basic data of the three calculation methods (RFO, FO and W) were significant according to the 16 main food taxa, so 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 occasion, season and sex. 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 occasion 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. The B_A values between the two survey occasions (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.

Diet composition calculation methods applied in the dissertation:

BC – calculated percentage biomass of food item consumed (in scat analysis)

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

RFO – percentage relative frequency of occurrence

W – percentage wet weight of all individual food remains found and separated in the samples (in stomach content analysis)

2.4. How successful bird nesting can be in a campus park?

Study area

The study area is the campus park of Kaposvár University is located on the area of 5 hectares. The campus is sorrounded by agricultural lands, tree alleys and forest patches.

Modeling

The survival chances of ground and shrub nesting bird species were tested with artificial nests and cluthes. Ground nests were formed by creating a depression in the soil using our heel. The artificial bush nests were cup-shaped made from wire mesh, attached to the foliage using wires at a height of 1-2 m and lined with grass litter. 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. Both years (2012, 2014) one quail egg and one plasticine egg of similar size were placed in each artificial nest.

Data collection and analysis

In both years the study was started on 10th May (second clutch period for many bird species) 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 and 08 h each time. Artificial nests were considered to be predated if at least one quail egg had disappeared or had been damaged. Nest predators were identified from the tooth or beak marks left by them on the plasticine eggs.

Daily survival rates of quail eggs were calculated with the Mayfield method and compared using the test proposed by Johnson. For the predation events of plasticine eggs, Chi-square test with Yates correction for continuity was applied.

3. RESULTS

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

In both surveys, small mammals (mainly *Microtus* voles and *Apodemus* mice) were the primary food type for the fox in the scat. The second important food was plants (mainly fruits), and the third was invertebrates (mainly beetles).

Based on the analysis from 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 (RFO, $P = 0.0022$; FO, $P = 0.0027$). When comparing the results from the second survey with those of the first survey, small mammals were consumed less frequently (RFO, 39.2% vs. FO, 26.8%), 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 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, $P = 0.030$).

There were also significant differences in the diet of the fox among seasons (RFO, $P = 0.009$; FO, $P = 0.0159$). The survey × season interaction was not significant (RFO, $P = 0.592$; FO, $P = 0.728$).

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

The golden jackal primarily consumed small mammals in all seasons (annual mean, RFO: 65.1 %, BC: 72.0 %). The main prey was the common vole. Other important food types were wild ungulates (annual mean, RFO: 7.6 %, BC: 13.2 %) and plants (annual mean, RFO: 17.8 %, BC: 12.8 %).

The consumption of cervids in winter and in spring was only detected in low proportions. By MANOVA no significant differences were found in consumption ratios depending on season (P = 0.825), year (P = 0.817) or these interactions (P = 0.901).

The red fox also primarily consumed small mammals (annual mean, RFO: 41.9 %, BC: 50.3 %), but their consumption dropped in summer and autumn. Most important prey species were also the common vole. Plants were a secondary important food item (annual mean: RFO: 30.2 %, BC: 29.7 %). Third most important items were ungulates (annual mean, RFO: 6.2 %, BC: 7.9 %, especially wild boar). The diet composition showed occasional significant differences (i.e. small mammals, invertebrates, plants) among seasons (log-linear analysis), 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 (P = 0.741), year (P = 0.622) or these interactions (P = 0.740).

Main effects of season were significant in the consumption of small mammals (P = 0.0004), and main effect of year was significant only in the consumption of wild boar (P = 0.0019), interactions were not significant.

The diet compositions of both predators were similar. Jackal and fox scat samples contained 33 and 32 different animal taxa. The standardized trophic niche (B_A) of both predators was equally very narrow (jackal vs. fox, occurrence: 0,13 vs 0,19, biomass: 0.09 vs. 0,09) 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. Significant interspecific differences were found 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 arboreal species than fox.

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

The total field-dressed mass of harvested big game was 271.6 kg year/km^2 in survey occasion 1 and 198.6 kg year/km^2 in survey 2. 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 survey occasions) showed a characteristic pattern, influenced by the hunting seasons. By ANCOVA, the estimated total mass of dead big game did not differ significantly between the first and second survey occasion (16.8 kg year/km^2 *vs.* 16.2 kg year/km^2, $P = 0.943$) and among seasons ($P = 0.639$).

The body mass of adult jackals did not differ between the survey occasions ($P = 0.513$), but differed depending on sex ($P < 0.001$) and season ($P = 0.006$). The survey occasion × sex interaction was significant ($P = 0.032$); 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 occasion than the first.

The proportion of empty stomachs (9.7% *vs*. 13.0%) did not differ significantly between the two survey occasions ($P = 0.498$). The weight of different food items in jackal stomachs was not significantly different between survey occasions ($P = 0.786$), season ($P = 0.912$) or sex ($P = 0.512$). The survey occasion × season interaction was significant for the December-April period ($P = 0.007$) as jackals had lower stomach content weights in the second survey occasion compared to the first.

In the first survey occasion, when food subsidies were present, the primary food of jackals was viscera and carrion (55% of diet). Adult wild boar was the second most important dietary component and cervids the third. In the

second survey occasion, 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.

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

In MANCOVA there was no significant difference in viscera and other carrion consumption either in the main effects (survey occasion, season, sex) or survey occasion × season interaction. In the first survey occasion, jackals consumed a higher proportion of adult wild boar (W: 11.6% *vs*. 1.3%), while in 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. Compared to other seasons, jackals in December-April consumed significantly higher proportions adult wild boar while in August-November they consumed more domestic animals, invertebrates and plants. The survey occasion × season interaction was significant in some cases. Significantly more adult wild boar consumption occurred in the first survey occasion 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 occasion in December-July.

Compared to the first survey occasion, 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, P = 0.256) and W data (0.10 ± 0.08 vs. 0.26 ± 0.03, P = 0.274). Compared to the first survey occasion, the stomachs in the second survey occasion contained significantly more food items (mean ± SE, 1.79 ± 0.15 and 2.55 ± 0.15, P = 0.002).

3.4. How successful bird nesting can be in a campus park?

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, P = 0.049). Inprints left on the plasticine eggs suggested small-sized bird and mammalian predators.

The daily survival rates of both nest types were significantly lower in the repeated survey in 2014, but the proportion of DSR of the two nest types were the other way round compared to the first study year. The daily survival rate of quial eggs in the ground nests was lower than in the shrub nests (0.833 and 0.912, respectively, P = 0.056) because of higher predation activity of small- and medium-sized mammals and birds. The results of our survey suggested that in the late breeding season nest predation was higher on ground nests than on elevated nests and the park maintanence had 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).

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. Domestic cats (*Felis catus*) were living and fed regularly by residents of the campus.

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 (maily corvids) accounted for almost all predation on shrub nests. Based on the tooth marks on the plasticine eggs, predation caused by mammals were frequent in both nest types.

4. CONCLUSIONS

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

There were significant differences in diet composition of foxes between the survey periods, supporting our hypothesis. 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 mammal decreased, while consumption of plants, invertebrates and wild boar increased. There were also significant differences in the diet of the fox among seasons. 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. The fox diet shifted (e.g consumption of wold boar increased) without the presence of a larger predator (e.g. golden jackal).

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

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 both predators were similar, with 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 in higher proportions wild ungulates (mainly wild boar, including piglets) in

winter and spring and plants in summer and autumn (mainly wild fruits). This experience confirms the jackal's relatively common choice of wild boar and, in comparison, the rare choice of cervids. The red fox consumed in higher proportions plants 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. Therefore, the first prediction was partially supported. Small-sized, terrestrial, open field living or habitat generalist and wild living animals were the most important food for both predators. In general, jackal, consumed higher ratios of forest-living and lower ratios arboreal species than fox. 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. The results did not support the second prediction, but partially supported the third one. Both carnivore species utilise many resource in varying degree 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.

The study confirmed the partial partitioning of food resources and opportunistic feeding of both canids.

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

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 survey occasions 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), while 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. All these only partially supported the second prediction.

Food removal, contrary to our first prediction, 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 jackal to the reduction of food subsidies were less pronounced than expected despite 50 kg of viscera removed per km^2 per year. Because in high big game density areas, wild ungulate carrion from different mortality causes are available in high

quantities throughout the year, predator populations can be maintained despite the high amount of viscera removal.

4.4. How successful bird nesting can be 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 the daily survival rate of ground nesting birds was significantly higher than the shrub nesting birds. The missing quail eggs were most likely taken away by corvids. 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 study the significant reduction of daily survival rates of both nest types can be explained by the increasing number of predators. The daily survival rates were high overall, which did not support the high bird nest loss expected (hypothesised) in the park.

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 rodents was frequent in both nest types. There was only one case of nest loss due to park management. We could not identify the red fox as a predator.

5. 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.

6. RECOMMENDATIONS

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

The dietary patterns and shifts in feeding habits over a long-term period of mesopredators, like the fox, 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 this could also help to gain a better understanding of the effects of change in the intensity of the agricultural production on trophic relationships 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.

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

Better knowledge of the ecological role of mesocarnivores may facilitate the choice of appropriate management approaches. Further field studies need to explore community level and area specific trophic interactions especially in human dominated habitats. The 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. It would be worthwhile to monitor the joint changes in the populations of the two canids.

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

To better understand the ecology of the jackal, during a long-term period, for example population size, reproduction and habitat use, parallel with feeding habits should be analysed in relation to food abundance (or amount of food available). 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. Leaving big game viscera or of domestic animal carcasses and garbage can maintain the population of scavengers.

4. How successful bird nesting can be in a campus park?

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, 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 (especially fall crops species for the winter bird guests). Many bird species prefer insects which are living in old, rotten trees, so it is necessary to not cut them in the park, or put some logs after security cutting, or place some new ones.

Should create undisturbed areas where no maintenance works can be tested, and these spaces should be impassable for dogs, cats or humans. Should create small lakes that increase the diversity and individual numbers of insects and water-bound or shyer birds. Parks provide shelter and favorable conditions for the breeding of many bird species, but in the case of high abundance of predators (mammals and birds), these habitats can operate as ecological traps.

7. PUBLICATION ON THE TOPIC OF DISSERTATION

Journal publications

Peer-reviewed papers published in journals

Nagyapáti N, Kurys A, Lanszki J, Purger JJ (2019): How Successfull Bird Nesting Can be in a Campus Park? Russian Journal of Ecology 50(6): 587–589.

Lanszki J, **Nagyapáti N**, Kurys A (2019): Long-term changes in the diet of the red fox in an agricultural area. Mammal Study 44(1): 33–40.

Lanszki J, Hayward MW, **Nagyapáti N** (2018): Feeding responses of the golden jackal after reduction of anthropogenic food subsidies. PloS ONE 13(12): e0208727.

Lanszki J, A Kurys, L Szabó L, **Nagyapáti N,** Porter LB, Heltai M (2016): Diet composition of the golden jackal and the sympatric red fox in an agricultural area (Hungary). Folia Zoologica 65(4): 310–322.

Scientific lectures

Nagyapáti N, Kurys A, Szabó L, Heltai M, Torbó L, Ćirović D, Penezić A, Lanszki J (2014): Study of the feeding habits of the golden jackal in Ormánság In: Zimmermann Z, Szabó G. (Eds.): „II. Sustainable development in the Carpathian Basin" international conference. Book of Abstracts, Szent István Egyetem, Gödöllő, pp. 104-106.

Nagyapáti N (2013): Az aranysakál és a vörös róka táplálkozási szokásainak összehasonlító vizsgálata az Ormánságban. In: Árgyalán T, Illyés Z, Nguyen DQ, Styevkó G, Szöllősi A (Szerk.): XXXI. Országos Tudományos Diákköri Konferencia Agrártudományi Szekció. Pályaművek Összefoglalói. Budapesti Corvinus Egyetem, Budapest.