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Diet composition of the long-legged buzzard (*Buteo rufinus*) in southeastern Bulgaria

Zloženie potravy myšiaka hrdzavého (*Buteo rufinus*) v juhovýchodnom Bulharsku

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Abstract: During 2018–2022, the local breeding population of the long-legged buzzard (*Buteo rufinus*) in southeastern Bulgaria was monitored in the territory of three districts of Sliven, Yambol and Burgas. Diet data were collected in 15 breeding pairs. Overall, we identified 290 prey items. We used three methods for diet analysis that produced different results: (1) collecting prey remains (68 individuals, 23.5%), (2) collecting pellets and skeletal materials (42 individuals, 14.5%), and (3) collecting data on a diet using trail cameras (180 individuals, 62.1%). The dominant part of the diet formed mammalian species (69.3%, ten species and some undetermined Rodentia and other Mammalia). Birds were less represented but with similar species richness (21.0%, 11 species and pigeons (*Columba* sp.), thrushes (*Turdus* sp.), undetermined Passeriformes and Galliformes). Compared to birds, the proportion of Reptilia was lower (9.3%, two species). Amphibia were represented only with one specimen of the common toad (*Bufo bufo*). The dominant diet of long-legged buzzards in southeastern Bulgaria was European souslik (*Spermophilus citellus*, 31.0%), followed by sibling vole (*Microtus mystacinus*, 25.5%). Less abundant taxa were undetermined Passeriformes (6.9%), lesser mole rat (*Nannospalax leucodon*, 5.9%), pigeons (4.5 %), blotched snake (*Elaphe sauromates*, 3.8%), Balkan green lizard (*Lacerta trilineata*, 3.5%), European hare (*Lepus europaeus*, 3.1%), common magpie (*Pica pica*, 2.8%), Colubridae (1.7%), common blackbird (*Turdus merula*, 1.4%), domestic chicken (*Gallus gallus domesticus*, 1.0%) and Eurasian skylark (*Alauda arvensis*, 1.0%). *Spermophilus citellus* was the most abundant species in the Yambol district samples and the most abundant species in the data obtained from trail cameras. In the Burgas district, the dominant species was *Microtus mystacinus*. When comparing the diet spectrum of *Buteo rufinus* from other authors, birds occurred more frequently than reptiles in our material.

Abstrakt: Počas rokov 2018–2022 bola sledovaná lokálna hniezdna populácia myšiakov hrdzavých (*Buteo rufinus*) v juhovýchodnom Bulharsku na území 3 okresov Sliven, Yambol a Burgas. Údaje o potrave boli zozbierané u 15 hniezdnych párov. Celkovo sme determinovali 290 vzoriek potravy. Použili sme tri metódy analýzy potravy, ktoré nám poskytli rozdielne výsledky: (1) zber zostatkov koristi (68 jedincov, 23,5 %), (2) zber vývržkov a kostrového materiálu (42 jedincov, 14,5 %) a (3) zber údajov o potrave fotopascami (180 jedincov, 62,1 %). Dominantnú zložku potravy tvorili cicavce (69,3 %, 10 druhov a niekoľko neurčených Rodentia a iné Mammalia). Vtáky boli menej zastúpené ale s podobnou bohatosťou druhov (21,0 %, 11 druhov a holuby (*Columba* sp.), drozdy (*Turdus* sp.), neurčené Passeriformes a Galliformes). V porovnaní s vtákmi bol podiel Reptilia nižší (9,3 %, 2 druhy). Amphibia boli prezentované jedným exemplárom druhu ropucha bradavičnatá (*Bufo bufo*). Dominantnou potravou myšiakov hrdzavých v juhovýchodnom Bulharsku bol syseľ pasienkový (*Spermophilus citellus*, 31,0 %), nasledovaný druhom hraboša (*Microtus mystacinus*, 25,5 %). Menej početné taxóny boli neurčené Passeriformes (6,9 %), slepec malý (*Nannospalax leucodon*, 5,9 %), holuby (4,5 %), užovka sarmatská (*Elaphe sauromates*, 3,8 %), jašterica smaragdová (*Lacerta trilineata*, 3,5 %), zajac poľný (*Lepus europaeus*, 3,1 %), straka obyčajná (*Pica pica*, 2,8 %), Colubridae (1,7 %), drozd čierny (*Turdus merula*, 1,4 %), kura domáca (*Gallus gallus domesticus*, 1,0 %) a škovránok poľný (*Alauda arvensis*, 1,0 %). *Spermophilus citellus* bol najpočetnejším druhom vo vzorkách z okresu Yambol a najčastešie sa vyskytoval v údajoch z fotopascí. V okrese Burgas bol dominantný druh *Microtus mystacinus*. Pri porovnaní potravných spektier *Buteo rufinus* od iných autorov sa v našom materiáli častejšie vyskytovali vtáky ako plazy.

Key words: long-legged buzzard, LLB, foraging, diet, prey, pellets, breeding biology, southeastern Bulgaria

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Introduction

Diet is an essential element for life and reproduction of species. The quantity, quality and availability of diet significantly affect not only individuals' overall fitness and physical and sexual activity but, ultimately, and most importantly, their survival and overall reproductive fitness (Trnka & Grim 2014). Diet studies provide information on prey species abundance and distribution (Bontzorlos et al. 2005). The food available is often a key factor affecting raptor population density and breeding performance. In species with varied diets, it is important to know the most frequent prey, as these will influence the predator most (Newton 1990). Each predator species uses specific hunting strategies to adapt to its particular environment. For the successful reproduction of raptors, especially at the edge of their range, it is necessary to know their foraging requirements. An understanding of the habitat and foraging requirements of raptors is essential for their conservation and management (Newton 1990).

The long-legged buzzard (*Buteo rufinus*) (LLB hereinafter) is a medium-sized raptor species with an estimated European population of approximately 13,000–23,000 pairs, making up approximately 17% of the total global population of this species. The global trend is considered stable with local fluctuations. Currently, the European trend is estimated to be increasing, and this is mainly due to range expansion to the north (Hagemeijer & Blair 1997, Demerdjiev et al. 2007, Daróczi & Zeitz 2008, Danko 2012, Birău et al. 2018, Keller et al. 2020, BirdLife International 2022). The population is thought to fluctuate in response to voles populations (Ferguson-Lees & Christie 2001), and the population of the species corresponds with that of European souslik (*Spermophilus citellus*) (Tucker & Heath 1994). It is a species of open areas, particularly steppe and semi-desert, rocky or stony habitats, also open woodland or woods with clearings, from plains and foothills to mountains; breeding from the coast up to at least 2,500 m a. s. l., and observed above 3,500 m a. s. l. (del Hoyo et al. 1994).

The LLB´s diet consists mainly of small mammals, e.g., gerbils (*Meriones*), rats (*Rattus*), voles (*Microtus*), young rabbits (*Oryctolagus*) and hares (*Lepus*), pikas (*Ochotona*); also reptiles, e.g., lizards (*Uromastix*, *Agama*) and snakes; some small birds, amphibians and large insects, e.g., locusts, grasshoppers (Orthoptera) and beetles (Coleoptera) (del Hoyo et al. 1994). Mammals include other smaller species such as the *Spermophilus*, hamsters (*Cricetus*), hedgehogs (*Hemiechinus*), and occasionally small *Lepus*, moles (*Talpa*), and weasels (*Mustela*). Reptiles regularly taken include lizards (*Lacerta*, *Eremias*) and snakes (*Natrix*, *Vipera*). Occasionally, frogs and toads (*Rana*, *Pelobates* and *Bufo*) are included in the diet and also birds whose size vary from larks (Alaudidae) to female common pheasant (*Phasianus colchicus*) and short-eared owl (*Asio flammeus*). In spring, summer, and autumn, larger insects may be an important part of the diet, especially Orthoptera and Coleoptera. In winter quarters, it eats carrion and attacks young poultry (*Gallus*) and wounded waterfowl (Anatidae) (Cramp & Simmons 1980).

The LLBs‘ diet composition was examined, for instance, in the northern limit of the species' breeding distribution from the lower Kuma River (Russia). Of 171 and 108 pellets collected over two summers, mammals were present in 85.9% and 69.4% of cases, respectively

– mainly little souslik (*Spermophilus pygmaeus*) rather fewer midday gerbils (*Meriones meridianus*) and tamarisk gerbils (*Meriones tamariscinus*), grey dwarf hamster (*Cricetulus migratorius*), house mouse (*Mus musculus*), social vole (*Microtus socialis*), northern mole vole (*Ellobius talpinus*), shrews (Soricidae), and in one, least weasel (*Mustela nivalis*); also reptiles 34.5% and 42.6%, insects 25.2% and 36.1%, amphibians 10.0% and 12.9%, and birds 7.0% and 16.6% (Cramp & Simmons 1980). In the diet spectrum of LLB in the Dnipropetrovsk region, Ukraine, the species *Spermophilus pygmaeus*, sand lizard (*Lacerta agilis*), *Microtus mystacinus* and European hare (*Lepus europaeus*) were found (Syzhko 2005). In the Mykolaiv region, Ukraine, the diet was dominated by mammals (60%), followed by reptiles (17.6%) including *Natrix* sp. and blotched snake (*Elaphe sauromates*), birds (9.5%), invertebrates (12.4%) and amphibians (0.5%) (Redinov 2010). Prevalent among the mammals were the Podolian souslik (*Spermophilus odessanus*) and Podolsk blind mole-rats (*Spalax zemni*), although in other parts of Ukraine *Microtus mystacinus* is the most common prey of the LLB (Redinov 2012). Among birds, *Phasianus colchicus*, red-footed falcon (*Falco vespertinus*) and common quail (*Coturnix coturnix*) were recorded (Redinov 2010). In Slovakia, during observation of LLB in the summer of 2012 on the Východoslovenská rovina Lowlands, all individuals exclusively hunted common vole (*Microtus arvalis*) on cultivated fields, in which year a population increase took place (Danko 2012). In Hungary, 14 LLB´s stomachs collected in August–November contained *Microtus arvalis* (6 individuals), *Spermophilus citellus* (4 inds.), young *Lepus europaeus* (1 ind.), unidentified taxa (2 inds.), *Rana* (2 inds.), *Pelobates* (1 ind.), green toad (*Bufotes viridis*, 1 ind.), *Lacerta* (1 ind.), small *Natrix* (1 inds.), locust (1 ind.), cricket (*Gryllus*, 1 ind.); in one stomach from March, *Talpa*, *Citellus*, *Mustela*, and *Gryllus* (Cramp & Simmons 1980). In the diet of a LLB on the territory of the Hortobágy Plain Kalotás (1992) found 94 separate taxa (67 insects, 72%), the most numerous of which (65 inds., 69.1%) were Coleoptera, from mammals the most numerous was *Spermophilus citellus* with 18 individuals. He found only seven *Microtus* individuals. In Romania, *Spermophilus citellus* was found as prey on the more occupied LLB´s nests in Dobrogea southeastern Romania (Dravecký in Danko 2012) and was considered the primary trophic source in southwestern Romania (Birău et al. 2018).

Diet of LLB has also been studied at the southwestern limit of the species breeding range in Greece, Iran and Cyprus (Alivizatos & Goutner 1997, Khaleghizadeh et al. 2005, Iezekiel et al. 2016, Kassinis 2009, Kassinis et al. 2022). Feeding of LLB was studied in the Evros province of NE Greece (Alivizatos & Goutner 1997). Regarding biomass, the diet consisted of mammals (59%), reptiles (27%), birds (13%), insects (0.6%) and centipedes (0.4%). Khaleghizadeh et al. (2005) studied the diet of LLB in Turan Biosphere Reserve, Iran. In that study, the percentage of mammals in the diet of the LLB was 61.5%, of birds 11.7%, and of reptiles 5.9% (only Mediterranean spur-thighed tortoise, *Testudo graeca*). Another study in SW Iran recorded high diversity of reptilians in the diet and the dominance of the Persian squirrel (*Sciurus anomalus*) among mammalian species (Shafaeipour 2015). Among the reptiles, three species were preferred by the LLB – spotted whip snake (*Hemorrhois ravergieri*), large-scaled rock agama (*Laudakia nupta*) and brilliant ground agama (*Trapelus agilis*). Bakaloudis et al. (2012) studied some biases in diet research methods for LLB in Cyprus. They found that the prey remains method differed significantly from pellet analysis due to more birds and fewer lizards, but it showed the broadest trophic spectrum. According to both study methods, the prevailing prey of the LLB in Cyprus were mammals, followed by reptiles and birds. Prey items were determined to family level. Lizards were found much more often in the diet compared to snakes. Kassinis et al. (2022) obtained similar results, but the prey items were determined to species level. The most numerous prey species were black rats (*Rattus rattus*), starred agamas (*Stellagama stelio*), *Mus musculus*, and large black whip snakes (*Dolichophis jugularis*). Still, regarding biomass, the most important prey items were *Rattus rattus*, *Dolichophis jugularis*, long-eared hedgehogs (*Hemiechinus auritus dorotheae*) and *Stellagama stelio*.

The diet of LLB in Bulgaria was studied by Milchev (2009). The research was carried out in the rocky habitats (three quarries) of southeastern Bulgaria (the Sliven district was not included in that research). The food remains (pellets, skin, feathers and bones) have been collected during three breeding seasons from two nests and from the resting places of the birds in two rocky quarries in St. Ilijski hills and Bakadzhik hills, and only from the resting site of the adults in the third quarry in Hisar hills. The diet of the breeding LLB included 34 taxa, mostly mammals (68.8%) followed by reptiles (13.2%) and birds (9.0%). *Microtus* sp. and *Spermophilus citellus* were the most abundant prey, with 22.2% and 18.5% of all prey items, respectively. Common rats (*Rattus norvegicus*) and water voles (*Arvicola amphibius*) were involved among the important prey – 10.6% and

8.5%, respectively. *Lepus europeus* was encountered on four occasions. Compared with birds, reptiles had a prevalence of 13.2%, and only two snakes (large whip snake (*Dolichophis caspius*) and *Natrix* sp.) and two lizards species (European green lizard, *Lacerta viridis* and Balkan green lizard, *Lacerta trilineata*) were found. Twelve species of birds (9.0%) were detected including passerines (Eurasian skylark, *Alauda arvensis*), crested lark (*Galerida cristata*), common starling (*Sturnus vulgaris*), trush (*Turdus* sp., juv.), Eurasian jay (*Garrulus glandarius*), hooded crow (*Corvus cornix*) but also quite big birds as chukar partridge (*Alectoris chukar*), Eurasian stone-curlew (*Burhinus oedicnemus*), common moorhen (*Gallinula chloropus*) and pigeons domestic pigeon (*Columba livia* f. *domestica*) and common wood pigeon (*Columba palumbus*). Invertebrates were found with a prevalence of 7.4% of all prey items.

In addition to the results on a diet from the three quarries, Milchev (2009) added the identified diet from the Sakar Mountains. He found five species (6 inds.) of birds – black-crowned night heron (*Nycticorax nycticorax*, 1 ind.), grey partridge (*Perdix perdix*, 1 ind.), common turtle dove (*Streptopelia turtur*, 1 ind.), calandra lark (*Melanocorypha calandra*, 2 inds.), barred warbler (*Sylvia nisoria*, 1 ind.), two species (2 inds.) of reptiles (Montpelier snake, *Malpolon monspessulanus* and sand viper, *Vipera amodytes*), one Orthoptera white-faced bush cricket (*Decticus albifrons*, 2 inds.).

The aim of our work was to contribute to the knowledge of the diet composition of the LLB from the territory of southeastern Bulgaria based on a study of the local population of the species within three districts of Sliven, Yambol and Burgas.

Material and methods

Studied species

The LLB is currently distributed almost throughout the whole territory of Bulgaria, especially in flat and low-mountain areas. It nests in ravines, hillsides, foothills, low mountains, but also in lowlands and plains where there are inland cliffs and exposed rocks, rarely on sea cliffs and trees, as well as on power line poles, abandoned quarries and slopes with eroded soil. Its breeding population in Bulgaria is estimated at 650–750 pairs (Demerdjiev et al. 2007).

Until the mid-20th century, the LLB was considered a rare migrant (Patev 1950). It might bred in Bulgaria as early as the 1940s (Boev 1962). Michev et al. (1984) and Simeonov et al. (1990) assumed it had been breeding in Bulgaria since 1950. A substantial increase in the number of breeding pairs in Bulgaria (up to ca. 300) has been recorded (Michev & Jankov 1993), to 200–300 pairs in 1997 (Kostadinova 1997, Hagemeijer & Blair 1997), 250–400 pairs for the period 1998–2002 (BirdLife International 2004), 700 pairs (Nankinov et al. 2004), 650–750 pairs in 2005 (Demerdjiev et al. 2007) and 800–1000 pairs in 2011 (Golemansky 2011, Mebs & Schmidt 2014). Several papers have been published on the biology, conservation and distribution of the species in Bulgaria (Michev et al. 1984, Vatev 1987, Borisov 1988, Karaivanov 2000, Milchev 2009, Milchev & Georgiev 2012, Demerdjiev et al. 2007, 2014, Vatev et al. 2015, Djorgova et al. 2021).

Study area

This study was conducted in the northern parts of the Tundzha River Plain and Burgas Plain, southeastern Bulgaria. It covers parts of three administrative districts – Sliven, Yambol, and Burgas (Fig. 1).

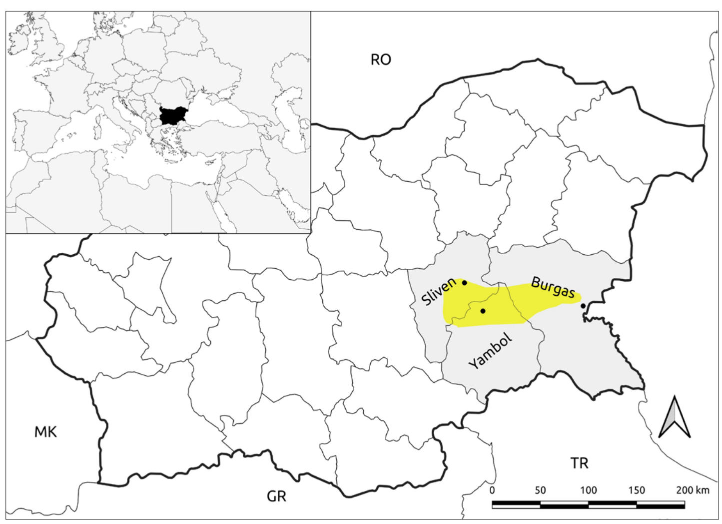

Fig. 1. The study area (marked in yellow) in southeastern Bulgaria on the territory of the three districts of Sliven, Yambol and Burgas.
Obr. 1. Územie výskumu (vyznačené žltou) v juhovýchodnom Bulharsku na území troch okresov Sliven, Yambol a Burgas.

The total area of the study was approximately 2000 square km. The area is primarily plain, with many hills and ridges. It borders low mountain areas to the north, part of the Stara Planina Mountains range. The average altitude of the Tudzha River Valley is 387 m. The vegetation is presented mainly by agricultural lands, orchards, pastures and steppes. Bushes and low oak forests cover the slopes. There are some bigger forest complexes - mainly in the Burgas district. Riparian forests are present along the Tundzha River. The climate of this area is transitional between Temperate and Mediterranean, with mild winters, almost without snow coverage, and hot, dry summers. The average winter temperature varies between 0 and 1.2°C. The average summer temperature ranges between 24 and 26°C. The area is characterized by strong winds, especially on the southern slopes of Stara Planina Mountains and close to the Black Sea (Burgas district) (Kopralev 2002). There are many small freshwater artificial lakes in the area. The western and central parts of the studied site belong to the Tundzha River Basin, while the eastern parts relate to the Black Sea Basin.

Data collection and analyses

During 2018–2022, the local breeding population of LLB in southeastern Bulgaria was monitored in the three districts of Sliven, Yambol and Burgas (Fig. 1). 21 breeding pairs (BP hereinafter) were confirmed with 30 nests found in an area of about 2000 squared km. Foraging data were collected for 15 checked BPs between 2018 and 2022, of which there were 4 BPs in Yambol district, 6 BPs in Sliven and 5 BPs in Burgas. Each locality was identified with an order number and pair code according to the location of the BP in each district - Yambol (Y) 4 BPs (order number 1–4, BP code Y1–Y4), Sliven (S) 6 BPs (order number 5–10, BP code S1–S6) and Burgas (B) 5 BPs (order number 11–15, BP code B1–B5) (Tab. 1). In each BP, at least one occupied nest was found. Fourteen BPs had one nest, and one BP (BP code S4) had two nests (S4a and S4b). Two breeding BPs had nests located in the quarry (BPs code Y4 and B3). The other 13 breeding pairs had nests built in trees (Tab. 1). One BP's breeding territory is considered one locality of food data collection. The locations of all nest sites found in the survey area were recorded using a GPS. The techniques for assessing raptor diets vary according to the species and its main prey (Newton 1990). We used three methods for the diet analysis:

1. Collecting prey remains

Prey remains were collected inside the nests during the ringing period of the chicks at about 21–40 days. Nest inspections for this purpose were carried out only once during the breeding season to avoid disturbing adults and the breeding process. Prey remains (whole or parts of animals body) were identified based on the shape and colour of the tarsus, bill, rectrices, remiges, and other notable characteristics of feathers of birds; the colour of the fur, skin, and hair of mammals; and the tail of mammals and reptiles. Overall, 68 prey remains samples from nests of 13 BPs (BP code S4 involves two nests, S4a and S4b) from all five study years, were included in subsequent analyses (Tab. 1).

2. Collecting pellets and skeletal materials

Pellets and skeletal materials were collected only inside the nests during the ringing period of chicks at about 21–40 days. The pellets were soaked in a 5% NaOH solution for one hour. After, hair and feather debris were dissolved, samples were rinsed on a dense sieve under running water and in a container with still water. Floating body parts of insects and hollow bird bones were collected. Using circular washing motion, all debris were washed out until only bones remained. After drying the washed sample, we sorted out the jaw bones (maxilla and mandible, as well as some teeth) of the mammals (Mammalia), the beaks, tarsometatarsi, humeral and metacarpal bones (*rostrum*, *tarsometatarsus*, *humerus* and *metacarpus*) of the birds (Aves), iliac bones (*os ilium*) of the frogs (Anura) and the jaws of the reptiles. The number of individuals of each taxon was calculated as the number of the most frequent body parts in the sample (e.g. left or right mandible or maxilla in mammals or reptiles, one out of four types of bones in birds, left or right iliac bone in frogs). The identification of bones was carried out according to the reference collections of vertebrate skeletons from captured or deceased animals and according to the published identification guides (Anděra & Horáček 1982, Mendellsohn & Yom-Tov 1987, Harrison & Bates 1991, Gromov & Erbajeva 1995, Kryštufek & Vohralík 2001, 2005, 2009). In total, 42 pellet and skeletal material samples from nests of 9 BPs from two years 2021 and 2022 were included in the follow-up analyses (Tab. 1).

3. Collecting data on a diet using trail cameras

During 2021–2022, trail cameras were used to collect feeding data from occupied nests. In 2021, the first trail camera was used on a trial basis and captured six prey items from one nest. In 2022, three trail cameras were installed in three nests before the start of the breeding season and captured data of 174 prey items delivered

Tab. 1. Three different methods R - collecting prey remains, P - collecting pellets and skeletal materials and TC - collecting data on diet using trail cameras used to collect diet data on nests of 15 pairs of the long-legged buzzard (*Buteo rufinus*) in southeastern Bulgaria in 2018–2022. BP - breeding pair, BP No - breeding pair number, Y1 - BP/nest code, Y - Yambol district, S - Sliven district, B - Burgas district, t - nest built on tree, q - nest built in quarry.

Tab. 1. Tri rozdielne metódy R - zber zostatkov koristi, P - zber vývržkov a kostrového materiálu a TC - zber údajov o potrave fotopascami použité na získanie údajov o potrave na hniezdach 15 párov myšiakov hrdzavých (*Buteo rufinus*) v juhovýchodnom Bulharsku v rokoch 2018–2022. BP - hniezdny pár, BP No - číslo hniezdneho páru, Y1 - kód hniezdneho páru/hniezda, Y - Yambol okres, S - Sliven okres, B - Burgas okres, t - hniezdo postavené na strome, q - hniezdo postavené v kamenolome.

BP No		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**		**9**	**10**	**11**	**12**	**13**	**14**	**15**			**Total**	
BP/nest code		Y1	Y2	Y3	Y4	S1	S2	S3	S4a	S4b	S5	S6	B1	B2	B3	B4	B5				
tree/quarry		t	t	t	q	t	t	t	t	t	t	t	t	t	q	t	t	**n**	**%**	**n**	**%**
Years	**Methods**																				
	R	1	0	0	0	2	2	1	2	0	0	0	2	0	0	0	0	10	3.45		
2018	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	10	3.45
	TC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00		
	R	1	8	0	0	0	0	0	0	0	0	0	1	0	0	0	0	10	3.45		
2019	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	10	3.45
	TC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00		
	R	0	0	0	0	0	0	4	0	0	0	0	6	0	0	0	0	10	3.45		
2020	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	10	3.45
	TC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00		
	R	0	0	2	1	0	0	1	0	3	0	0	1	3	4	3	0	18	6.21		
2021	P	1	0	5	0	0	0	1	0	0	2	0	4	0	0	1	0	14	4.83	38	13.0
	TC	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	6	2.07		
	R	1	0	3	0	0	0	0	7	0	0	1	0	0	5	3	0	20	6.89		
2022	P	8	0	3	0	0	0	3	5	0	0	1	0	0	0	0	8	28	9.65	222	76.55
	TC	0	0	72	0	0	0	42	0	0	0	0	0	0	0	0	60	174	60.00		
	R	3	8	5	1	2	2	6	9	3	0	1	10	3	9	6	0	68	23.45		
2018–22	P	9	0	8	0	0	0	4	5	0	2	1	4	0	0	1	8	42	14.48	290	100
	TC	0	0	72	0	0	0	42	0	0	0	0	6	0	0	0	60	180	62.07		
∑		12	8	85	1	2	2	52	17		2	2	20	3	9	7	68	290	100		

to the chicks by the parents. In several cases, the male delivered the diet to the incubating female. Denver WCS 5020 trail cameras were used to monitor diet delivery to the nest by the adults. The trail cameras were installed before the start of the breeding season on 12–15 March 2022 and removed on 31 July 2022. Pictures of nests were taken at 30-minute intervals over 3.5 months.

Overall, 180 data on a diet using trail cameras from nests of 4 BPs from 2021 and 2022 were included in subsequent analyses (Tab. 1).

Collecting prey remains on the nest was implemented during all five years of our research from 2018–2022. It was the only method used in the foraging survey in 2018–2020. In 2021 and 2022, two additional research methods were added: collecting pellets and skeletal materials and collecting data on a diet using trail cameras. In these years, two or three methods were used simultaneously on some nests of breeding pairs (Tab. 1). With a combination of 2 methods (collecting prey remains and collecting pellets and skeletal materials) carried out once a year at the same time on a nest, it is unlikely that there will be duplication of data in prey determination. The first method assesses fresh food brought to the nestlings, either whole bodies or significant parts of them, while the second method collects pellets and bones simultaneously. It is unlikely that at the same time part of the food is fresh on the nest and at the same time part of the food has already been consumed, digested and discarded in the form of pellets. From this we assume that for this combination of the two methods (in this particular situation), overlapping of methods and duplication of results is unlikely. In the case of a combination of all three methods used simultaneously on a nest, if the collecting prey remains method confirms the same prey species during nest inspection as the trail camera method, then such prey samples are excluded from further analyses. In case the collected pellets and skeletal materials from the nest confirm new prey species that were not detected by the trail camera method, these species are included in the LLB diet composition results.

Data evaluation

Tables 3–5 display the evaluated data using MDFM method (The method marked differences from the mean) (Obuch 2001). The symbol "+" means significantly higher abundance than the mean value of species in the evaluating file. The mean value was expressed as a sum and its percentage value in the last columns of the table. The values with significantly lower abundance than the mean are marked with the symbol "-". Numbers "1+, 2+..." and "1-, 2-..." indicate the degree of differences from the mean. In Tabs. 3–5, species are placed in order so that positive (+) values of MDFM created clusters highlighted by grey color in a particular data field. More abundant species without MDFM are placed in order under the dashed line from the most abundant to less abundant. Other species are listed below the table. At the bottom of the tables are sums for the classes of Vertebrata and Evertebrata as well as Shannon & Weaver (1949) biodiversity index. Our study compares the results with those of the authors from neighbouring countries such as Ukraine, Bulgaria, Iran and Cyprus.

Results

We determined 290 prey items of LLB in southeastern Bulgaria. The dominant part of the diet formed mammalian species (69.3%, ten species and some undetermined Rodentia and other Mammalia) (Tab. 2, Fig. 2). Birds were less represented but with the similar species richness (21.0%, 11 species and *Columba* sp., *Turdus* sp., undetermined Passeriformes and Galliformes). Compared to birds, the proportion of Reptilia was lower (9.3%, two species). Amphibia were represented only with one specimen of the *Bufo bufo*. The dominant diet of LLB in southeastern Bulgaria was *Spermophilus citellus* (31.0%) (Fig. 3), followed by *Microtus mystacinus* (25.5%). Less abundant taxa were undetermined Passeriformes (6.9%), the lesser mole rat (*Nannospalax leucodon*, 5.9%) (Fig. 4), *Columba* sp. (4.5%), *Elaphe sauromates* (3.8%) (Fig. 5), *Lacerta trilineata* (3.5%) (Fig. 6), *Lepus europaeus* (3.1%), common magpie (*Pica pica*, 2.8%) (Fig. 2), Colubridae (1.7%) (Fig. 7), the common blackbird (*Turdus merula*, 1.4%), the domestic chicken (*Gallus gallus domesticus*, 1.0%) and *Alauda arvensis* (1.0 %) (Tab. 2).

Fig. 2. Mammals and birds remains identified during nest inspection (*Lepus*, *Martes*, *Alauda*, *Pica*). Yambol district, breeding pair/nest code - Y2, 26 May 2019. Photo: M. Dravecký.
Obr. 2. Zvyšky cicavcov a vtákov určených pri kontrole hniezda (*Lepus*, *Martes*, *Alauda*, *Pica*). Yambol okres, kód hniezdneho páru/hniezda - Y2, 26 Máj 2019. Foto: M. Dravecký.

Fig. 3. *Spermophilus citellus* (3 individuals in the nest) dominant prey for *Buteo rufinus* in southeastern Bulgaria. Yambol district, breeding pair/nest code - Y3, 29 June 2022. Photo: M. Dravecký / Trail camera Denver WCS 5020.
Obr. 3. *Spermophilus citellus* (3 jedince v hniezde) dominantná potrava *Buteo rufinus* v juhovýchodnom Bulharsku. Yambol okres, kód hniezdneho páru/hniezda - Y3, 29 Jún 2022. Foto: M. Dravecký / Fotopasca Denver WCS 5020.

Tab. 2. Diet composition of the long-legged buzzard (*Buteo rufinus*) in the nests of breeding pairs studied in southeastern Bulgaria in 2018–2022. BP - breeding pair, BP No - breeding pair number, Y1 - breeding pair code, Y - Yambol district, S - Sliven district, B - Burgas district, N - number of prey items.

Tab. 2. Zloženie potravy myšiaka hrdzavého (*Buteo rufinus*) v hniezdach hniezdnych párov skúmaných v juhovýchodnom Bulharsku v rokoch 2018–2022. BP - hniezdny pár, BP No - číslo hniezdneho páru, Y1 - kód hniezdneho páru, Y - Yambol okres, S - Sliven okres, B - Burgas okres, N - počet objektov potravy.

BP No	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**∑**	**%**
Species / BP code N	**Y1**	**Y2**	**Y3**	**Y4**	**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**B1**	**B2**	**B3**	**B4**	**B5**		
Talpa europaea	1														1	2	0.69
Lepus europaeus		1					1	2			2	1		2		9	3.1
Spermophilus citellus	1		44		1		29	1		1			5		8	90	31.03
Nannospalax leucodon	1		10				1			1	4					17	5.86
Mus musculus			1					1								2	0.69
Apodemus sylvaticus							1									1	0.34
Apodemus microps								1								1	0.34
Microtus mystacinus	6		15				12				2				39	74	25.52
Rodentia			2													2	0.69
Martes martes		1														1	0.34
Mustela nivalis			1													1	0.34
other Mammalia							1									1	0.34
Mammalia	**9**	**2**	**73**	**0**	**1**	**0**	**45**	**5**	**0**	**2**	**8**	**1**	**5**	**2**	**48**	**201**	**69.31**
Accipiter nisus															1	1	0.34
Buteo rufinus															1	1	0.34
Falco tinnunculus											1				1	2	0.69
Perdix perdix			1													1	0.34
Gallus gallus dom.		2						1								3	1.03
Galliformes		1														1	0.34
Columba oenas			1													1	0.34
Columba sp.	1	1	2	1		1	1	2			2	1	1			13	4.48
Alauda arvensis		1						2								3	1.03
Turdus merula			1										1	2		4	1.38
Turdus sp.											1					1	0.34
Troglodytes troglodytes			1													1	0.34
Passer hispaniolensis											1					1	0.34
Pica pica		1	1			1		2					1		2	8	2.76
Passeriformes	2		1		1		3		1		7	1	1	2	1	20	6.9
Aves	**3**	**6**	**8**	**1**	**1**	**2**	**4**	**7**	**1**	**0**	**12**	**2**	**4**	**4**	**6**	**61**	**21.03**
Bufo bufo									1							1	0.34
Lacerta trilineata			1				4								5	10	3.45
Elaphe sauromates			2					1							8	11	3.79
Coluber sp.															1	1	0.34
Colubridae			1					3						1		5	1.72
Amphibia, Reptilia	**0**	**0**	**4**	**0**	**0**	**0**	**4**	**4**	**1**	**0**	**0**	**0**	**0**	**1**	**14**	**28**	**9.66**
∑	**12**	**8**	**85**	**1**	**2**	**2**	**53**	**16**	**2**	**2**	**20**	**3**	**9**	**7**	**68**	**290**	**100**

Based on the analysis of prey remains from nests, *Lepus europaeus*, *Columba* sp. and unidentified species of small songbirds (order Passeriformes) were more frequently detected. The trail cameras recorded the delivery of *Spermophilus citellus* to the nests more frequently. Less prey items were recovered from the osteological remains in the pellets, but more individuals could be detected to species level. Therefore, this method's diversity index (H′ = 2.38) is the highest (Tab. 3).

The comparison of summary results from three neighboring districts shows the food spectra to be quite similar. Only, *Spermophilus citellus* in the Yambol district and the *Microtus mystacinus* in the Burgas district were more abundant (Tab. 4).

Tab. 3. Comparison of the long-legged buzzard (*Buteo rufinus*) diet composition in the nests investigated in southeastern Bulgaria in 2018–2022 obtained by different methods - identification of food remains on the nests, analysis of pellets and trail cameras. Method No - method number, N - number of prey items.
Tab. 3. Porovnanie zloženia potravy myšiaka hrdzavého (*Buteo rufinus*) v hniezdach skúmaných v juhovýchodnom Bulharsku v rokoch 2018–2022 získané rozdielnými metódami - identifikáciou zbytkov potravy na hniezde, rozborom vývržkov a fotopascami. Method No - číslo metódy, N - počet objektov potravy.

Method No		**1**		**3**		**2**		
Species / Method N		**Remains**		**Trail cameras**		**Pellets**	∑	%
Lepus europaeus	1+	7	1-	1		1	9	3.1
Columba sp.	1+	13	1-	0			13	4.48
Passeriformes	1+	15	1-	3		2	20	6.9
Spermophilus citellus	1-	10	1+	78	2-	2	90	31.0
Microtus mystacinus	2-	2		56		17	75	25.9
Nannospalax leucodon		1		13		3	17	5.86
Elaphe sauromates				9		2	11	3.79
Lacerta trilineata				9		1	10	3.45
Pica pica		6		2			8	2.76
Colubridae		3				2	5	1.72
Mammalia	1-	21		152		28	201	69.3
Aves	2+	44	2-	9		8	61	21.0
Amphibia, Reptilia		3		19		6	28	9.66
∑		68		180		42	290	100
Diversity Index H’		2.25		1.53		2.38	2.28	

Legend / Legenda:
Other species / Ostatné druhy (**Method Number / metóda číslo** – number / počet): *Talpa europaea* (**3**-1; **2**-1), *Mus musculus* (**3**-1; **2**-1), *Apodemus sylvaticus* (**2**-1), *Apodemus microps* (**2**-1), Rodentia (**3**-2), *Martes martes* (**1**-1), *Mustela nivalis* (**2**-1), *Accipiter nisus* (**3**-1), *Buteo rufinus* (**2**-1), *Falco tinnunculus* (**3**-1; **2**-1), *Perdix perdix* (**2**-1), *Gallus gallus domestica* (**1**-3), Galliformes (**1**-1), *Columba oenas* (**2**-1), *Alauda arvensis* (**1**-3), *Turdus merula* (**1**-3; **3**-1), *Turdus* sp. (**2**-1), *Troglodytes troglodytes* (**3**-1), *Passer hispaniolensis* (**2**-1), *Bufo bufo* (**2**-1), *Coluber* sp. (**3**-1).

Tab. 4. Diet composition of the long-legged buzzard (*Buteo rufinus*) in the nests of breeding pairs investigated in southeastern Bulgaria in 2018–2022 in Yambol, Sliven and Burgas districts. District No - district number, N - number of prey items.
Tab. 4. Zloženie potravy myšiaka hrdzavého (*Buteo rufinus*) v hniezdach hniezdnych párov skúmaných v juhovýchodnom Bulharsku v rokoch 2018–2022 v okresoch Yambol, Sliven a Burgas. District No - číslo okresu, N - počet objektov potravy.

District No		**1**		**2**		**3**		
Species / District N		**Yambol**		**Sliven**		**Burgas**	∑	%
Spermophilus citellus	1+	45		32	1-	13	90	31.0
Microtus mystacinus		21	1-	12	1+	41	74	25.5
Passeriformes		3		5		12	20	6.9
Nannospalax leucodon		11		2		4	17	5.86
Columba sp.		5		4		4	13	4.48
Elaphe sauromates		2		1		8	11	3.79
Lacerta trilineata		1		4		5	10	3.45
Lepus europaeus		1		3		5	9	3.1
Pica pica		2		3		3	8	2.76
Colubridae		1		3		1	5	1.72
Mammalia		84		53		64	201	69.3
Aves		18		15		28	61	21.0
Amphibia, Reptilia	1-	4		9		15	28	9.66
∑		106		77		107	290	100
Diversity Index H’		2.04		2.1		2.18	2.3	

Legend / Legenda:
Other species / Ostatné druhy (**District Number / okres číslo** – number / počet): *Talpa europaea* (**1**-1; **3**-1), *Mus musculus* (**1**-1; **2**-1), *Apodemus sylvaticus* (**2**-1), *Apodemus microps* (**2**-1), Rodentia (**1**-2), *Martes martes* (**1**-1), *Mustela nivalis* (**1**-1), iné Mammalia (**2**-1), *Accipiter nisus* (**3**-1), *Buteo rufinus* (**3**-1), *Falco tinnunculus* (**3**-2), *Perdix perdix* (**1**-1), *Gallus gallus domesticus* (**1**-2; **2**-1), Galliformes (**1**-1), *Columba oenas* (**1**-1), *Alauda arvensis* (**1**-1; **2**-2), *Turdus merula* (**1**-1; **3**-3), *Turdus* sp. (**3**-1), *Troglodytes troglodytes* (**1**-1), *Passer hispaniolensis* (**3**-1), *Bufo bufo* (**2**-1), *Coluber* sp. (**3**-1)

Discussion

The comparison of summary results from three neighbouring districts shows that the food spectra are quite similar. Only in the Yambol district, *Spermophilus citellus* and in the Burgas district the *Microtus mystacinus* were more abundant.

Comparing the efficiency of collecting diet composition data by the three different methods, the efficiency was highest for the method using trail cameras, but with less accurate determination at the species level. In 2021 and 2022, trail cameras recorded 180 prey items, representing 62.1% of all LLB diet data collected collectively by all three methods. The advantage of this method was the ability to collect data on food brought to the nestlings on nests by adults throughout the whole breeding season. In the trail cameras, we recorded the delivery of *Spermophilus citellus* to the nests more frequently.

Diet at nests, at 21-40 days of age of the juvenile, is consumed relatively quickly by the nestlings and food remains are rarely left at the nest. For that reason, only 68 individuals (23.4%) were detected by this method during the five years of this study. Based on the analysis of prey remains from nests, *Lepus europaeus*, *Columba* sp. and unidentified species of small songbirds (Passeriformes) were more frequently detected.

Fewer prey items were recovered from the osteological remains in the pellets, as bones are strongly degraded in the digestive tract of the buzzards. Still, this method could detect more individuals to the species level. Therefore, this method’s diversity index (H′ = 2.38) is the highest.

Fig. 4. *Nannospalax leucodon* (rare species) was relativelly often confirmed in the nests as a prey (detail). Burgas district, breeding pair/nest code - B1, 10 June 2020. Photo: G. Dilovski
Obr. 4. *Nannospalax leucodon* (zriedkavý druh) bol relatívne často potvrdený na hniezde ako korisť (detail). Burgas okres, kód hniezdneho páru/hniezda - B1, 10 Jún 2020. Foto: G. Dilovski

Fig. 6. *Lacerta trilineata* in the nest confirmed by instaled trail camera. Burgas district, breeding pair/nest code - B5, 26 May 2022. Photo: M. Dravecký / Trail camera Denver WCS 5020.
Obr. 6. *Lacerta trilineata* v hniezde potvrdená fotopascou. Burgas okres, kód hniezdneho páru/hniezda - B5, 26 Máj 2022. Foto: M. Dravecký / Fotopasca Denver WCS 5020.

Fig. 5. *Elaphe sauromates* app. 100–120 cm long snake in the nest as a prey. Yambol district, breeding pair/nest code - Y3, 1 June 2022. Photo: M. Dravecký / Trail camera Denver WCS 5020.
Obr. 5. *Elaphe sauromates* približne 100–120 cm dlhý had v hniezde ako potrava. Yambol okres, kód hniezdneho páru/hniezda - Y3, 1 Jún 2022. Foto: M. Dravecký / Fotopasca Denver WCS 5020.

Fig. 7. Colubridae (app. 3–4 inds. complette skeletons / vertebrae), *Lepus europaeus* (two legs) and *Columb*a sp. Sliven district, breeding pair/nest code - S4a, 21 June 2022. Photo: G. Dilovski
Obr. 7. Colubridae (približne 3–4 kompletné kostry jedincov / stavce), *Lepus europaeus* (dve nohy) a *Columba* sp. Sliven okres, kód hniezdneho páru/hniezda - S4a, 21 Jún 2022. Foto: G. Dilovski

Pellets were collected only inside the nests during the ringing period of chicks at about 21–40 days. Rarely were entire pellets preserved and found at the nests at this time of the nestlings' age. In most cases, pellets were crushed and pushed between twigs of the nest structure, and the total mass of pellets inside and around the nest was difficult to obtain. Therefore, in the two years of this research, 2021 and 2022, only 42 individuals (14.5%) were detected by this method.

In our work, we used the collection of food remains, pellets and skeletal remains exclusively from the interior of occupied nests of LLB, in most cases while the chicks were still present at the nest or just after the nestlings fledged. Alternatively, the trail cameras captured food data as the parents delivered food to the chicks throughout the nestling period. We did not collect food remains and pellets from under the nest, under the tree, or the adults' perching sites to avoid inaccuracy of food data. Remnants of any prey, skeletal material, and parts or whole bodies of animals may also reach the collection site through other predators that bring their prey from elsewhere under the tree, rock, or nest; they may drop their prey while perching on a solitary tree where the nest is located. In some cases, tree nests may be used for nesting, alternately by different species. For example, LLB has alternated tree nest use with black kite (*Milvus migrans*) (our study) or on cliff nests with Eurasian eagle-owl (*Bubo bubo*) (Miltschev 2003). In five locations (quarries and natural rocks) LLB bred jointly with the *Bubo bubo*, at a distance of 60–650 m from their nests (Milchev 2009).

According to published knowledge on the feeding ecology (Cramp & Simmons 1980, Alivizatos & Goutner 1997, Milchev 2009, Redinov 2010, Bakaloudis et al. 2012, Kassinis et al. 2022), mammals and reptiles are the most abundant prey items in the diet of LLB from southeastern Europe and Iran. In accordance with these published results, mammals 69.3% are the most dominant part of the diet of LLB in our study from southeastern Bulgaria.

An important component of the LLB diet of the family Sciuridae are the sousliks: in Bulgaria, Romania and Hungary, *Spermophilus citellus* (Kalotás 1992, Milchev 2009, Danko 2012, Birău et al. 2018) and in Ukraine *Spermophilus pygmaeus*, *Spermophilus suslicus*, *Spermophilus odessanus* (Cramp & Simmons 1980, Syzhko 2005, Redinov 2010, 2012). In accordance with these published results, *Spermophilus citellus* followed by *Microtus mystacinus* are the dominant part of the diet of LLB in our study from SE Bulgaria. In SW Iran, sousliks are replaced by the *Sciurus anomalus*. In the steppes, mole-rats are also hunted: *Nannospalax leucodon* in Bulgaria and *Spalax zemni* with a higher proportion in Ukraine. Of the larger mammals, the more important prey is *Lepus europaeus*, the brown rat *Rattus norvegicus* or common hamster *Cricetus cricetus*. On the island of Cyprus, there is a different species supply of mammals which explains why LLB preys more on *Hemiechinus auritus dorotheae* and *Rattus rattus*. Of the smaller rodents, *Microtus mystacinus* is a frequent prey in Bulgaria and Ukraine, and in Iran it is replaced by the species of *Microtus irani*. Birds are rarer prey of LLB (average prey abundance is about 10%, Tab. 5), but were more abundant in our material from southeastern Bulgaria (21%). Reptiles of the families Lacertidae and Colubridae are more important prey (about 20%, Table 5) than birds across the LLB range of breeding distribution with their high incidence in LLB food spectrum in Cyprus and Iran, but were less abundant in our study (9.3%). The more abundant Coleoptera are reported by authors from Hungary (Kalotás 1992), Ukraine and Cyprus (Tab. 5).

By comparing the results of Milchev (2009) from southeastern Bulgaria with our results also from SE Bulgaria, we can state that both showed relatively equal mammal abundance of 68.8%, 12 species and 69.3%, 10 species. Unlike Milchev (2009), we did not observe a single individual of *Rattus norvegicus* on the nests, even though LLB were observed foraging near human settlements.

Different results were found in the representation of reptiles and birds. Reptiles were predominant in Milchev's (13.2%, four species) followed by birds (9.0%, 12 species). In our results, birds dominated (21.0 %, 11 species), followed by reptiles (9.3%, two species). This comparison was based on a comparison of our results with those obtained by Milchev from three quarries on the northern boundary of his study area. If to these results we add identified diet from the Sakar Mountains which consisted of 5 bird species (6 inds.), 2 species of reptiles (2 inds.) and 1 species of Orthoptera (2 inds.), the ratio between reptiles and birds would be reduced. In that case, reptiles would account for 13.56% and birds for 11.55%, and the difference between them would be lower.

By comparing our results to Milchev's in the differential representation of reptiles and birds, the divergence of our results can be explained as follows. Although both research was carried out in southeastern Bulgaria, our research plots were not identical and did not overlap. From the line of St. Ilijski hills, Bakadzhik hills, Hisar hills, Burgas south to Turkey's border, the study area of Milchev was established (see map Milchev 2009). From this line north to the foot of the Stara Planina Mountains and the town of Sliven east past the towns of Karnobat, Aytos and Burgas was established our study area. In Milchev's work, almost all nests were located on massive rock sites in three gorges of rivers in the Sakar Mountains and one gorge of Thundzha River near the border with Turkey. In four cases, the birds selected quarries. Only two nests were built on trees. In our study of 15 breeding pairs, 13 breeding pairs had nests built in trees, and only two breeding pairs had nests built in quarries. Breeding pairs in our study are found in environments presented mostly by agricultural lands, orchards, pastures and

Tab. 5. Comparison of the long-legged buzzard (*Buteo rufinus*) diet composition in different countries. N - number of prey items.
Tab. 5. Porovnanie zloženia potravy myšiaka hrdzavého (*Buteo rufinus*) v rôznych krajinách. N - počet objektov potravy.

Country	**Bulgaria**		**Bulgaria**		**Ukraine**		**Cyprus**		**Iran**			
Author	**This study**		**Milchev**		**Redinov**		**Kassinis et al.**		**Shafaeipour**		**∑**	**%**
Species \ Year N	**2022**		**2009**		**2010**		**2022**		**2015**			
Spermophilus citellus	2+	90	1+	35	3-	0	4-	0	3-	0	125	10.13
Spermophilus suslicus	1-	0			2+	23	1-	0			23	1.86
Sciurus anomalus	2-	0	1-	0	2-	0	2-	0	2+	52	52	4.21
Nannospalax leucodon	1+	17		5			1-	0			22	1.78
Spalax zemni	2-	0	1-	0	2+	36	2-	0	1-	0	36	2.92
Lepus europaeus	1+	9		4		1		1			15	1.22
Hemiechinus auritus	1-	0					1+	19			19	1.54
Rattus norvegicus	1-	0	2+	20			1-	0			20	1.62
Cricetus cricetus					1+	8					8	0.65
Rattus rattus	4-	0	3-	0	4-	0	2+	200	3-	0	200	16.21
Mus musculus	1-	2		2	1-	0	1+	31	1-	0	35	2.84
Microtus mystacinus	1+	74	1+	42	1-	13	4-	0	3-	0	129	10.45
Arvicola amphibius			2+	16			1-	0			16	1.3
Microtus irani									1+	8	8	0.65
Rodentia	1-	2	1-	0	2+	37	2-	0		8	47	3.81
Pica pica	1+	8				1					9	0.73
Columba sp.	1+	13									13	1.05
Passeriformes	1+	20		4		2	1-	0			26	2.11
Elaphe sauromates	1+	11				2					13	1.05
Coluber sp.		1		2					1+	9	12	0.97
Natrix sp.				6	1+	11	1-	0			17	1.38
Colubridae		5			1-	0	1+	21			26	2.11
Lacerta trilineata		10	1+	17	1-	0	2-	0			27	2.19
Lacerta agilis					1+	12					12	0.97
Lacertidae	2-	0	1-	0	1-	0	2+	41	1-	0	41	3.32
Reptilia	3-	0	2-	0		12	3-	0	3+	88	100	8.1
Coleoptera	2-	0	2-	0	1+	26	1+	34	2-	0	60	4.86
Orthoptera			1+	13				1			14	1.13
Turdus merula		4								5	9	0.73
Alauda arvensis		3		1		3					7	0.57
Athene noctua				1				4			5	0.41
Mustela nivalis		1				4					5	0.41
Mammalia		**201**		**130**		**126**		**253**	**1-**	**68**	**778**	**63.05**
Aves	**1+**	**61**		**17**		**20**	**1-**	**16**		**13**	**127**	**10.29**
Amphibia, Reptilia	**1-**	**28**	**1-**	**28**		**38**		**63**	**2+**	**97**	**254**	**20.58**
Evertebrata	**3-**	**0**		**14**	**1+**	**26**	**1+**	**35**	**2-**	**0**	**75**	**6.08**
∑		290		189		210		367		178	1234	100
Diversity Index H'		2.3		2.57		2.57		1.63		1.41	3.26	

Legend: Bulgaria, SE: this study, years 2018–2022; **Bulgaria, SE:** years 1994–2007, Milchev 2009; **Ukraine, SW:** Mykolaiv region, years 2000–2010, Redinov 2010; **Cyprus, S:** years 2005–2018, Kassinis et al. 2022; **Iran, SW:** years 2012–2013, Shafaeipour 2013.

Legenda: Bulharsko, JV: táto štúdia, roky 2018–2022; **Bulharsko, JV:** roky1994–2007, Milchev 2009; **Ukrajina, JZ:** Mykolaivska oblasť, roky 2000–2010, Redinov 2010; **Cyprus, J:** roky 2005–2018, Kassinis et al. 2022; **Irán, JZ:** roky 2012–2013, Shafaeipour 2013.

steppes. Several nests of breeding pairs were located very close to villages. The nearest occupied nest was found only 120 meters from the edge of the village. Adults of LLB are commonly observed flying over an open landscape, human settlements, cultivated fields, gardens, and orchards, and hunting prey in the vicinity. Such environments provide a more extensive food supply consisting of birds than reptiles. Such bird species include

Columba sp., *Pica pica*, S*turnus vulgaris*, *Turdus merula*, *Turdus* sp., *Alauda arvensis*, undetermined Paseriformes and sometimes *Gallus gallus domesticus* on the edges of villages. For this reason, there is a higher proportion of birds in the diet compared to reptiles in our study, which contrasts the results of Milchev 2009 and other authors (Cramp & Simmons 1980, Alivizatos & Goutner 1997, Redinov 2010, Bakaloudis et al. 2012, Kassinis et al. 2022).

Diurnal birds of prey *Falco vespertinu*s (Redinov 2010), common kestrel (*Falco tinnunculus*, 2 inds.) and Eurasian sparrowhawk (*Accipiter nisus*, 1 ind.) (our study) were also detected in the diet of LLB. An interesting finding was the determination of *Buteo rufinus* (juv.) in the diet of LLB from skeletal materials. This specific diet was detected in a breeding pair (BP code B5), for which the method of collecting data on diet using trail cameras was used in parallel that year. The trail camera on the nest confirmed that one of the three chicks, aged about three weeks, had died on the nest. The female and the other two chicks consumed the entire dead chick within a day of death. The chick's death was due to cold and rainy weather, when the female was unable both to warm the three three-week-old chicks on the nest and provide food in inclement weather. The second of the three chicks also died on the nest within a few days due to drenching and hypothermia. It remained untouched on the nest until the last third chick fled. There is little direct evidence in the literature obtained from wildlife live streams, video cameras or trail cameras from nests to confirm this phenomenon of parents and siblings consuming a dead chick on the nest together.

Spermophilus is a very important component in the diet of LLB throughout much of its breeding range (Cramp & Simmons 1980, Kalotás 1992, Syzhko 2005, Milchev 2009, Redinov 2010, 2012, Danko 2012, Birău et al. 2018, our study). The gradual decline in the populations of *Spermophilus citellus* in Europe may lead to the endangerment of the species and, thus, indirectly to the degradation of such an important food source, not only for the LLB but also for rare species such as the eastern imperial eagle (*Aquila heliaca*), booted eagle (*Hieraaetus pennatus*), saker falcon (*Falco cherrug*) and other species. For that reason, the European Commission approved an international project, LIFE19 NAT/SK/001069, entitled „Conservation of the European Ground Squirrel (*Spermophilus citellus*) at the northwestern border of its range“, which aims to conserve the endangered species of European importance - the sousliks and improve the unfavourable status of its populations at the northwestern edge of its range in Europe (Webgate.ec.europa.eu/life/ 2023).

The results of our study on the food ecology of LLB contributed to the knowledge of the basic components of the diet of this species from Bulgaria. Together with the results of the work of Milchev (2009), they provided an increase in the level of knowledge of the diet composition of this species focused on research in the area of southeastern Bulgaria. Our results and those of other authors, confirm the wide range of LLB diet represented mainly by mammals, reptiles and birds, which allows them to adapt to different environments.

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Temporal variation in the peregrine falcons (*Falco peregrinus*) diet after the extinction of the original population and the emergence of a new population in Slovakia

Časové zmeny v potrave sokola sťahovavého (*Falco peregrinus*) na Slovensku v súvislosti so zánikom pôvodnej a vznikom novej populácie

Ján OBUCH & Jozef CHAVKO

Abstract: We made an analysis of the osteological remains of prey that had been captured by the peregrine falcon (*Falco peregrinus*) and was collected from eyries perched high in rocky cliffs of Slovakia. Birds dominated the 7,233 vertebrates identified (class Aves, with minimum of 98 species and 97.2% of the total). Bones from mammals (class Mammalia, 24 species, 2.5%) were rarely found, and sporadic remains from lower vertebrate species (classes Amphibia, Reptilia, Pisces, 0.3%) were also noted. The collected specimens were divided over three distinct periods. Before domestic pigeons became a major component in the juvenile peregrine falcon diet (Period A), wild pigeons and doves were the most common prey; specifically stock doves (*Columba oenas*) caught at lower elevations, and wood pigeons (*Columba palumbus*) in mountainous areas. The Eurasian woodcock (*Scolopax rusticola*) was a frequent prey . The diversity of peregrine falcon diet reached its maximum between the 1930s and the 1950s (Period B), with the domestic pigeon (*Columba livia domestica*) present in the diet at a similar abundance (16.1%) to wild pigeons and doves. The peregrine falcon population tailed off in the 1960s as pesticides became more commonly used in agriculture. A new population started expanding from Western Europe during the 1990s and has stabilised at around 150 breeding pairs in recent years. Since the turn of the millennium (Period C), domestic pigeons have become the dominant prey (51.1%) along with smaller songbirds such as hawfinches (*Coccothraustes coccothraustes*) and common starlings (*Sturnus vulgaris*), at 15.5% and 14.6% of total osteological remains collected, respectively.

Abstrakt: Analyzujeme osteologické zvyšky koristi sokola sťahovavého (*Falco peregrinus*), zbierané na jeho skalných hniezdach na Slovensku. Z determinovaných 7 233 kusov stavovcov dominujú vtáky (Aves, minimálne 98 druhov, 97.2%). Zriedkavé sú kosti z cicavcov (Mammalia, 24 druhov, 2.5%) a sporadické zvyšky z nižších druhov stavovcov (Amphibia, Reptilia, Pisces, 0.3%). Zbery sme rozdelili do 3 časových období. Skôr, než sa stali domáce holuby významnou zložkou výživy mláďat sokolov sťahovavých (obdobie A), ich najčastejšou potravou boli divé holuby holub plúžik (*Columba oenas*) v nižších polohách a holub hrivnák (*Columba palumbus*) vyššie v horách. Častou korisťou bola sluka hôrna Scolopax rusticola. V období 30. až 50. rokov 20. storočia (obdobie B) bola diverzita koristi sokolov sťahovavých najvyššia a domáce holuby (*Columba livia domestica*, 16.1%) boli v potrave zastúpené v podobnom množstve, ako divé holuby. Táto populácia zanikla v 60. rokoch 20. storočia v dôsledku používania pesticídov v poľnohospodárstve. Nová populácia sa začala šíriť zo západnej Európy v 90. rokoch 20. storočia a v posledných rokoch sa ustálila na počte okolo 150 hniezdnych párov. V novom miléniu (obdobie C) sú domáce holuby dominantnou korisťou (51.1%) spolu s menšími druhmi spevavcov glezgom obyčajným (*Coccothraustes coccothraustes*, 15.5%) a škorcom obyčajným (*Sturnus vulgaris*, 14.6%).

Key words: prey diversity, dominant prey, Central Europe, reintroduction, Falconidae

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Introduction

Peregrine falcons (*Falco peregrinus)*, swiftly swooping down on other birds flying above the ground, have always fascinated people. This method of attacking has long been exploited by falconers, who have been training them to hunt prey since the medieval era. On the other side, fanciers of racing and homing pigeons would get annoyed at these falcons outpacing and catching their fastest birds. The pigeons became a fatal attraction to these raptors in the 1950s when the former started feeding on pesticide-dressed grain that had been sown in fields. During the 1960s and 1970s, the falcon population collapsed in most of Europe after the raptors died of toxins they had ingested from contaminated pigeons (Newton, 1988). After the spraying of harmful pesticides was prohibited, and some Western European countries launched breeding programmes in the 1990s to rescue the peregrine falcon, the birds started returning to Slovakia and, since the turn of the 21st Century, the population has rebounded to the level at which it stood in the early 1950s.

Between 1977 and 1982, an intensive search was conducted in mountainous parts of Slovakia for nests that peregrine falcons had previously used. The remains of their prey were collected from eighteen identified eyries, where the bones of birds dominated among the findings (Obuch, 1982, 1996). These were published especially from studies of collections that had been brought from the Choč Mountains (Obuch 1981), the Malá Fatra mountain range (Obuch, 1985a) and from the Muránska Planina (Muráň Plateau) National Park (Obuch, 1985b). The first analysis of food remnants found around a newer peregrine falcon nest in the Malé Karpaty Mts. , carried out in 1993-95, was published in a study of the falcon's diet (Obuch & Chavko, 1997).

Historical data sets on peregrine falcon breeding in Slovakia were summarised by Ferianc (1964, 1977), along with more information coming from Mošanský (1972) and Hudec & Černý (1977). Peregrine falcons breed in most of Slovakia's mountain ranges, except those few situated in lowland regions, where the highest concentration of breeding sites are found in the central part of the country. The earliest data on peregrine falcons breeding in central and east Slovakia were published by Schenk (1918). Probably the highest abundance of the species in Slovakia was recorded between 1930s and 1950s (Hudec & Černý, 1977), with numbers slowly declining at first and then dramatically falling after 1960s (Ferianc, 1977). The intensity of the drop in population was such that by 1970s it had reached a critically low level. In subsequent years, an apparent absence of this species was evident at all known eyries in Slovakia where the falcons bred. In addition, adult falcons were rarely observed in Slovakia between 1970 and 1993, while juvenile birds were hardly seen during the breeding season (Chavko, 2008). The occurrence at eyries was only observed again in 1992, with the first nesting and breeding recorded only two years later in the Malé Karpaty Mts and Veľká Fatra Mts range farther north.

The diet of peregrine falcons was studied intensively in interwar Germany. Uttendörfer (1952) summarised results he had obtained from the determination of skeletal remains and feathers of prey collected at breeding sites, and Schnurre (1973, 1996) continued his research after the World War II. Sladek & Mošanský (1957) surveyed peregrine falcons foraging (1953-55) similarly from feather remains at a nest located in central Slovakia. A study of peregrine falcon diets in Europe at the beginning of the 21st Century provides evidence of how the current population has adapted to hunting domestic pigeons (e.g. López-López et al. 2009; Dixon et al., 2018). Attracted by the abundant supply of birds in urban environments, some pairs have been breeding directly in urban areas (Mlíkovský & Hruška, 2000; Rejt, 2001; Drewitt & Dixon, 2008).

The actual study is directed to evaluate the diet trend taken by current Slovakia's peregrine falcon population between 1994 and 2021. Further, to compare its food spectra with earlier peregrine falcon populations in the two defined periods (A and B) and, in the case of the current population, also with seasonal changes in the population's diet between 2003 and 2018 throughout the actual peregrine falcon's range in Slovakia (Period C).

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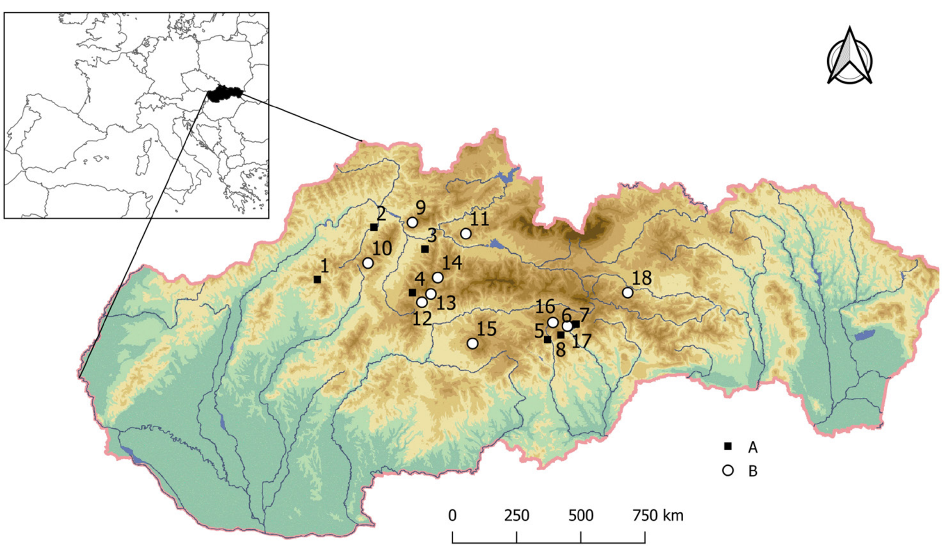
Material and methods

Members of Raptor Protection of Slovakia monitored the breeding population of peregrine falcons in Slovakia between 1994 and 2021. The birds were observed in the field by 25-30 members of the organisation. They directly searched nests they had first located after reading historical data in the references and subsequently referred to observations that had been recorded of falcon occurrence. Several occupied nesting grounds and eyries that had been detected, along with successfully breeding pairs, were observed, and the number of fledglings was counted and watched.

Appendix 1 provides an overview of the food remnants found at the sites with findings from previous Periods A and B. Figure 1 shows the locations in mountainous areas and plots them on a physical map of Slovakia. Radiocarbon analysis of the oldest habitat (No. 2 on the map) above Rajecké Teplice has dated it to 1,360 years ago with an error factor of ± 50 years (Kaizer et al., 2018). We estimate that all of the samples are older than 100 years. Nine collections were from Period A, wherein 1,585 specimens were determined to be from the diet of peregrine falcons. Period B, is defined by the data on the rings around the pigeons' legs , predominantly from the twenty years between 1931 and 1951. Only one ring came from a later date – 1961. The years during which the samples have been eaten range between 1920 and 1965. There are 11 collections from which 2,018 food items were identified. Food remains were collected from 264 samples over a wider area during Period C – the most recent period in our study, running mainly between 2003 and 2018.

Material from the older collections was washed in water. After it dried, the bones were then sorted for determination. Meat residues were stripped from fresh food scraps, taken at peregrine falcon eyries, by putting them in a 5% sodium hydroxide (NaOH) solution. We determined four types of bones coming from the parts of birds: the rostrum (beak), tarsometatarsus (lower leg), humerus, and metatarsus (digits). Mammals were determined from the mandible and maxilla found in cranial remains to have constituted only a minor diet component (2.5%). Among the lower vertebrates, remains of frogs were identified from the sacral vertebra, while reptiles and fish were identified from the jawbones. Our comparative collection of vertebrate skeletons was used in the determination. The minimum number of individuals (MNI) for each species collected was set as the least possible number that could be determined from the most abundant part of the skeleton. The results are presented in tables adjusted for marked differences from the mean (MDFM) (Obuch, 2001), i.e., the relative abundance of the species in the whole set, expressed as a percentage in the right-hand most column of the tables. Species in the assessed set with a significantly higher abundance than the mean (1+, 2+) are shown at the top of the tables in blocks whose are in grey color. The numbers before the plus (+) or minus (-) sign indicate the degree of deviation from the mean. Below the dashed line, more abundant species with no significant deviation are ranked from the highest total abundance to less abundant species. The remaining less abundant species or species assigned to higher taxonomic units are listed below in an appendix of the Table 1. These species are not listed



Fig,1. Location of sites where older peregrine falcon food was found (A – period before the introduction of domestic pigeons (more than 100 years before the present); B – introduction of domestic pigeons (1920–1965)).

Obr. 1. Poloha nálezísk staršej potravy sokola sťahovavého. (A – obdobie pred výskytom domácich holubov (> 100 rokov BP), B – obdobie s výskytom domácich holubov (1920–1965)).

in Tables 2-5 because Table 1 already presents them. The diversity index H' was calculated from the formula used by Shannon & Weaver (1949). ZBER, a local database software programme, was used to compile the tables (Šipöcz 2004).

Results and discussion

Comparing the diet of peregrine falcons from three different periods

For all three observed periods, birds (class Aves, 97.2%, minimum 98 species) dominated the diet of peregrine falcons breeding in the mountainous regions of Slovakia. Yet mammal bones were also found at food sites (class Mammalia, 2.5%, 24 species) mixed with sporadic amounts of lower vertebrate bones (classes Amphibia, Reptilia, Pisces, 0.3%). The most common prey items were three species from the pigeon and dove family: the domestic pigeon (*Columba livia domestica*, 30.1%, the stock dove (*Columba oenas*, 8.9%) and the common wood pigeon (*Columba palumbus*, 5.5%). Other birds more frequently hunted by the falcons were the Eurasian woodcock (Scolopax rusticola, 6.2%), several passerine species from the Corvidae family and, from among smaller prey, the hawfinch (*Coccothraustes coccothraustes*, 11.9%) and the common starling (*Sturnus vulgaris*, 7.8%).

Before free-ranging domestic pigeons appeared (Period A), the peregrine falcon's dominant prey was stock doves and wood pigeons, together with woodcocks abundant during their spring migration when the falcons were breeding. Among larger prey, waterfowl were more abundant, especially ducks from the family Anatidae, the European honey buzzard (*Pernis apivorus*) from among the raptors and the Eurasian jay (*Garrulus glandarius*) from among the passerine birds. Significant numbers of wild pigeons and doves persisted in the diet even into the period from the 1930s to the 1950s (Period B) along with domestic pigeons (16.1%). This period was distinguished from the others by the highest diversity of prey, mainly composed of an increasing amount of the common kestrel (*Falco tinnunculus*), northern lapwing (*Vanellus vanellus*), and common cuckoo (*Cuculus canorus*) in the diet along with several species from the corvid family (Corvidae) and the true thrushes (genus *Turdus*). In the most recent period (Period C), prey diversity fell as domestic pigeons (51.1%), and the smaller hawfinches and starlings grew more dominant in the diet (Table 1). Overall, Table 1 shows species diversity in the diet of peregrine falcon H' to have fallen from 3.13 in Period B to 1.90 in Period C, while the European turtle dove (*Streptopelia turtur*) and common blackbird (*Turdus merula*) remained relatively stable prey in all three periods.

Compared to other osteological sites on rocks, bird bones are dominantly represented among the remnants found in the peregrine falcon's diet (Obuch, 1994). They are primarily uneaten remains of the birds preyed upon by the falcons. The humerus was the predominant bone among the bird bones that had been determined, often pierced from the beak when the flesh was separated from the bone (Larouladie, 2002). Carpal (*metacarpus*) and lower leg (*tarsometatarsus*) bones were rare as they offer little meat and the falcons tend to consume and digest them whole. The mixture of mammal and lower vertebrate bones at the sites may have been partly due to falcons because other predators could have eaten their prey and deposited droppings there. For example, Mošanský (l959) reported ravens foraging at peregrine falcon nests. The occurrence of food from other vertebrae classes was also found at more recently constructed peregrine falcon nests. Likewise, Heredia et al. (1988) found in Spain bones from mammals, primarily bats but also the black rat (*Rattus rattus*), and the European rabbit (*Oryctolagus cuniculus*) and from lower vertebrates, also frogs and lizards.

Oldest Period (A)

Before domestic pigeons flew freely in Slovakia, the main prey for peregrine falcons consisted of stock doves (18.8%) and wood pigeons (13.1%), with woodcocks (15.5%) comprising the remaining larger prey and hawfinches (14.3%) the smaller one. By comparing peregrine falcon food from eight foraging sites, we found that the main difference was that stock doves were the dominant prey in nests located in warmer sections of Slovakia. Smaller species, such as hawfinches, starlings and the mistle thrush (*Turdus viscivorus*), were more frequently hunted at the southern edge of the Strážov Mountains. At eyries in higher elevations, wood pigeons and woodcocks were the most common prey. The oldest site above Rajecké Teplice (No. 2, Tab. 2, Fig. 1) contained more ducks (Anatidae) and other aquatic bird species, reflecting the period 1,400 years ago when the basin of the Rajčanka River between Rajecká Lesná and Turie had extensive wetlands. The number of honey buzzards counted from this site was exceptionally high. Corvidae were more often hunted above the Turiec basin at Katova skala in the Veľká Fatra Mountains. There were no significant deviations from the mean in the percentages

Tab. 1. Comparison of peregrine falcon diets in Slovakia from three different periods.
Tab. 1. Porovnanie potravy sokola sťahovavého na Slovensku z 3 období.

Years		**1920<**		**1920 - 1965**		**1999 - 2018**		
Species \ Period		**1 /A/**		**2 /B/**		**3 /C/**	**Total**	**%**
Anas platyrhynchos	1+	14		3	2-	0	17	0.24
Anas crecca	1+	7		3	1-	1	11	0.15
Anas querquedula	1+	11		4	1-	1	16	0.22
Pernis apivorus	1+	13		4	2-	0	17	0.24
Upupa epops	1+	8		4	1-	0	12	0.17
Coturnix coturnix	1+	6		1		0	7	0.10
Scolopax rusticola	2+	243	1+	186	4-	17	446	6.17
Columba oenas	1+	296	1+	288	3-	56	640	8.85
Columba palumbus	1+	208	1+	167	3-	23	398	5.50
Coloeus monedula	1+	74	1+	111	3-	11	196	2.71
Garrulus glandarius	1+	37	1+	44	1-	22	103	1.42
Falco tinnunculus		3	1+	14	1-	1	18	0.25
Vanellus vanellus		4	1+	12	1-	3	19	0.26
Cuculus canorus		15	1+	37	2-	5	57	0.79
Asio otus		1	1+	7	1-	0	8	0.11
Turdus viscivorus		36	1+	61	1-	34	131	1.81
Turdus pilaris		14	1+	38		32	84	1.16
Turdus torquatus		4	1+	29	1-	5	38	0.53
Nucifraga caryocatactes		3	1+	11	1-	1	15	0.21
Pica pica	1-	4	1+	32	1-	11	47	0.65
Corvus cornix+frugilegus		54	1+	188	2-	52	294	4.6
Columba livia dom. N	7-	0	1-	325	1+	1854	2179	30.13
%		0.00		16.11		51.07		
Coccothraustes coccothr.	2-	225	2-	79	1+	556	860	11.89
Sturnus vulgaris	3-	27	3-	18	1+	518	563	7.78
Carduelis chloris	1-	2	1-	0	1+	20	22	0.30
Dendrocopos major	1-	2	1-	2	1+	22	26	0.36
Dryocopus martius		6		7	1-	2	15	0.21
Crex crex		5		3	1-	0	8	0.11
Picus canus		3		6	1-	0	9	0.12
Alauda arvensis		8		11	1-	7	26	0.36
Streptopelia turtur	1-	23		43		90	156	2.16
Turdus merula		26		26		63	115	1.59
Turdus philomelos		15		29		31	75	1.4
Fringilla coelebs		9		14		25	48	0.66
Loxia curvirostra		9		13		13	35	0.48
Perdix perdix		6		9		7	22	0.30
Picus viridis		7		5		3	15	0.21
Oriolus oriolus		3		3		8	14	0.19
Pyrrhula pyrrhula		2		4		6	12	0.17
Apus apus		3		4		5	12	0.17
Strix aluco		5		4		2	11	0.15
Mammalia, 24 species		**50**	**1+**	**85**	**1-**	**48**	**183**	**2.53**
Aves, 98 species		**1529**		**1921**		**3578**	**7028**	**97.17**
Amphibia,Reptilia,Pisces		**6**	**1+**	**12**	**1-**	**2**	**20**	**0.28**
Evertebrata		**0**		**0**		**2**	**2**	**0.03**
Total		**1585**		**2018**		**3630**	**7233**	**100.00**
Diversity Inex H’		2.94		3.13		1.89	2.86	

Tab. 1. Continuation
Tab. 1. Pokračovanie

Other species 1(**Period No** - number of individuals) / Ostatné druhy (**Obdobie č**.-počet):
Erinaceus roumanicus (**1**-5; **2**-2); *Talpa europaea* (**1**-2; **2**-9; **3**-2), *Myotis bechsteinii* (**2**-1), *Vespertilio murinus* (**1**-2; **3**-1), *Eptesicus serotinus* (**1**-1; **2**-2; **3**-1), *Nyctalus noctula* (**1**-1; **2**-5; **3**-10), Chiroptera sp. (**1**-1), *Lepus europaeus* (**1**-1; **2**-1; **3**-1), *Sciurus vulgaris* (**2**-1), *Spermophilus citellus* (**1**-2; **2**-2; **3**-9), *Glis glis* (**1**-6; **2**-4; **3**-2), *Eliomys quercinus* (**2**-1), *Muscardinus avellanarius* (**1**-1; **2**-2), M*us musculus* (**2**-1), *Apodemus flavicollis* (**3**-1), *Apodemus* sp. (**1**-6; **2**-9), *Rattus norvegicus* (**2**-2; 3-4), *Cricetus cricetus* (**2**-1), *Myodes glareolus* (**1**-5; **2**-7; **3**-1), *Arvicola amphibius* (**1**-5; **2**-12; **3**-3), *Terricola subterraneus* (**1**-1; **2**-3), *Microtus arvalis* (**1**-9; **2**-19; **3**-10), *Microtus agrestis* (**2**-1), *Mustela nivalis* (**1**-1; **3**-2), *Meles meles* (**1**-1), *Felis catus dom*. (**3**-1), *Podiceps nigricollis* (**2**-1; **3**-1), *Anas strepera* (**1**-5; **2**-1), *Aythya fuligula* (**2**-1), Anatidae sp. (**1**-7; **2**-5), *Accipiter gentilis* (**2**-1), *Accipiter nisus* (**1**-2; **2**-3; **3**-2), *Buteo buteo* (**3**-1), *Circus* sp. (**1**-2), *Falco peregrinus* (**2**-4; **3**-4), *Falco sp.* (**1**-4; **2**-5), *Tetrastes bonasia* (**1**-3; 3-1), *Lyrurus tetrix* (**1**-3; **2**-1), *Phasianus colchicus* (**3**-1), *Gallus gallus dom.* (**1**-3), Galliformes sp. (**2**-2), *Rallus aquaticus* (**1**-1; **2**-1), *Gallinula chloropus* (**2**-2; **3**-1), *Fulica atra* (**1**-1; **2**-2), *Charadrius dubius* (**2**-1), *Tringa sp.* (**2**-1), *Philomachus pugnax* (**1**-1; **2**-1), *Numenius arquata* (**1**-2; **2**-1), *Gallinago* sp. (**1**-1), Limicolae sp. (**1**-3), *Chroicocephalus ridibundus* (**1**-1), *Sterna hirundo* (**1**-1; **2**-5), *Chlidonias niger* (**2**-1), *Streptopelia decaocto* (**2**-1; **3**-7), *Otus scops* (**3**-1), *Glaucidium passerinum* (**2**-1), *Aegolius funereus* (**1**-2; **2**-1), *Athene noctua* (**2**-3), *Caprimulgus europaeus* (**1**-1), *Coracias garrulus* (**1**-1; **2**-1), Psittacidae sp. (**3**-1), *Dendrocopos syriacus* (**1**-1), *Dendrocopos medius* (**3**-1), *Dendrocopos leucotos* (**3**-2), *Jynx torquilla* (**1**-1; **3**-3), *Lullula arborea* (**2**-1), *Galerida cristata* (**3**-1), *Hirundo rustica* (**2**-1), *Anthus trivialis* (**3**-1), *Anthus* sp. (**1**-1), *Motacilla alba* (**3**-5), *Motacilla cinerea* (**3**-1), *Lanius excubitor* (**1**-1), *Lanius minor* (**1**-2), *Lanius collurio* (**2**-1), *Sylvia communis* (**3**-1), *Sylvia atricapilla* (**3**-1), *Sylvia* sp. (**3**-1), *Erithacus rubecula* (**3**-1), *Parus major* (**2**-1; **3**-2), *Periparus ater* (**2**-1), *Poecile palustris* (**3**-1), *Poecile montanus* (**3**-1), *Sitta europaea* (**3**-1), *Cinclus cinclus* (**3**-2), *Emberiza citrinella* (1-3; 2-1; 3-3), *Emberiza calandra* (**1**-1; **3**-2), *Emberiza schoeniclus* (**3**-1), *Carduelis carduelis* (**3**-1), *Carduelis cannabina* (**3**-1), *Passer domesticus* (**2**-1; **3**-7), *Passer montanus* (**2**-1; **3**-3), *Corvus corax* (**3**-1), Passeriformes sp. (**1**-8; **2**-8; **3**-6), Aves sp. (**1**-5; **3**-1), Aves sp.juv. (**1**-21; **2**-10), *Bufo bufo* (**2**-2; **3**-1), *Rana temporaria* (**1**-3; **2**-8; **3**-1), *Lacerta viridis* (**1**-1), *Lacerta agilis* (**1**-2; **2**-1), *Salmo trutta* (**2**-1), *Lucanus cervu*s (**3**-1), Limacidae sp. (**3**-1)

of species from findings at smaller sites in the Veľká Fatra range at the valley around Žarnovica and on the Muráň Plateau (Kášter, Šance) (Table 2).

Predominant diet between the 1930s and 1950s (Period B)

Ten sites were studied whose domestic pigeon remnants were dated from their rings to the period between 1930 and 1960. There were similar numbers of domestic pigeons (15.8%), stock doves (14.3%) and wood pigeons (8.4%) found. Eurasian woodcocks and corvids were also abundant. Significant differences were only evident among the five more numerous samples of the peregrine falcon diet. On the rocks above the Hoskora valley (No. 9, Tab. 3, Fig. 1) in the Malá Fatra Mountains, peregrine falcons have nested high in the narrow gorge through which the Váh river flows. It was here where they could follow the Eurasian woodcock’s spring migratory route. This species and wild pigeons and doves formed the falcon’s main prey. The rock wall at Sokol above the Ružomberok, Liptov Region (No. 11) once hosted nesting grounds for a colony of western jackdaws (*Coloeus monedula*). These were the most accessible prey for falcons whose eyries lay at the same location. The falcons in the cliffs above Dolný Harmanec, Veľká Fatra Mts (No. 12) hunted for the hooded crow (*Corvus cornix*), turtle doves and hawfinches along the Hron river valley near Banská Bystrica and domestic pigeons flying through the mountain pass at Šturec to the Turiec Region. Domestic pigeons were likewise common prey for the falcons bred at Majerová skala in the south-eastern Veľká Fatra Mts (No. 13). At higher elevations, common prey was the ring ouzel (*Turdus torquatus*). Falcons nesting in the enclosed valley below Mála Stožka (No. 16) in the Muránska planina Mts would hunt carrier pigeons flying from various directions. Rings on these birds indicated that they had been caught, banded and then released in Hungary, the Czech Republic and Košice further east. The nest located at Site 16 was abandoned after one falcon of the pair died. Its skeleton was found at the bottom of a deep chasm in the eastern face of Mála Stožka, along with the skeleton of a pigeon banded in 1950 (Tab. 3).

The most comprehensive material about food that had been foraged by peregrine falcons from 221 breeding sites in Germany was collected during the interwar period by Uttendörfer (1952). Table 4 thus summarises our material from Period B and of a similar age, which differs mainly in the higher abundance of stock doves, wood pigeons, woodcocks and crows. Being predominately flat, Germany already had a lot of domestic pigeons, starlings and wetland species, particularly the northern lapwing (*Vanellus vanellus*) and the black-headed gull (*Chroicocephalus ridibundus*) during that period. Although smaller songbird species had already become abundant by that time, too. The peregrine falcon diet was subsequently studied in eastern Germany by Schnurre (1966, 1973). Even after 1950, the diet was dominated by three species mentioned earlier: domestic pigeons, common starlings and northern lapwings, with a high diversity of other bird species.

The presence of domestic pigeons in the samples was used to distinguish the earlier Period A from Period B. Even though they had been bred since medieval times, the pigeons used to be kept in closed aviaries. Among

Tab 2. Peregrine falcon diet before the introduction of domestic pigeons (Period A).
Tab 2. Potrava sokola sťahovavého pred výskytom domácich holubov (obdobie A).

Species \ Locality No	1	7	8	2	3	4	5	6	Total	%
Turdus viscivorus	1+ 19	1	2	6	4	1	3		36	2.29
Sturnus vulgaris	1+ 20		1	1- 0	1		3	2	27	1.72
Coccothraustes coccothr.	1+ 115	2- 2	20	54	1- 10	1- 0	1- 1	22	224	14.28
Columba oenas	1+ 127	1+ 29	1+ 80	2- 15	2- 7	8	9	1- 20	295	18.80
Streptopelia turtur	5	4	1+ 9	1	1		1	2	23	1.47
Anas platyrhynchos	3			1+ 8	2	1			14	0.89
Pernis apivorus	1			1+ 11	1				13	0.83
Scolopax rusticola	1- 61	12	1- 10	1+ 86	1+ 41	6	1- 2	25	243	15.49
Columba palumbus	1- 50	16	1- 7	56	1+ 36	10	3	28	206	13.13
Corvus cornix+frugilegus	1- 7	2	8	13	1+ 13	5		2	50	3.19
Coloeus monedula	24	1	1- 2	12	1+ 22	5	2	3	71	4.53
Turdus philomelos	1- 0		3	3	6	1	1	1	15	0.96
Garrulus glandarius	11	3	6	9	3		2	3	37	2.36
Turdus merula	6	2	6	4	3		3	2	26	1.66
Cuculus canorus	7	3		2	1			2	15	0.96
Turdus pilaris	5		3	1	2			1	12	0.76
Anas querquedula	4	1	1	3				2	11	0.70
Fringilla coelebs	2		2	3	1		1		9	0.57
Loxia curvirostra	3			4	1	1			9	0.57
Upupa epops	2	1	3				1	1	8	0.51
Alauda arvensis	3	3	1					1	8	0.51
Anas crecca	2			3		1		1	7	0.45
Perdix perdix	2			1	2		1		6	0.38
Coturnix coturnix	1	1		3			1		6	0.38
Dryocopus martius	1		1	1	1			2	6	0.38
Picus viridis	2		1	1	1	1			6	0.38
Mammalia	**12**	**6**	**3**	**11**	**1- 0**	**0**	**5**	**1+ 13**	**50**	**3.19**
Aves	**517**	**87**	**171**	**333**	**180**	**44**	**40**	**141**	**1513**	**96.43**
Amphibia, Reptilia	**0**	**0**	**0**	**4**	**0**	**0**	**1**	**1**	**6**	**0.38**
Total	**529**	**93**	**174**	**348**	**180**	**44**	**46**	**155**	**1569**	**100.00**
Diversity Index H'	2.60	2.44	2.17	2.81	2.64	2.24	2.99	2.86	2.94	

Locations, date of collection/ **Lokality,** dátum zberu: **1** - Čierna Lehota, Sokolie skaly, 3.3.1979, **7** – Muráň, Šance, right edge, 11.10.1979, **8** – Muráň, Javorníčkova dolina, 15.5.1979, **2** - Rajecké Teplice, Skalky, 26.7.1978, **3** – Sklabinský podzámok, Katova skala, 4.9.1979, **4** – Čremošné, Žarnovická dolina, 8.6.1995, **5** – Tisovec, Kášter, 30.7.1980, **6** – Muráň, Šance, left edge, 23.9.1980.

free-flying pigeons, homing pigeons released beyond the borders of former Czechoslovakia for training flights and racing pigeons in the competition became attractive prey for the peregrine falcons nesting in the country. In 1921, the Racing Pigeon Union of Czechoslovakia (CHPV) was established in Prague. Two years later, a law was adopted, which vested in the interior ministry the authority to protect racing and homing pigeons and required them to be registered. The first meeting of the CHPV was held in Liptovský Mikuláš, Slovakia, in 1923, followed by another meeting in Zvolen a year later and in the Spiš region in 1928 (Alexaj 1971). Breeders would often complain at these meetings about huge losses of pigeons caught by birds of prey whenever the route of races took them over central Slovakia. These complaints would appear in the local carrier pigeon magazine. The breeders were calling for raptors to be eliminated by all means possible. Matoušek (1947) explained that most birds of prey catch pigeons only in exceptional circumstances, and the relatively rare peregrine falcons were at the time protected by law. Hudec & Šťastný (2005) mentioned that falcon numbers slowly increased after the peregrine falcon received protection in 1929. Likewise, World War II contributed to the limited shooting of these birds. The population continued to rise until 1950 when numbers started falling again. Newton (1988) cites the agricultural use of DDT and mainly cyclodienes, including aldrin and dieldrin dressings in grain, as the cause of the decline in the falcon population in most European countries

Tab. 3. Predominant peregrine falcon diet in the period from 1930s to 1960s (Period B).
Tab. 3. Potrava sokola sťahovavého prevažne z 30. až 50. rokov 20. storočia (obdobie B).

Rings, Years	**1942 - 52**		**1944 - 54**		**1933 - 51**		**1931 - 46**		**1932 - 51**			**1932 - 34**		**1961**				**1939 - 52**		
Species \ Locality No		**9**		**11**		**12**		**13**		**16**	**10**		**14**		**15**		**17**	**18**	**Total**	**%**
Turdus philomelos	1+	11		3		5				5			1		1		3		29	1.46
Scolopax rusticola	1+	79		38	1-	38	1-	6	1-	4	4		1		3		10	1	184	9.25
Columba oenas	1+	95		68	1-	64	2-	1		26	4	1-	1		5		15	5	284	14.27
Columba palumbus	1+	43	1+	48	1-	29		15	1-	5	4		1		3		11	8	167	8.39
Coloeus monedula		22	1+	45		28	1-	2	1-	0	6				1		3	4	111	5.58
Nucifraga caryocatactes			1+	7		1		1							1			1	11	0.55
Streptopelia turtur		9	1-	3	1+	20		1		5	2				1		1	1	43	2.16
Corvus cornix + frugilegus	1-	13		30	1+	105		11	1-	6	4		1		3		10	4	187	9.40
Coccothraustes coccothr.		11		12	1+	40		4	1-	1			1		4		3	3	79	3.97
Columba livia domestica	2-	13		57	1+	121	1+	62		29	6		6		7	2-	2	11	314	15.78
Turdus torquatus		3		2	1-	1	2+	15					4				3		28	1.41
Turdus viscivorus		9		10		14		2	1+	14	5		2		2		2		60	3.2
Cuculus canorus		7		4		12			1+	9	1				1		1	1	36	1.81
Turdus pilaris	1-	1		12		15		3		1							1	3	36	1.81
Turdus merula		4		4	1-	3				2	4		2		1		4	2	26	1.31
Garrulus glandarius		8		10	1-	5		3		3	2		1		4		3	2	41	2.6
Pica pica		9		12		5		1			4						1		32	1.61
Sturnus vulgaris		1		5		7					3						2		18	0.90
Falco tinnunculus		2		2		5		2					1				2		14	0.70
Fringilla coelebs		4		2		4				1			1		2				14	0.70
Vanellus vanellus		1		7				1			1				1			1	12	0.60
Loxia curvirostra		3		3		5									1				12	0.60
Alauda arvensis		4		3		1		2			1								11	0.55
Perdix perdix				2		3									2		1	1	9	0.45
Asio otus		1		1		4		1											7	0.35
Dryocopus martius		1		4		1		1											7	0.35
Picus canus		1		3		1												1	6	0.30
Mammalia	**3-**	**0**	**1-**	**7**	**1-**	**9**		**7**	**1+**	**16**	**2**	**2+**	**17**	**1+**	**14**	**1+**	**11**	**2**	**85**	**4.27**
Aves		**376**		**416**		**578**		**138**		**116**	**56**	**1-**	**28**		**48**		**87**	**50**	**1893**	**95.13**
Amphibia,Reptilia,Pisces		**0**		**0**		**3**		**0**		**2**	**1**		**0**		**1**	**1+**	**5**	**0**	**12**	**0.60**
Total		**376**		**423**		**590**		**145**		**134**	**59**		**45**		**63**		**103**	**52**	**1990**	**100.00**
Diversity Index H'		2.60		2.90		2.85		2.24		2.67	2.91		2.77		3.24		3.9	2.58	3.13	

Locations, date of collection/ **Lokality,** dátum zberu: **9** – Turčianske Kľačany, Nad Hoskorou, 11.6.1980; **11** – Valaská Dubová, Sokol, 1.7.1977; **12** – Dolný Harmanec, Bystrická dolina, 4.11.1978 + 17.7.2004; **13** – Staré Hory, Majerova skala, 15.4.1980; **16** – Závadka nad Hronom, Malá Stožka, 16.5.1979; **10** – Vrícko, Vrania skala, 27.6.1982; **14** – Liptovské Revúce, Čierny Kameň, 13.5.1980; **15** - Hrochoť, Jánošíkova skala, 10.7.1978; **17** - Muráň, Klin, 29.7.1980; **18** - Smižany, Klauzy, 14.9.1980.

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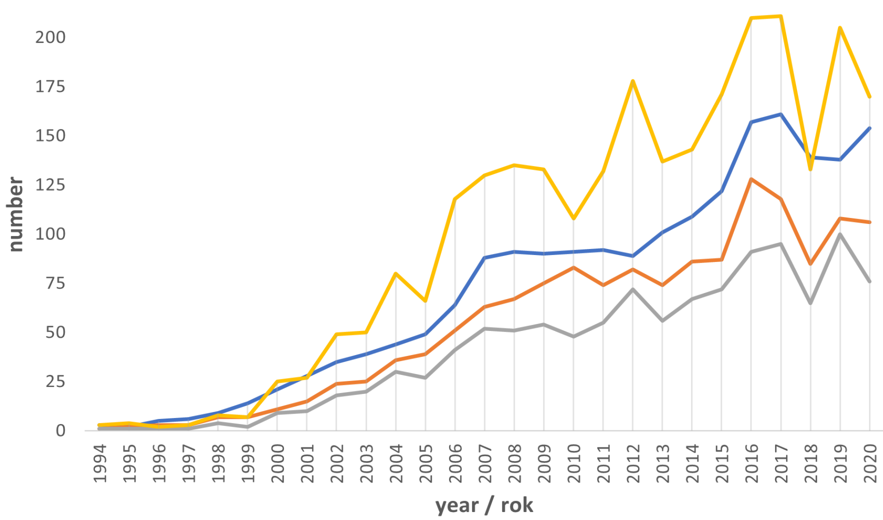

Fig. 2. Peregrine falcon monitoring results for 1994-2021 (collection of results from 2021 was curtailed by the reduction of biotope mapping staff caused by measures to combat the COVID-19 pandemic).

Obr. 2. Výsledky monitoringu populácie sokola sťahovavého za obdobie rokov 1994 – 2021 (výsledky z roku 2021 boli čiastočne ovplyvnené znížením počtu mapovateľov v dôsledku COVID-19 opatrení).

starting in the 1950s. These organochlorine compounds were banned in Western Europe during the 1980s and the peregrine falcon population began to soar with the ban. Kubiš (1946) promoted DDT as an excellent means against pigeon ectoparasites, recommending that crops be dusted with it several times a year. Hudec (1988) estimated the peregrine falcon population in Czechoslovakia in the early 1970S as 10-20 pairs, falling between 1975 and 1985 to 2-4 pairs.

New populations and their diet in recent decades (Period C)

Chavko (2002) reported the regular breeding of peregrine falcons in western Slovakia starting in 1993 and spreading of other pairs were further east. In 1994-2001, 272 nesting pairs were recorded in Slovakia that had raised young 1,941 times. After subtracting nesting successes that could not be checked, only 1,460 active cases of breeding were evaluated by us, of which 1,119 were successful and 2,638 chicks fledged from the nests. For all breeding, the average success rate index covering all years was 1.8 chicks, and 2.5 chicks per successful breeding. Figure 2 shows an increase observed in the peregrine falcon population during the period studied, with first gradual and subsequently dynamic growth in breeding abundance until 2016. Breeding was also recorded by us at new, previously unpublished sites in Slovakia (Fig. 3). A similar upward trend in the development of new populations and colonisation of earlier breeding sites over the last three decades is shown in Figures 4, 5 and 6 for other European countries (Keller et al. 2020).

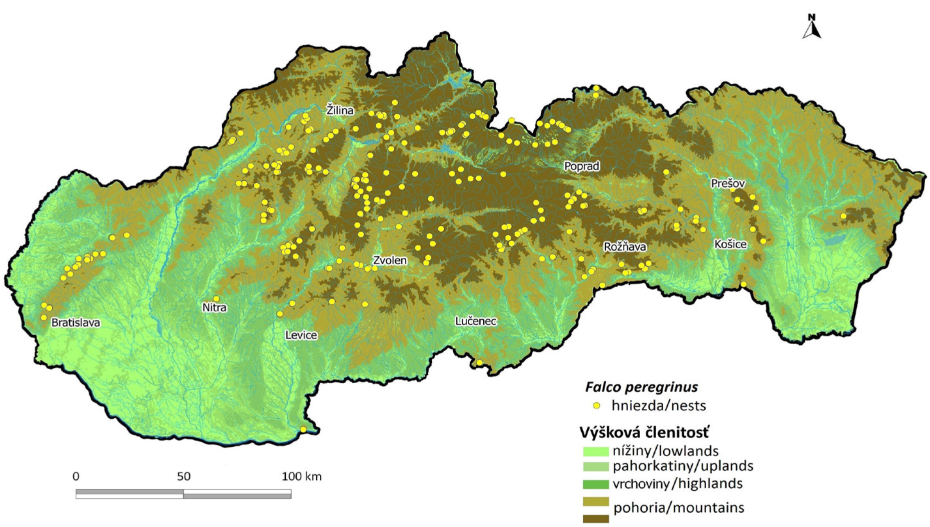

Fig. 3. Recent distribution of peregrine falcon nests (status up to 2016).

Obr. 3. Recentná distribúcia hniezd sokola sťahovavého (stav do roku 2016).

Tab. 4. Comparing the earlier diet of peregrine falcons in Slovakia (Period B) to findings by Uttendörfer (1952) in Germany
Tab. 4. Porovnanie staršej potravy sokola sťahovavého (obdobie B) s výsledkami Uttendörfera (1952) z Nemecka

Species \ Country	Slovakia		Germany		Total	%
Coloeus monedula	2+	111	2-	42	153	1.83
Scolopax rusticola	2+	186	4-	10	196	2.35
Coccothraustes coccothr.	2+	79	2-	15	94	1.13
Turdus torquatus	2+	29	3-	0	29	0.35
Columba oenas	2+	288	3-	41	329	3.94
Columba palumbus	1+	167	1-	122	289	3.46
Streptopelia turtur	1+	43	1-	51	94	1.13
Corvus cornix+frugilegus	1+	188	1-	123	311	3.72
Pica pica	1+	32	1-	17	49	0.59
Nucifraga caryocatactes	1+	11	2-	0	11	0.13
Cuculus canorus	1+	37	1-	21	58	0.69
Falco tinnunculus	1+	14	1-	2	16	0.19
Asio otus	1+	7	1-	1	8	0.10
Loxia curvirostra	1+	13	1-	8	21	0.25
Vanellus vanellus	3-	12	1+	489	501	6.00
Chroicocephalus ridibundus	4-	0	1+	168	168	2.1
Alauda arvensis	3-	11	1+	298	309	3.70
Turdus iliacus	3-	0	1+	88	88	1.5
Emberiza citrinella	2-	1	1+	82	83	0.99
Sturnus vulgaris	4-	18	1+	1209	1227	14.69
Parus major	2-	1		47	48	0.57
Fringilla coelebs	2-	14		181	195	2.34
Columba livia dom.	1-	325		2039	2364	28.3
Perdix perdix	1-	9		90	99	1.19
Sterna hirundo	1-	5		39	44	0.53
Dendrocopos major	1-	2		26	28	0.34
Turdus philomelos	1-	29		137	166	1.99
Carduelis chloris	1-	0		28	28	0.34
Passer domesticus	1-	1		28	29	0.35
Passer montanus	1-	1		23	24	0.29
Garrulus glandarius		44		170	214	2.56
Turdus viscivorus		61		148	209	2.50
Turdus pilaris		38		139	177	2.12
Turdus merula		26		105	131	1.57
Mammalia	2+	**85**	3-	**8**	**93**	**1.11**
Aves		**1921**		**6325**	**8246**	**98.74**
Amphibia,Reptilia,Pisces	1+	**12**	2-	**0**	**12**	**0.14**
Total		**2018**		**6333**	**8351**	**100.0**
Diversity Index H'		3.13		2.69	3.2	

Out of 264 collections between 2003 and 2018, evenly distributed over the peregrine falcon's range in Slovakia, 3,537 prey items were identified, of which birds constituted 98.6% and mammals 1.3%. The dominant component in Period C was domestic pigeons (*Columba livia domestica*, 51.0%), which was more abundant in the earlier seasons from 2003 to 2008 and at the end of the observation period in 2015-18. In the first year of monitoring (2003), the hooded crow (*Corvus cornix*), the rook (*Corvus frugilegus*) and the European turtle dove (*Streptopelia turtur*) were the most common prey found in the peregrine falcon diet. The stock dove (*Columba oenas*) was the most common prey in the second year (2004) and the common blackbird (*Turdus merula*) during the subsequent year. In the second decade of Period C (starting from 2010), there were alternate years when there was a higher proportion of hawfinches (15.5%) and common starlings (14.6%), while the dominance of other species was less than 1%. Compared to earlier periods, the percentage of the common noctule (*Nyctalus noctula*) rose to 0.3% of prey items collected, while the proportion

Fig. 4. The Eurasian golden oriole (*Oriolus oriolus)* as prey in the nest of a peregrine falcon.
Obr. 4. Vlha obyčajná (*Oriolus oriolus*) ako korisť na hniezde sokola sťahovavého.

Fig. 5. Peregrine falcon flying with prey.
Obr. 5. Let sokola sťahovavého s korisťou.

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Tab. 5. Peregrine falcon recent diet in the period from 2003 to 2018 (Period C).
Tab. 5. Potrava sokola sťahovavého v recentnom období (sezóny 2003 – 2018, obdobie C).

Number of samples	**22**	**25**	**22**	**17**	**35**	**13**	**9**	**30**	**19**	**14**	**30**	**9**	**16**	**3**		
Species / Season	**2003**	**2004**	**2005**	**2006**	**2008**	**2009**	**2010**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**∑**	**%**
Corvus cornix+frugilegus	2+ 18	7	2	6	2	1		3	2		1- 3				44	1.24
Streptopelia turtur	1+ 16	13	7	1	9		1	17	6	3	1- 9	2	3		87	2.46
Columba livia dom. N	156	1+ 226	123	112	261	53	37	1- 182	1- 84	1- 42	333	81	64	51	1805	51.03
%	55.8	63.7	60.6	59.3	54.6	44.2	50.7	38.4	38.4	33.1	52.2	55.9	40.5	66.2		
Columba oenas	3	1+ 11	4	7	5	1	1	4	6		1- 3	3	2	1	51	1.44
Turdus merula	3	8	1+ 10	8	6	4	2	10	3		7		1	1	63	1.78
Nyctalus noctula						1+ 5			2	2	1				10	0.28
Sturnus vulgaris	2- 11	1- 34	1- 10	1- 12	75	18	1+ 19	1+ 108	38	1+ 32	91	29	1+ 35	1- 5	517	14.62
Coccothraustes coccothr.	1- 29	1- 27	1- 18	1- 16	65	15	1- 3	88	1+ 49	25	1+ 133	24	1+ 37	18	547	15.47
Carduelis chloris	2				5			2	1+ 6		2	1	2		20	0.57
Turdus viscivorus	6	6	3	2	7	1	1	3	1	2	2				34	0.96
Turdus pilaris	4	4	2	1	1	5	2	5	2	1	3				30	0.85
Turdus philomelos	3	2	5	5	3	3		4			3		2		30	0.85
Fringilla coelebs	3		1	3	6			3	1	3	5				25	0.71
Dendrocopos major	1				6	1	2	5		1	4	1	1		22	0.62
Garrulus glandarius	1	1	5	1	2	2		3			4		2		21	0.59
Columba palumbus	2	3	2		2	2		6	1						18	0.51
Scolopax rusticola	3	1	3	1	3			2	1		2		1		17	0.48
Loxia curvirostra	2	2			1	1		1	1	1	1		1	1	12	0.34
Pica pica		2	1	1	2			2			1	1			10	0.28
Coloeus monedula	4		1	1		1		1	1		1				10	0.28
Spermophilus citellus					3		1	1	2		1		1		9	0.25
Oriolus oriolus				1	4		1	1			1				8	0.23
Perdix perdix	1		1		1	1		1			1		1		7	0.20
Streptopelia decaocto		1			1	1					4				7	0.20
Alauda arvensis	1		1								4		1		7	0.20
Passer domesticus				1					1	2	3				7	0.20
Microtus arvalis	1		1			1				1	2		1		7	0.20
Pyrrhula pyrrhula									2	3	1				6	0.17
Cuculus canorus								3	1				1		5	0.14
Motacilla alba				1				1	1	1	1				5	0.14
Mammalia	4	2	1	1	5	1+ 7	1	3	5	4	9	0	3	0	45	1.27
Aves	276	353	202	188	473	113	72	470	213	123	628	145	155	77	3488	98.61
Amphibia	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0.06
Evertebrata	1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0.06
Total	281	355	203	189	478	120	73	474	219	127	638	145	158	77	3537	100
Diversity Index H'	1.89	1.51	1.69	1.77	1.67	2.3	1.57	1.99	1.99	1.98	1.62	1.29	1.69	0.96	1.89	

Fig 6. Peregrine falcon with catch brought to the nest to feed its young.

Obr. 6. Sokol sťahovavý s úlovkom, prineseným na hniezdo mláďatám.

of wild pigeons and doves fell significantly, with stock doves dropping to 1.4% and wood pigeons to 0.5%. There were also a low number of Eurasian woodcocks (0.5%) and corvids, as seen in Table 5.

The current population of peregrine falcons in Central and Western Europe heavily depends on the predation of domestic pigeons. A study of the diet in eastern Spain by López-López et al. (2009) implies that the peregrine falcon population increases in direct proportion to the percentage of domestic pigeons measured in their diet. Some studies of their foraging are from pairs nesting in urban areas, where domestic pigeons comprise more than 40% of their prey (e.g., Mlíkovský & Hruška, 2000; Rejt, 2001; Drewitt & Dixon, 2008).

Assessment of population trends of some prey species eaten by peregrine falcons in Slovakia

Comparing the foraging spectra of peregrine falcons in three different periods indicated changes in the relevant abundance of birds in Slovakia over the last 100 years. The most significant finding is the decline in the European woodcocks abundance during Period C, the most recent of the periods studied. Karaska (2002) considered it a species of least concern with a stable population trend. Water birds have also declined in the diet of peregrine falcons, although when comparing the changes to the diet of Eurasian eagle-owl, the opposite trend was observed (Obuch, 2021). There has likewise been a significant decline in crows in the diet, especially of western jackdaws, which were still nesting in colonies on rock cliffs in the 1980s. The population of hooded crows was severely reduced in the 1970s due to hunters' poisoning and pesticides sprayed on fields. The northern lapwing population also decreased with the reclamation of wetlands where they used to nest (Krištín, 2002). Conversely, there has been a marked rise in the abundance of smaller bird species, especially hawfinches and starlings, in the most recent Period C, in addition to domestic pigeons, whose increase has mostly come from growth in urban populations. This increase may also be due to samples from earlier periods (A and B) having come from higher elevations, while lower elevations in neighbouring lowland meadows and rolling hills lowlands have figured in recent collections. Among mammals, bats from the species *Nyctalus noctula* have recently been predominant. Their hibernating colonies use cavities found in panel houses built in urban housing estates during the socialist era (1948-89). The higher densities are reflected in the diet of several raptor and owl species (Danko et al., 2012). In comparative periods, the turtle dove (*Streptopelia turtur*) has been a similar rise in the abundance of about 2%. Even though the Eurasian collar dove (*Streptopelia decaocto*) arrived in Slovakia in the 1950s, the species remains low in the diet of many predators. An exception to that rule was the abundant hunting by the Ural owl (*Strix uralensis*) in the centre of Košice winters (Dravecký & Obuch, 2009).

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Appendix 1. Overview of old peregrine falcon diet collections in Slovakia.
Príloha 1. Prehľad starých zberov potravy sokola sťahovavého na Slovensku.

ID	Mountain / Pohorie	Cadaster / Kataster	Lokality / Lokalita	Date of collection / Dátum zberu	
A. Collections without domestic pigeons / Zbery bez výskytu domácich holubov					
1	Strážovské vrchy	Černa Lehota	Sokolie skaly	3.3.1979	
2	Súľovské vrchy	Rajecké Teplice	Skalky	26.7.1978	
3	Veľká Fatra	Sklabinský Podzámok	Katova skala	4.9.1979	
4	Veľká Fatra	Čremošné	Žarnovická dolina	8.6.1995	
5	Muránska planina	Tisovec	Kášter	30.7.1980	
6	Muránska planina	Muráň	Šance ľavý okraj	23.9.1980	
7	Muránska planina	Muráň	Šance pravý okraj	11.10.1979	
8	Muránska planina	Muráň	Javorníčkova dolina	15.5.1979	
	Malá Fatra	Terchová	Poludňpvé skaly	4.6.1997	
B. Collections with domestic pigeons / Zbery s výskytom domácich holubov					Rings - Years Krúžky-Roky
9	Malá Fatra	Turčianske Kľačany	Nad Hoskorou	11.6.1980	1942 - 52
10	Malá Fatra	Vrícko	Vrania skala	27.6.1982	
11	Chočské vrchy	Valaská Dubová	Sokol	1.7.1977	1944 - 54
12	Veľká Fatra	Dolný Harmanec	Bystrická dolina	4.11.1978	1933 - 51
13	Veľká Fatra	Staré Hory	Majerova skala	15.4.1980	1931 - 46
14	Veľká Fatra	Liptovské Revúce	Čierny Kameň	13.5.1980	1932 - 34
15	Poľana	Hrochoť	Jánošíkova skala	10.7.1978	1961
16	Muránska planina	Závadka n. Hronom	Malá Stožka	16.5.1979	1932 - 51
17	Muránska planina	Muráň	Klin	29.7.1980	
18	Slovenský Raj	Smižany	Klauzy	14.9.1980	1939,1952
	Nízke Tatry	Liptovský Ján	Bielo	18.9.2008	

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Roadside hawk (*Rupornis magnirostris*) hit by an oncoming vehicle while capturing a striped snake (*Lygophis anomalus*)

Myšiak zobatý (*Rupornis magnirostris*) zasiahnutý protiidúcim vozidlom pri love *Lygophis anomalus*

Sebastián LYONS & Diego O. Di PIETRO

Abstract: One of the most apparent origins of biodiversity loss caused by humans is infrastructural development of roads. Yet they offer certain benefits for some animals, such as hunting opportunities with lower energy costs and consumption of carrion earlier hit by vehicles. Raptors find roads a particularly favorable environment, perching on poles or overhead cables and waiting to attack their prey as it crosses a road. This paper describes the first ever recorded predation by a roadside hawk (*Rupornis magnirostris*) of a striped snake (*Lygophis anomalus*) supportable by material evidence, when both the raptor and the snake were hit by a vehicle immediately after the snake was caught. The study contributes to knowledge about the roadside hawk's diet and illuminates the problem these human infrastructures pose for animals. Future research on roads birds of prey use as hunting sites could contribute toward improvements in conservation programs for birds of prey species.

Abstrakt: Jednou zo zjavných príčin straty biodiverzity spôsobenej ľuďmi je rozvoj cestnej infraštruktúry. Niektorým druhom zvierat však ponúka výhody, ako sú energeticky menej náročný lov či konzumácia uhynutých živočíchov zasiahnutých vozidlami. Dravce vyhľadávajú cesty ako mimoriadne vhodné prostredie. Sedia na stĺpoch či vedeniach, kde vyčkávajú aby zaútočili na korisť križujúcu cestu. Tento článok popisuje vôbec prvú zaznamenanú predáciu hada (*Lygophis anomalus*) myšiakom zobatým (*Rupornis magnirostris*) keď dravca aj korisť zrazilo vozidlo bezprostredne po útoku. Štúdia prispieva k poznatkom o potrave myšiaka zobatého a zvýrazňuje problémovosť cestnej infraštruktúry pre zvieratá. Ďalší výskum dravých vtákov využívajúcich cesty ako lovné plochy by mohol prispieť k zlepšeniu programov ochrany týchto druhov.

Key words: human-wildlife conflict, roadkill, diet, conservation,accipitridae, dipsadidae

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Road networks are attractive locations for a variety of wildlife and, in some cases, present apparent benefits, which have a substantial impact on the species that take advantage of roads for obtaining food (Meunier et al. 2000; St. Clair et al. 2019). For example, they can serve as foraging habitats for predators and allow especially raptors and owls a place to perch while they are scouting for prey (Morelli et al. 2014). The availability of perches and a high abundance of small vertebrates (Dean & Milton 2003) make roads important wildlife corridors (Bennett 1990). The roadsides may be major foraging sites for small animal predators, with raptors and scavengers likely to forage at these sites, too (Dean & Milton 2003). However, mortality caused by vehicles is among the most commonly reported effects of roads on wildlife, and traffic speed appears to be related to bird mortality (e.g., Meunier et al. 2000; Benítez-López et al. 2010). Several studies have reported the presence of raptors near roads that had been hit by vehicles while searching for animal carrion (Lambertucci et al. 2009) or actively hunting for prey (Dean & Milton 2003). Nonetheless, the majority of studies on the mortality of birds of prey on roads have focused on the Strigidae family, probably because owls have been the birds most found as roadkill (Anderson 2006; Arnold et al. 2019; Boves & Belthoff 2012; Guinard et al. 2012; Illner 1992). There have also been studies where barn owls (*Tyto alba*) and spotted eagle-owls (*Bubo africanus*) (Arnold et al. 2019; Bullock et al. 2011; Dean & Milton 2003) were the birds most commonly killed on roads. It is also well evident that many vehicle-killed raptors had been feeding on either live prey captured on a road or on carrion found there because of the high concentration of invertebrates, small vertebrates and/or road-killed carcasses noticeable on or near them (Bullock et al. 2011; Cuyckens et al. 2016; Dean & Milton 2003; Donázar et al. 1993; Eakle 1994; Ellis et al. 1990; Knight & Kawashima 1993; Marin & Schmitt 1996; Thompson et al. 2013; Travaini et al. 1995; Visagie & Anderson 2006). For instance, the southern pale chanting goshawk (*Melierax canorus*) is the most frequently observed raptor killed on roads in Southern Africa (Oschadleus & Harebottle 2002).

The roadside hawk (*Rupornis magnirostris*) is a common, medium-sized species widespread in the Neotropical region (Baladrón et al. 2016), which ranges from northern Mexico to the Río Negro valley in central Argentina (Thiollay 1994). It inhabits open fields, forests, and urbanized areas (dos Santos & Rosado 2009). The species is closely associated with agroecosystems and natural grasslands (Mazar-Barnett & Pearman 2001).

This raptor is opportunistic (Panasci & Whitacre 2000), preferring easy-to-capture prey like the young of other birds (dos Santos & Rosado 2009). They also take advantage of special opportunities, such as hunting insects escaping from army-ant swarms, capturing frogs immediately after rain, and prey fleeing from fires (Panasci and Whitacre 2000). In addition, the roadside hawk is a passive-seeking predator (Baladrón et al. 2016) that employs a sit-and-wait strategy. Its hunting behaviour consists of perching on branches, utility poles, and overhead electric cables; waiting, and springing onto its prey (Panasci & Whitacre 2000; dos Santos and Rosado 2009).

The geographical distribution of the striped snake (*Lygophis anomalus*) is restricted to the Pampean grasslands of Uruguay, southern Brazil, and east-central Argentina (Panzera et al. 2017; Williams et al. 2021). There are few confirmed cases of predation of snakes by birds of prey (e.g., Martins et al. 2003; DuVal et al. 2006; Costa et al. 2009, 2014; Medrano-Vizcaíno 2019; Sawaya et al. 2003; Travaglia-Cardoso & Almeida-Santos 2012), which include studies of roadside hawks hunting the two-headed sipo snake *Chironius bicarinatus* (Zocche et al. 2018) and snakes of the genera *Apostolepis*, *Philodryas*, *Erythrolamprus* and *Rhachidelus* (de Souza et al. 2022). Although there are equivocal reports of roadside hawk preying on striped snakes (Salvador et al. 2017) and other unidentified snakes (de la Peña 2011), this paper provides the first documented case of a roadside hawk preying upon a striped snake that is supportable by material evidence.

Both the roadside hawk and the striped snake were most likely hit together by a vehicle just after the snake had been captured by the hawk. This event was observed in central Argentina at a peri-urban patch of National Highway 168

Fig. 1. Landscape next to National Highway 168 where the striped snake was caught by the roadside hawk and both animals were then hit.
Obr. 1. Krajina vedľa štátnej cesty 168, kde myšiak zobatý (*Rupornis magnirostris*) ulovil hada *Lygophis anomalus* a obe zvieratá následne zrazilo vozidlo.

(31°43'S, 60°28'W, Elevation 77 m) in the city of Paraná, Entre Ríos Province. The area is in the Argentine Espinal bioregion (Cabrera 1976), more recently described as a subtropical riparian forest (Oyarzabal et al. 2018) which is mostly devoted to agricultural production. Various species of grasses can be found between these fields and the road, as well as trees and utility poles supporting power lines (Fig. 1).

The specimens were found dead on the side of the paved road in October 2010, and both were collected and deposited at the Herpetological Collection curated by the Museo de la Plata (Collection number MLP.R.7000).

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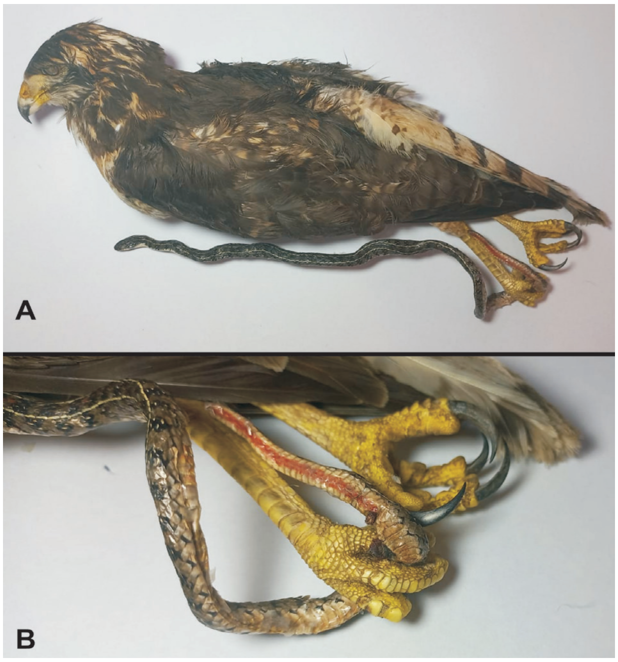

Fig. 2 A - Roadside hawk (*Rupornis magnirostris*) collected at the side of the road with a male striped snake (*Lygophis anomalus*). B - Close-up of the roadside hawk's left talon grasping the striped snake.
Obr. 2. Myšiak zobatý (*Rupornis magnirostris*) spolu so samcom *Lygophis anomalus*. B – Detailný záber na ľavý pazúr myšiaka zobatého, s uloveným *Lygophis anomalus*.

The raptor's left talon had held the snake by the caudal part of its body (Fig. 2a), with a lateroventral puncture wound appearing on the snake's right side that the roadside hawk's hallux claw had made. An evisceration was present approximately three centimeters cranially from cloaca and the hemipenes were everted (Fig. 2b). Neither animal had been stepped upon, which infers that the evisceration occurred from the force exerted by the claws squeezing hard on the snake (Fig. 2b). Of course, the eversion of the hemipenes could have been caused by the force of impact delivered by the vehicle, too.

Though observations of these events are scarce (Zocche et al. 2018), they provide meaningful knowledge about the diet of birds of prey worldwide and particularly in regions with scarce information about trophic ecology, such as among the Neotropical birds of prey group (del Hoyo et al. 1994; Bierregaard 1998; Bó et al. 2007). Finally, there has been great effort expended in recent years to conserve raptor and owl species as the pest control abilities of these predators and scavengers become recognized (Donázar et al. 2016). In this sense, the rapid increase in human infrastructure generates the need for increased knowledge about how these birds utilize roads as hunting sites, which would contribute to the development of conservation programs. Studying this topic further would enable the planning stages of future road development to be appropriately defined to generate the least possible impact on wildlife (Bennett 2017).

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The second egg in the lesser spotted eagle (*Clanga pomarina*) clutch as a nesting insurance

Druhé vajce v znáške orla krikľavého (*Clanga pomarina*) ako hniezdna poistka

Ján Kicko

Abstract: Over an interval of 16 days, two eggs were laid by the same lesser spotted eagle female in her nest in the west-central Slovakia in 2021. The first egg failed to hatch, and the female ate it on the 45th day after she had laid it. Thereafter, the chick hatched from the second egg and later successfully fledged. The case contributes toward explaining why the species lays a second egg, even though the younger hatched chick is almost always prone to siblicide. In this case, the second egg acts as a reserve or an insurance if the first egg should not hatch, enabling the parents to breed successfully.

Abstrakt: V roku 2021 bolo zistené na hniezde orla krikľavého na západe stredného Slovenska znesenie dvoch vajec s odstupom až 16 dní tou istou samicou. Prvé vajce sa nevyliahlo a samica ho na 45. deň po znesení skonzumovala. Mláďa z druhého vajca sa vyliahlo a neskôr z hniezda úspešne vyletelo. Prípad prispieva k vysvetleniu príčiny znášania dvoch vajec u tohto druhu, hoci mladšie mláďa skoro vždy podlieha siblicíde. V tomto prípade druhé vajce poslúžilo ako rezerva alebo poistka, keď po nevyliahnutí mláďaťa z prvého vajca umožnilo páru úspešne vyhniezdiť.

Key words: belated second egg laying, cainism, Abel rearing

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Introduction

The main evolutionary advantage of siblicide in birds of prey is to increase the surviving nestlings' share of food from their parents (Simmons 2002). The lesser spotted eagle is one of the raptor species where obligate siblicide, also known as cainism (Wendland 1958), regularly occurs (Simmons 1988) - e.g. harpy eagle (*Harpia harpyja*), bearded vulture (*Gypaetus barbatus*), crowned eagle (*Stephanoaetus coronatus*), Verreaux's eagle (*Aquila verreauxii*), tawny eagle (*Aquila rapax*), and the African hawk-eagle (*Aquila spilogaster*). Obligate siblicide reduces these species' brood size to one in virtually all (> 90%) cases, and food stress was never found to be the proximate cause of this behaviour in any season (Gerhardt et al. 1997). Although the complete lesser spotted eagle clutch consists mostly (81%) of two eggs, sometimes (16%) of one egg, and, in exceptional cases (2%) of three eggs (n = 178, Meyburg 1969), the percentage of nests found with two fledged young ranged from only 0.1% in Germany (Meyburg et al. 2008, n = 1305) to 3.6% in Slovakia (Maderič et al. 2008, n = 1775). The interval from when the female laid her first to her second egg, calculated from the timing between when they hatched, would reach three to four days (Meyburg 1970, Sládek 1959) and occasionally up to six days (Meyburg 2002). Scheller & Meyburg (1996) estimated the interval between the first and second egg at 5-7 days, and Matsone et al. (1996) measured the difference in captivity as seven days. Väli (2017) calculated the median difference between the laying of the first (n = 21) and the second egg (n = 8) as five days. The incubation period was estimated at 37-41 days (Sládek 1957, Scheller & Meyburg 1996). The young from the egg that hatched later (Ábel, Wendland 1958) would be attacked by its older sibling (Cain), with the smaller chick usually fleeing to the edge of the nest to die of exposure to cold or starvation or falling out of it (Meyburg 1974). The older chick would continue to attack even if there is a sufficient food reserve in the nest (Sládek 1959). The younger chick sometimes receives no food and dies within a few days after hatching (Sládek 1959). The female could then rip the dead chick and feed the pieces to the older chick or eat it herself (Meyburg 1974).

The amount of food correlates negatively with sibling aggression and brood reduction (Estes et al. 1999) in facultative siblicide species, such as the northern goshawk (*Accipiter gentilis*) and American kestrel (*Falco sparverius*). The young or the parents could subsequently feed upon the dead brood (Boal & Bacorn 1994). Cannibalism is more frequent in years of food scarcity (Bortolotti et al. 1991).

Modern optical recording devices enable the observation of the breeding biology in raptor species in which siblicide has evolved and to learn how either the younger chick dies or, on the contrary, survives with minimal disturbance.

Methods

A KeepGuard 680V camera trap was used to study the lesser spotted eagle's breeding biology (cf. Väli 2017). An external power source, a car battery, was placed at the base of the nesting tree. The camera trap was installed on 29 March 2021, before the eagles' arrival from their wintering grounds, to minimise human disturbance (cf. Dombrovski 2019). It was placed directly over the nest and pointed downwards. The minimum trigger interval was set at 30 seconds. The camera was removed from the nest after the young had fledged on 9 September 2021. The nest is located on a fir (*Abies alba*) tree in the Veľká Fatra Mountains, in the Turiec region in the west-central Slovakia, at 660 m.a.s.l.

Results

Both the male and female first appeared at the nest on 12 April. On 26 April, the female laid her first egg, followed 16 days later, on 12 May, by a second egg. The eggs could easily be distinguished from each other because the earlier-laid egg was lighter, rounder and slightly larger than the latter egg. On May 13-17, rainfall occured, and temperatures were cooler than average on May 13-17. On the evening of 14 May, neither egg was incubated while it was raining for over one hour because the adult eagles were not at the nest, so the eggs got wet. On 10 June, 45 days after the first egg was laid, the female cracked the first egg and consumed its contents. The chick never hatched. Since the egg was already 5-6 days after its estimated hatching date and still contained a lot of yolk, the embryo had probably not been fully developed. On June 18, the camera trap memory card became full, and the hatching of the second chick could not be recorded. Nevertheless, the "Abel" had hatched and was observed from the ground as a fully feathered chick in the nest on 3 August 2021, shortly before it fledged. Subsequently, on 9 September, the young was observed again already flying in the forest around the nest.

Discussion

Contrary to previous knowledge, a 16-day interval between laying two eggs is relatively large. At first, a possible explanation for the late laying of the second egg was that it had been laid by another female. Polygyny was found in a closely related Indian spotted eagle (*Clanga hastata*) (Sant et al. 2017), where one male bred with two females in two different nests. In lesser spotted eagles, females visit foreign nests in the later stages of breeding, and it is assumed that they do not exhibit territorial behaviour towards other females therein (Meybrug et al. 2007). There are, however, no known data on polygyny in lesser spotted eagles. Although in the case described, there were no individual markings on the female (either a ring or a wing marking), it is clear from the individual colour signs on her back, shoulders and upper parts of her wings that both eggs were laid and the first egg also consumed by the same female, and no polygyny was involved in this case. In 2020, a breeding male most likely disappeared at this site during the breeding season and a new male probably nested here a year later. The methods used did not determine whether the female had two partners. There are no data on polyandry in lesser spotted eagles either. The female's laying of a second egg 16 days later probably cannot be considered a replacement clutch, for which longer intervals have been found in other raptors, ranging from 25 days in ospreys (*Pandion haliaetus*) to 60 days in bald eagles (*Haliaeetus leucocephalus*) (Morrison & Walton 1980, cf. Moleón et al. 2009). It is not exactly known why the laying of the second egg was delayed.

The date when the second egg was laid, 12 May, is not exceptional. For instance, one case was found by me in 2019 when a chick fledged as late as 18 August, and in another case, Bergmanis (Latvijas Sabiedriskie Mediji 2022) observed young hatching even as late as around 7 July.

The interruption in the earlier-laid egg's embryonic development may have been caused by exposure to hypothermia on 14 May, the 18th day after the first egg had been laid. The second egg was then at a different stage of development, being laid only two days before. Although the survival of the developing embryo is significantly influenced by its age (Webb 1987), recent research suggests that many bird species can tolerate egg hypothermia as low as 10 °C (Zhao et al. 2017).

In several respects, the lesser spotted eagle does not fall into the category of cainistic species. These are typically large, have long life spans, are tropical and sedentary, with high sub-adult mortalities, extremely stable territories and low rates of adult turnover within them, thus limiting opportunities to breed (Simmons 1988). Therefore, the reasons why siblicide developed in lesser spotted eagle are probably different from other above-mentioned obligate cainists.

Factors that allow for siblicide in obligate cainists (Edwards & Collopy 1983) include a few days hatching asynchrony, the size difference of the eggs and consequently the chicks' size when they hatch, the sex of the chicks and the order in which they hatch. The age difference gives the earlier-hatching chick a substantial size development advantage. The first egg laid is almost always larger, and so is the chick that hatches from it, although female chicks also happen to be larger overall. In lesser spotted eagles, these factors are complemented by mutual aggression between the chicks (apparently the larger chick usually against the smaller one) and the lesser attention the mother gives to the smaller and less active chick (Meyburg 2002). The second egg laid in species with obligate siblicide serves as insurance (Edwards & Collopy 1983, Meyburg 1974). It is a parental response to the pressure of floaters in the population, where the proportion of two-egg clutches declines as their number increases (Simmons 1988, 1997). Meyburg (2002) supposes that the lesser spotted eagle is in an evolutionary transitional phase, laying one egg instead of two.

This unusual case offers a possible explanation of the two laid eggs where the second egg can be an insurance policy for the lesser spotted eagle, allowing the parents to raise Abel and let him successfully fledge after the earlier-laid egg fails.

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Distribution, abundance, and breeding of the imperial eagle (*Aquila heliaca*) in Western Slovakia in 1977–2022

Rozšírenie, početnosť a hniezdenie orla kráľovského (*Aquila heliaca*) na západnom Slovensku v rokoch 1977–2022

Jozef CHAVKO, Leonidas PREŠINSKÝ & Roman SLOBODNÍK

Abstract: The distribution, abundance, breeding success, and habitats of the imperial eagle in the mountains and adjacent lowlands of Western Slovakia were studied over the last 45 years (1977–2022), with a total of 65 breeding pairs documented. Of the 589 breeding attempts (range 2–42 per year) that were recorded, 420 were successful (74%) and produced 718 chicks altogether. Breeding success varied considerably across the years, with an average of 1.2 chicks per initiated and 1.7 chicks per successful breeding attempt. Three chicks fledged from 10.7% of the successful breeding attempts, two chicks from 50.2%, and one chick from 39.1% of them. Breeding numbers increased slowly between 1977 and 1997, with a marked increase after 1998. In two of the most recent years, 2020 and 2021, breeding numbers more than doubled. Since 2000, we have observed changes in breeding habitat preferences, where the population has shown more preference for lowland regions than mountains. Natural factors are probably driving the upward population trend, but there has also been action taken with several management measures. The conservation measures involved and their impact on population and range trends are analysed and discussed here.

Abstrakt: Rozšírenie, početnosť, hniezdny úspech a biotopy orla kráľovského boli skúmané za posledných 45 rokov (1977 – 2022) v pohoriach a priľahlých nížinách západného Slovenska. Celkovo sme zaznamenali 65 hniezdiacich párov a 589 zahniezdení (2 – 42 ročne), z toho 420 úspešných (74%). Z úspešných hniezd vyletelo spolu 718 mláďat. Úspešnosť hniezdenia v jednotlivých rokoch bola veľmi variabilná s priemerom 1,2 mláďaťa na započatý hniezdny pokus a 1,7 mláďaťa na úspešný hniezdny pokus. V 10.7% úspešných pokusov o hniezdenie vyleteli tri mláďatá, v 50.2% dve a v 39.1% jedno mláďa. V období rokov 1977 až 1997 početnosť hniezdení pozvoľne stúpala, od roku 1998 začal počet hniezdení výraznejšie stúpať a v posledných dvoch rokoch 2020 a 2021 stúpol počet hniezdení viac ako dvojnásobne. Od roku 2000 sme pozorovali zmenu preferencie hniezdísk, kde populácia začala preferovať nížiny pred pohoriami. Vzostupný populačný trend pravdepodobne súvisí s prirodzenými faktormi, ale aj s viacerými ochranárskymi opatreniami, ktoré sme zrealizovali.

Key words: birds of prey, breeding biology, distribution, Central Europe, population

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Introduction

The eastern imperial eagle (*Aquila heliaca*) inhabits the central and western Palaearctic realm from southern Moravia and Austria at the western edge of its range to Lake Baikal at its easternmost extent (Heredia 1996). In Europe, it occurs only in Pannonia, on the islets of the southern Balkans, central and eastern Ukraine, central and southern Russia, and western Kazakhstan (Keller et al. 2020). Population size was estimated between 1994 and 1996 for 363 to 604 pairs (Heredia 1996). Since then, the European population has risen to between 1,768 and 2,229 pairs (Demerdzhiev et al. 2011). Historical data on the raptor's occurrence in Slovakia had been previously summarised by Ferianc (1964), Mošanský (1972), Sládek (1959), and Hudec & Černý (1977). The eastern imperial eagle nests in two regions within Slovakia, approximately 160 kilometres apart from each other (Fig. 1). The distribution of the species continuously runs southward to breeding areas in Hungary (Horváth et al. 2020), western and north-western Austria and into the Czech Republic (Schmidt & Horal 2018).

The earliest reference to the eastern imperial eagle's presence in Western Slovakia comes from Tonhauzer (1954), who mentioned sightings in the Little Carpathian Mountains in 1953. Between 1963 and 1965, five breeding pairs were documented there (Ferianc 1964, Kalivodová & Brtek 1977), and an overview of the total occurrence of this species in Slovakia was later published by Danko and Chavko (1966, 2002) and Chavko et al. (2014). The causes for the expansion of the eagle's range in Central Europe and breeding in Slovakia were described by Sládek (1959), who mentioned the gradually warming climate as the main factor driving the expanded distribution.

Until recently, the Little Carpathians were considered to be the western limit of the eastern imperial eagle. In the last two decades, the frontier has shifted (e.g., Mikuš et al. 2008 Horal, 2008) to southern Moravia, almost to the White Carpathians, and even further west to breeding sites in Lower Austria. These areas are now regarded as the north-westernmost boundary for the Pannonian subpopulation (Šťastný et al. 2021, Schmidt & Horal, 2018, Vili et al. 2009).

Over 45 years (1977–2022), selected data was processed from all breeding records for the species documented in Western Slovakia since previously published data were only partial and breeding over recent decades had not been analysed in a continuous time series (Chavko 2002, Danko et al. 2011). Eastern imperial eagle population trends are accordingly described to underscore factors causing mortality. The discussion evaluates the impact of selected actions to conserve the species and confronts our results from western Slovakia with results from a study conducted in eastern Slovakia (Danko et al. 2020).

Methodology

Distribution and abundance

In Western Slovakia, the breeding range of eastern imperial eagles has been systematically monitored since 1977, with a total of 28 people involved over the years. Nests were directly searched to determine breeding distribution and abundance, using historical data from references and subsequently recording occurrences. While observations were made from selected observation posts that offered a good view, during the autumn and winter, nests were sought in forest growth at anticipated locations and then checked for occupancy in the spring. The distribution of the species was monitored annually by counting the number of occupied nests. Each nest was documented for breeding habitat, species of nesting tree, and interactions with other raptor species nesting in the same territory. Every breeding site was also photographically documented.

Breeding success

Nests were visited only once during the breeding season. Any further checking was carried out with a monocular and later, starting in 2019, with drones (e.g., Galleago & Sarasola 2021). Nests were physically inspected to band the chicks (Slobodník & Jenčo 2020), collect biological samples, and fit the chicks with satellite transmitters (Danko et al. 2011). Breeding was considered unsuccessful when the pair had nested and the female had laid eggs, but the pair produced no fledglings. Reproductive success was expressed as the ratio of the number of fledglings from 1) initiated and 2) successful breeding attempts. Factors causing nesting failure were recorded.

Mortality and conservation measures

Data was collected on cases of poisoning, unlawful shooting, and other illegal activities between 2003 and 2015 and again in 2016-22. During 2003-15, during a lower abundance of eastern imperial eagles, the mortality was monitored by volunteers. From 2016, mortality was monitored during the preventive conservation of bird populations starting with major projects like LIFE ENERGY, LIFE PANNON EAGLE, and LIFE DANUBE FREE SKY. Other activities under the aegis of these large projects included mapping the nesting sites, establishing protection zones around the nests, safeguarding the nests electronically, searching foraging and nesting territories

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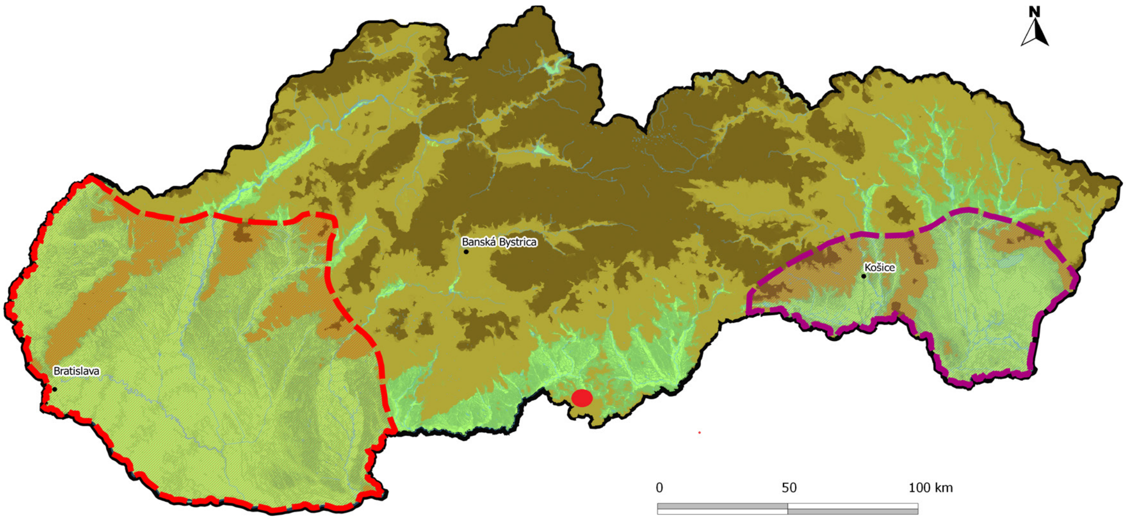

Fig. 1. Range of the eastern imperial eagle in Slovakia. The red dashed line indicates the range of the eastern imperial eagle's western population in Slovakia, the purple dashed line the eastern population, and the red circle marks an solitary nesting of an eastern imperial eagle pair in south part of cestral Slovakia.
Obr. 1. Výskyt orla kráľovského na Slovensku. Červená prerušovaná čiara označuje areál výskytu západnej populácie orla kráľovského na Slovensku, fialová prerušovaná čiara východnú populáciu a červený kruh označuje solitérne hniezdisko páru orla kráľovského na juhu stredného Slovensku.

for poisoned baits, banding the birds, tagging the chicks with satellite telemetry and subsequently ascertaining the causes of mortality as part of the monitoring. LIFE PANNON EAGLE has been partnering with Slovakia's national police authority since 2019 to organise field patrols, where trained sniffer dogs inspect for the presence of contaminated bait. Hunting grounds, in which repeated incidents of poisoning and other cases of bird crime had been reported in the past, were specifically targeted. Approximately 25-30% of eagle nesting and foraging territories in western Slovakia were checked yearly. Most police findings involving killed birds were subsequently published in the media to encourage prevention.

Electrocution mortality and mortality caused by collisions with power lines were monitored in 1993, 2006, and again in 2014-19, according to a methodology subsequently published by Galis (2020). In the earlier period, conservation measures were realized to less extent compared to the second period. Conservation measures were represented by the installation of protective and warning devices. Mortality data were obtained during the Life Energy project realization (2014-2019).

Results

Distribution and abundance

The first two occupied nests were discovered in 1977, one in the Little Carpathians (situated at an elevation of 600 metres) and the other in Považský Inovec Mountain (190 metres). Other nesting sites were later found in Považský Inovec Mountain (420 m.a.s.l.) and Tribeč Mountain (280 m.a.s.l.) and in the mountains of the Strážovské (740 m.a.s.l.). Until 2000, there were only two cases documented of eastern imperial eagles breeding in lower elevations. The first was recorded in the Danubian Plain (Pair 4 at 130 m.a.s.l., see Appendix 1) and the second in 1995 at a highland agrocenosis above the Žitava Žitavská highlands (Pair 34 at 200 m.a.s.l. in the Žitavská highlands pahorkatina, Krištín, 1999). As eastern imperial eagles slowly moved into new territories, the number of breeding pairs gradually rose. The bigger increase in numbers came after 2018, when 21 pairs bred, followed in 2019 by 31 pairs, then 37 pairs in 2020, 42 pairs in 2021, and finally, 46 pairs in 2022 (Fig. 2). Between 1977 and 2022, a total of 65 breeding sites were identified in Western Slovakia (Fig. 3, see details in Appendix 1). However, the first-ever successful breeding of an isolated pair was also recorded in 2021 and 2022 within the district of Rimavská Sobota in the south-central region of Slovakia (red circle in Fig. 1) and breeding was documented in 13 orographic units. In the 45 years of population monitoring, 589 cases of breeding were registered among the 65 known pairs. The closest active nests were 1.56 kilometres apart from each other. When the population of eastern imperial eagles started to be monitored, there were only two to ten pairs registered. But the number of known pairs grew after 2000 as they settled in lower elevations. In 2016, there were 19 pairs, and by 2022 the number had risen remarkably to 46 breeding pairs (Fig. 2).

Breeding success

Of the total 589 observed breeding attempts, 420 (74%) were successful. These successful breedings (pairs) produced 718 fledglings (Fig. 2) in total, although nesting success rates varied from year to year (Fig. 5). The average nesting success was 1.2 fledglings per initiated and 1.7 fledglings per successful nesting attempt. When the nesting pairs were successful, they produced 164 broods (39.1%) with a single fledgling, 211 broods (50.2%) with two fledglings, and 45 broods (10.7%) with three fledglings. In the twenty years between 2002 and 2022, a total of 348 chicks were banded.

Changes in breeding habitats

Of the 589 known breedings, 381 pairs nested in mountainous areas and 208 pairs nested in lower elevations. In the early years of monitoring, nests were found predominately in the mountains and rarely in lower elevations (see above). A more pronounced settlement of the lowlands has been observed since 2000 and, starting in 2018, most pairs have been nesting in lowland regions, mostly in agrocenoses (Fig. 6). Seven pairs moved from mountainous areas to lowland regions (marked by an asterisk in Appendix 1). While the average elevation of the nests in the mountains was 423 ± 170.1 metres (± SD), ranging from 260 to 740 m, the mean elevation of the nests in lowland regions was 147 ± 145.1 m (mean ± SD, range 110 – 280 m). During the study period eastern imperial eagles nested on 14 different tree species used in different proportions (Fig. 7).

Mortality and conservation measures

Between 2003 and 2015, 17 eastern imperial eagles were found dead. Four of them had been poisoned with carbofuran and three were shot, including two individuals shot directly in their nests. In addition, there was one case where three chicks had been stolen from a nest and four cases where eagles were found dead but the cause remained unknown. In two cases, chicks were found dead in their nests where it was probable that the parents had been poisoned.

A total of 153 raptors from different species were unlawfully injured or killed in 2016-22. In eight of those cases (5%), the victims were eastern imperial eagles. The birds had either been poisoned or shot. Starting in 2017, we sought to document the mortality of eastern imperial

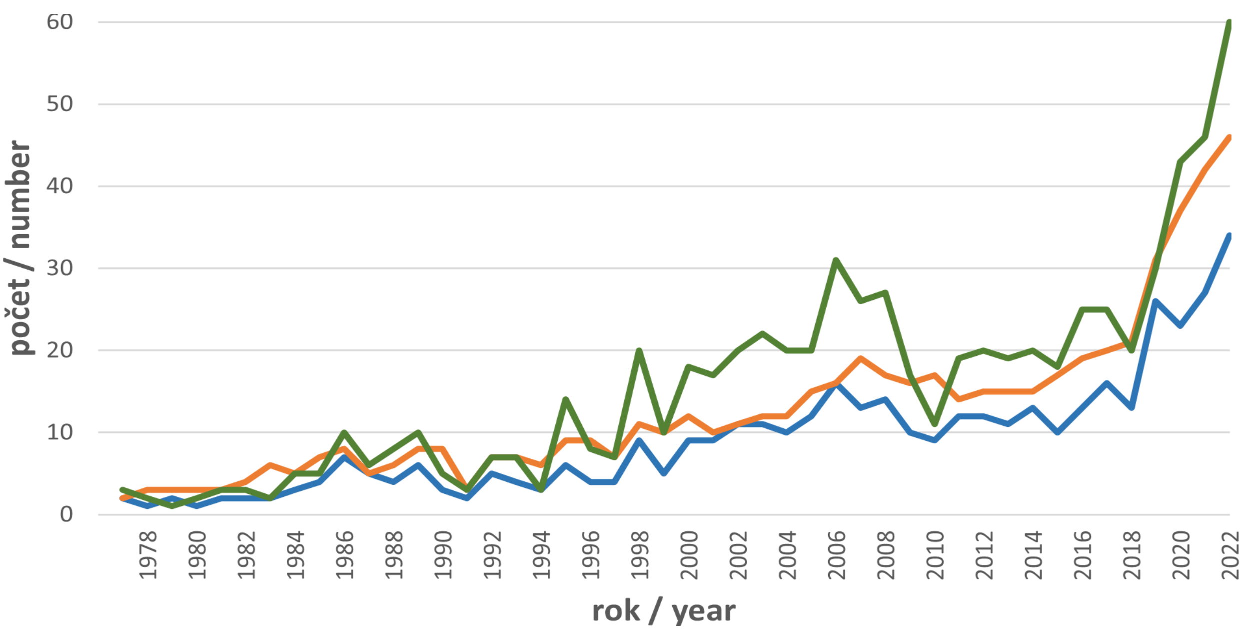

Fig. 2. Population trends for eastern imperial eagle in Western Slovakia (1977 – 2022). The blue line shows the number of successful breedings, the orange line shows the number of known breeding pairs, and the green line the number of chicks fledged.

Obr. 2. Populačný trend orla kráľovského na západnom Slovensku (1977 – 2022). Modrá čiara zobrazuje počet úspešných hniezdení, oranžová počet známych hniezdiacich párov a zelená čiara počet vyletených mláďat.

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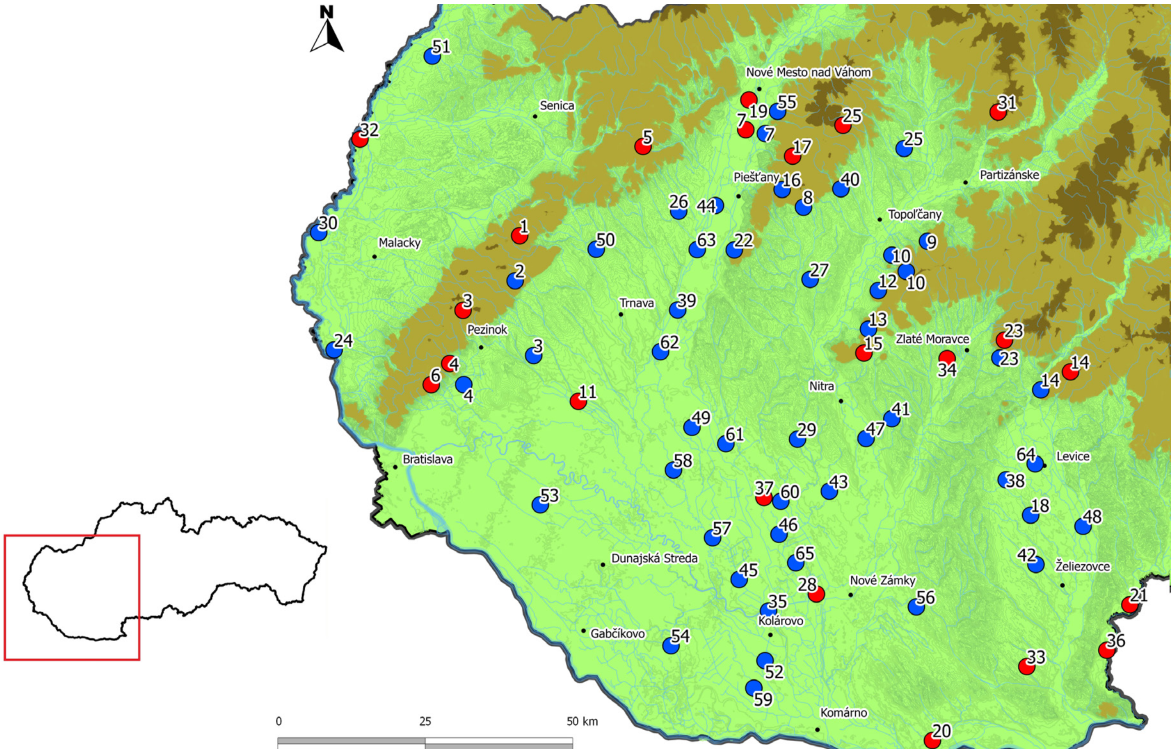

Fig. 3. Breeding places of eastern imperial eagles in Western Slovakia between 1977 and 2022 (each breeding pair was assigned a number). Pairs 4, 7, 8, 13, 16, and 25 had previously bred in mountainous areas. The blue dots are breeding places that were occupied in 2022, red dots indicate the other nesting places occupied since 1977 to 2021.

Obr. 3. Hniezdiská orla kráľovského na západnom Slovensku v rokoch 1977 až 2022 (každý hniezdny pár mal pridelené číslo). Páry 4, 7, 8, 13, 16 a 25 predtým hniezdili v pohoriach. Modré body sú hniezdiská, ktoré boli obsadené v roku 2022, červené body označujú ostatné hniezdiská obsadené od roku 1977 až 2021.

Fig. 4. Pair 16's nest, located in a European larch at the Považsky Inovec Mountain range, July 2009.

Obr. 4. Hniezdo páru 16, nachádzajúce sa na smrekovci opadavom pohorí Považský Inovec, júl 2009.

eagles annually. There were a total of three cases in 2017, two cases each in 2018 and 2019, one case in 2020, and none in 2021. Except for a single shooting, all of these cases involved carbofuran poisoning. A significant threat of injury or death for eastern imperial eagles has come from electrocution on 22-kilovolt power lines. In the period from 1993 to 2006, five eastern imperial eagles were found dead beneath high-voltage pylons, while six were likewise discovered dead during a shorter period between 2014 and 2019. In both of these periods, they were all juvenile and sub-adult individuals. No mortality of adult eastern imperial eagles was observed.

Discussion

Sládek (1959) mentioned eastern imperial eagles nesting in both western and eastern Slovakia in 1941-50, documented four nesting sites, and presumed the existence of a further

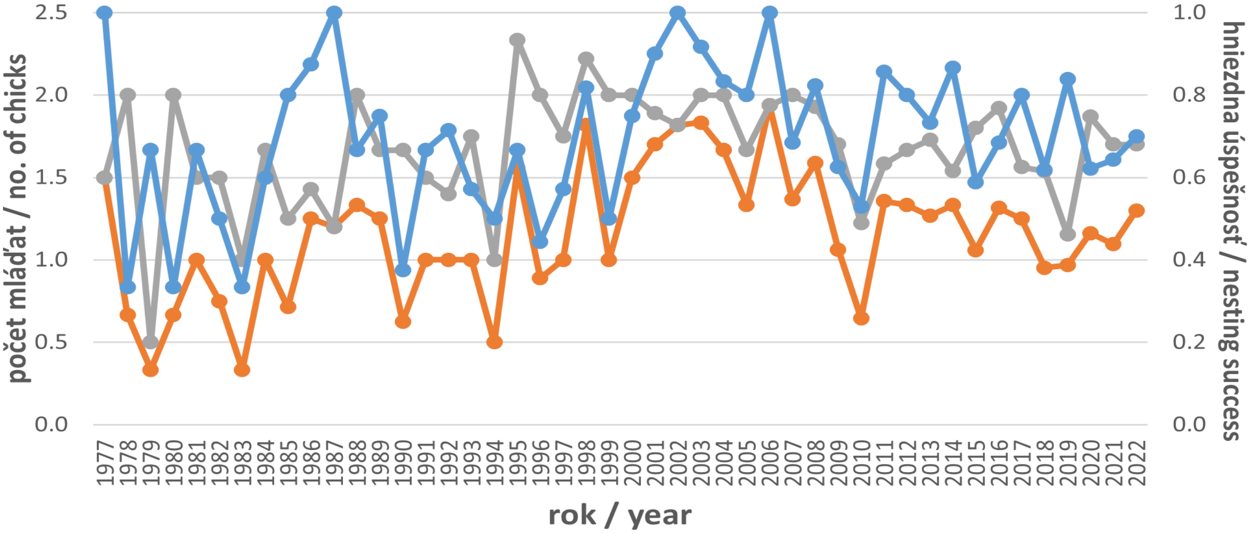

Fig. 5. Breeding success of the eastern imperial eagle in Western Slovakia (1977 – 2022). The orange line indicates the number of fledglings per initiated nesting and the grey line the number of fledglings per successful nesting (left axis), while the blue line indicates the nesting success ratio (right axis).

Obr. 5. Hniezdna úspešnosť orla kráľovského na západnom Slovensku (1977 – 2022). Oranžová čiara označuje počet mláďat na začaté hniezdenie a sivá čiara počet mláďat na úspešné hniezdenie (ľavá os), modrá čiara označuje pomer úspešnosti hniezdenia z daný rok (pravá os).

two sites. Even before then, Turček (1946) had published data on repeated shootings since 1932 of eastern imperial eagles in Western Slovakia, which occurred in the area around Veľký Tríbeč Mountain. Foresters provided evidence of a nest they had noticed in a tall beech tree on its eastern slope, which was the first recorded case of eastern imperial eagles nesting inside the territory of today's Slovakia. Although reports of breeding in the Považský Inovec range date back to 1945 (Kaňuščák 1988), it was only in 1955 that demonstrated breeding was documented (Víťaz & Kaňuščák 1999). Špaček & Kovář (1967) likewise found an occupied nest in the Považský Inovec range in 1958. Another remarkable finding was of a nest with four chicks, again in the Považský Inovec range, this time in 1973 (Víťaz & Kanuščák 2004).

The facts described above, and our results show the initial gradual increase of the eastern imperial eagle's population in Western Slovakia changed markedly trending upward after 2000. This positive trend consistently follows developments in Hungary, where the population had been rising since the 1980s. By 2019, it had grown to 282 known nesting pairs in Hungary (Horváth et al. 2020). The progressive increase of Western Slovakia's population corresponds to the trend seen in the study species in both Eastern Slovakia (Danko 2020) and across all of Europe (Demerdzhiev et al. 2011). There were 542 (70.4%) successful breeding attempts from 770 known cases of breeding and 883 fledglings in Eastern Slovakia between 1971 and 2018. The breeding success rate in the western population was 1.1 chicks per initiated and 1.6 chicks per successful nesting (Danko, 2020). Our results are in line with this study.

Generally higher breeding successes have been recently observed in Central Europe for other species in the same environment, especially at agrocenoses, such as the saker falcon (*Falco cherrug*) (Chavko 2019), the great bustard (*Otis tarda*) (Nagy 2018), the red-footed falcon (*Falco vespertinus*) (Slobodník et al. 2021), and the European roller (*Coracias garrulous*) (Repel et al. 2022). Measures to manage these species may have had a positive impact on their population (e.g., Chavko et al. 2014, Palatitz et al. 2015). Kovács et al. (2005) highlighted the eastern imperial eagle's upward population trend in recent years with the implementation of management measures and their survival has become increasingly dependent upon them. The overall positive impact of targeted conservation measures has led to a rise in the eastern imperial eagle population throughout

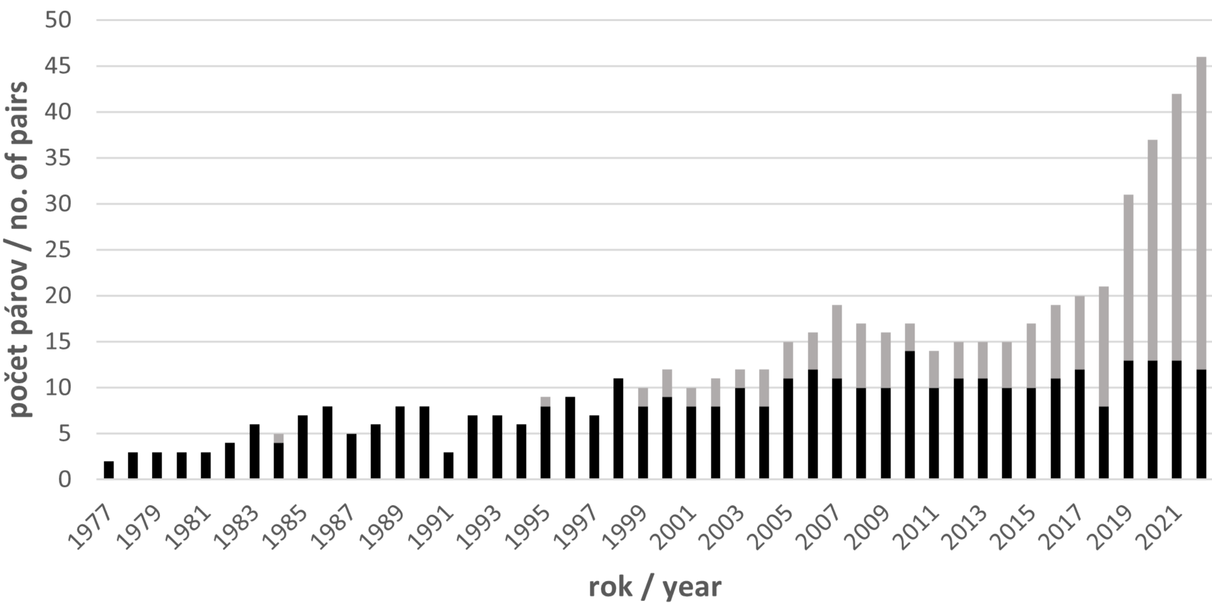

Fig. 6. Changes in breeding habitats of the eastern imperial eagle in Western Slovakia during 1977 – 2022 (black – mountains, grey – lowlands).

Obr. 6. Zmeny hniezdnych biotopov orla kráľovského na západnom Slovensku v rokoch 1977 – 2022 (čierna farba – pohoria, šedá farba – nížiny).

the Pannonian Basin (Keller et al. 2020, Schmidt & Horal, 2018). Alongside climatic conditions during the eagle's reproductive period, especially weather with little rainfall (e.g., Takagi, 2001, Weatherhead, 2005), these management measures are considered by us to be the key factors driving population growth.

From a management perspective, the success of the monitored population in western Slovakia has been limited by three following major anthropic factors. The most significant threats of eastern imperial eagles face are poisoned baits and illegal shooting, as direct mortality affects non-selectively both adults of reproductive age and also prospective juveniles (Abuladze, 1996, Heredia, 1996). Priorities to protect small game species against raptors have caused them to be persecuted and come into conflict with raptor conservation interests. The introduction of conservation measures like regular checking for the presence of poisoned baits (Fig. 8) and media coverage of confirmed cases demonstrated increased numbers of eastern imperial eagle breeding pairs and individuals occupying lowland regions (Horváth et al. 2020). This also corresponds with our results.

The second significant hazard is the high mortality caused by unsafe 22-kilowatt power lines (e.g., Gális et al. 2020, Horváth et al. 2006, Lazarová et al.

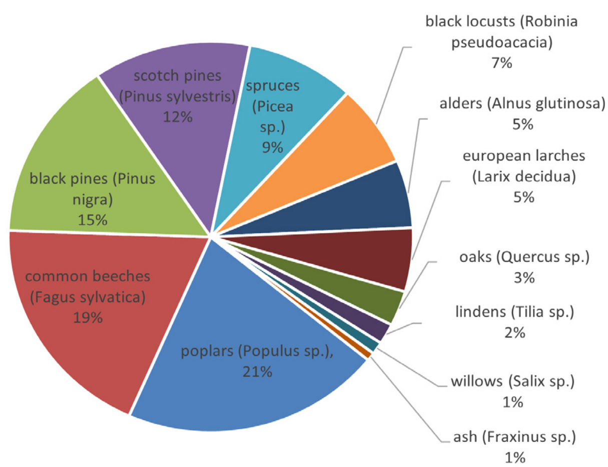

Fig. 7. Tree species of eastern imperial eagle nests [maple (*Acer* sp.) and elm (*Ulmus* sp.), each 0.17% of the total are not visualized in the figure.

Obr. 7. Druhy hniezdnych stromov orla kráľovského (javor (*Acer* sp.) a brest (*Ulmus* sp.), po 0,17% z celkového počtu nie sú na obrázku znázornené).

2020, Fig. 9). In response, a more efficient approach was taken to counteract the danger by involving the electricity network operator, Západoslovenská distribučná a.s., several implemented projects.

In recent years, protective elements have been installed at crucial points within the eastern imperial eagle's range to prevent injuries to the birds when they perch on high-voltage pylons and utility poles (Fig. 10 and 11). A total of 1,100 twenty-two-volt poles were treated by protective devices in territories of the eastern imperial eagle between 2018 and 2022 (Gális et al. 2020).

Changes in land use represent the third threat. The prioritization of commercial interests over primary environmental concerns has consequently diminished biodiversity in general and shrunk natural food sources for the eagles (Donald 2001, Vermouzek 2017). Critical declines in the abundance of European ground squirrels (*Spermophilus citellus*) and black-bellied hamsters (*Cricetus cricetus*) were particularly significant. Both species can be regarded as key prey species for eastern imperial eagles (Chavko et al. 2012). Rodenticides applied against small mammals, which are a major component of the eastern imperial eagle's diet, also remain a significant threat to the birds (Demerdzhiev et al. 2022). The balancing of agrosystems' productive, ecological, and environmental functions can be considered inadequate even in terms of habitat protection. Non-forest vegetation has been degraded and trees eradicated to make land more accessible to agricultural machinery and for the production of woodchips. Not enough new trees have been planted to compensate for what has been removed. In combination with the degradation and decay of old stands, this leads to a reduction of nesting opportunities for eastern imperial eagles in lower elevations.

Fig. 8. Police officer with a dog trained to search for poisoned bait.

Obr. 8. Policajt so psom vycvičeným na vyhľadávanie otrávených návnad.

Fig. 9. Eastern imperial eagle electrocuted. Trnavská pahorkatina Higlands, April 2006.

Obr. 9. Orol kráľovský usmrtený elektrickým prúdom. Trnavská pahorkatina, apríl 2006.

Katzner et al. (2003) recorded the displacement of eastern imperial eagles to the periphery or the occupation of their original nests by golden eagles (*Aquila chrysaetos*), which corresponds to our observations. There were three cases recorded of eastern imperial eagle pairs displaced from their breeding territories by golden eagles after either directly occupying their nests or building new nests in their territories. Golden eagles began nesting at the breeding site of the eastern imperial eagle (Pair 14) in the Štiavnické mountains in 2011. The pair was found in 2022 at a newly occupied nest located on a black pine about six kilometres southwest of the original nest. At Považský Inovec Mountain, golden eagles began nesting at Pair 17's breeding territory in 2019 and at the breeding site of Pair 25 in 2016.

Fig. 10. Straight-line protective perch.

Obr 10. Priamy ochranný prvok.

Fig. 11. Triangular protective perch.
Obr. 11. Trojuholníková zábran.

A gradual transition in breeding habitat preference from mountainous areas to lowlands has also been documented in Hungary (Bagyura et al. 2002, Horváth et al. 2011). This gradual increase in the number of breeding sites in lowland regions (Fig. 12, 13) led to changes in the distribution of the trees where the nests were located, with trees that tend to grow in lower elevations such as poplars, black locusts, and alders beginning to predominate. In contrast, the proportion of nests in beeches and spruces declined markedly. To conclude, it is important to stress the importance of continued prevention of bird crime and the risk of injury from power lines (Kern et al. 2022, Lazarová et al. 2020), which have markedly impacted not only the population of eastern imperial eagles but also many other raptor species (Gonzalez et al. 2007, Smart et al. 2010, Demerdzhiev, 2014, Demeter et al. 2018, Dwyer et al. 2015).

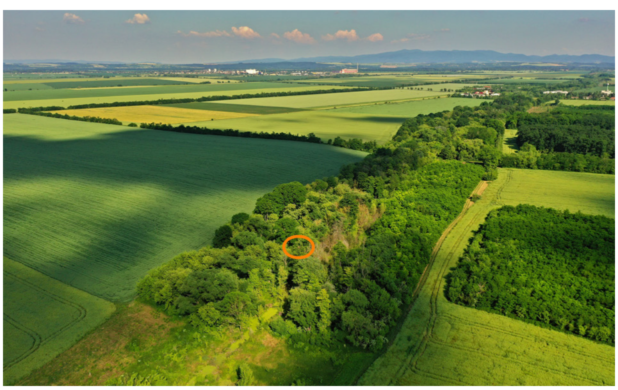

Fig. 12. Breeding habitat of the eastern imperial eagle (Pair 42), Danubian Plain, May 2021. The nesting tree is marked with a orange circle.
Obr 12. Hniezdny biotop orla kráľovského (Pár 42), Podunajská nížina, máj 2021. Hniezdny strom je označený krúžkom.

Fig. 13. Breeding habitat of the eastern imperial eagle (Pair 56), Hronská pahorkatina Highlands, June 2021. The nesting tree is marked with a orange circle.
Obr 13. Hniezdny biotop orla kráľovského (Pár 56), Hronská pahorkatina, jún 2021. Hniezdny strom je označený krúžkom.

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Príloha 1 Zoznam hniezdisk a časový priebeh hniezdenia jednotlivých párov za celé obdobie monitoringu 1977 – 2022.

Appendix 1. List of breeding places and breeding process of particular nesting pairs during years 1997 - 2022

pair´s ID	orographic unit	habitat	breeding period	pair´s ID	orographic unit	habitat	breeding period
kód páru	**orografický celok**	**biotop**	**obdobie hniezdenia**	**kód páru**	**orografický celok**	**biotop**	**obd. hniezdenia**
1	Malé Karpaty	mountains	1977-1989, 1990-2007	30	Borská nížina	lowlands	2016, 2018-2022
2	Malé Karpaty	mountains	1980-1994, 1998, 2000-2001, 2010-2012,2016-2022	31	Strážovské vrchy	mountains	1986, 1988-1990
3*	Malé Karpaty	mountains	1982-1990, 1995-1996, 2005-2006, 2008-2010, 2012-2013	32	Borská nížina	lowlands	2009, 2020
	Trnavská pahorkatina	lowlands	2004, 2014-2016, 2020-2021	33	Podunajská rovina	lowlands	2004
4*	Malé Karpaty	mountains	1989-1999	34	Žitavská pahorkatina	lowlands	1995
	Podunajská rovina	lowlands	1984, 2000-2022	35	Podunajská rovina	lowlands	2007, 2019-2022
5	Malé Karpaty	mountains	1985, 1990, 1992-1993, 1998-1999	36	Ipeľská pahorkatina	lowlands	2007
6	Malé Karpaty	mountains	1995-1998, 2000-2006	37	Podunajská rovina	lowlands	2010
7*	Považský Inovec	mountains	1977-1979, 1983-1987,1988-1998,2000-2012, 2017, 2019-2022	38	Pohronská pahorkatina	lowlands	2017-2022
	Trnavská pahorkatina	lowlands	1999	39	Trnavská pahorkatina	lowlands	2017-2022
8*	Považský Inovec	mountains	1990, 1992-2007, 2009-2010, 2012-2013, 2016-2017, 2019-2022	40	Považský Inovec	mountains	2018-2022
	Nitrianská pahorkatina	lowlands	2008	41	Nitrianská pahorkatina	lowlands	2018-2019, 2022
9	Tríbeč	mountains	1978-1983, 1996, 1998-2008, 2010-2011, 2014-2021	42	Pohronská pahorkatina	lowlands	2018-2022
10	Tríbeč	mountains	1979, 1985-1989, 1992-2010, 2012-2022	43	Nitrianská pahorkatina	lowlands	2018-2022
11	Trnavská pahorkatina	lowlands	1999-2000	44	Trnavská pahorkatina	lowlands	2018-2022
12	Tríbeč	mountains	1995-2022	45	Podunajská rovina	lowlands	2019-2022
13*	Nitrianská pahorkatina	lowlands	2007-2010	46	Podunajská rovina	lowlands	2019-2022
	Tríbeč	mountains	2013-2015, 2016-2021	47	Žitavská pahorkatina	lowlands	2020-2022
14	Štiavnické vrchy	mountains	1999-2010, 2022	48	Ipeľská pahorkatina	lowlands	2019-2022
15	Tríbeč	mountains	2015	49	Podunajská rovina	lowlands	2019-2022
16*	Považský Inovec	mountains	1986, 2003-2005,2008-2022	50	Trnavská pahorkatina	lowlands	2021-2022
	Trnavská pahorkatina	lowlands	2000, 2002	51	Borská nížina	lowlands	2019-2022
17	Považský Inovec	mountain	2002,2003,2005-2015	52	Podunajská rovina	lowland	2020-2022
18	Pohronská pahorkatina	lowlands	2001-2013, 2015-2022	53	Podunajská rovina	lowlands	2020-2022
19	Trnavská pahorkatina	lowlands	2003, 2005-2013,2014-2016	54	Podunajská rovina	lowlands	2020-2022
20	Pohronská pahorkatina	lowlands	2007-2008	55	Považský Inovec	lowlands	2019-2022
21	Ipeľská pahorkatina	lowlands	2005-2010, 2012-2013, 2015-2016	56	Podunajská rovina	lowlands	2021-2022
22	Považský Inovec	mountains	2006-2017, 2019-2022	57	Podunajská rovina	lowlands	2021-2022
23	Pohronský Inovec	mountains	2006-2022	58	Podunajská rovina	lowlands	2021-2022
24	Borská nížina	lowlands	2007-2009, 2011-2022	59	Podunajská rovina	lowlands	2021
25*	Považský Inovec	mountains	2012-2014	60	Podunajská rovina	lowlands	2022
	Nitrianská pahorkatina	lowlands	2017, 2019-2022	61	Podunajská rovina	lowlands	2022
26	Trnavská pahorkatina	lowlands	2014-2022	62	Trnavská pahorkatina	lowlands	2022
27	Nitrianská pahorkatina	lowlands	2015, 2017-2022	63	Trnavská pahorkatina	lowlands	2022
28	Podunajská rovina	lowlands	2016-2017	64	Ipeľská pahorkatina	lowlands	2022
29	Nitrianská pahorkatina	lowlands	2016, 2018, 2020-2022	65	Podunajská rovina	lowlands	2022

* pairs moved from mountains to lowland / páry presťahové z pohorí do nížin

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Hunger sweetens the beans: evidence of opportunistic feeding behaviour of the little owl (*Athene noctua*, Scopoli 1769) from Peloponnese, Greece

Hladnému chutí všetko: dôkaz oportunistického potravného správania kuvika obyčajného (*Athene noctua*, Scopoli 1769) z Peloponézu, Grécko

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Abstract: The little owl (*Athene noctua*) is a common raptor in Mediterranean habitats. To acquire more information on its diet, this study identified cranial and post-cranial skeletal material from 70 owl pellets collected during the 2016 and 2017 breeding seasons. The material was used to quantify the little owl's relative prey abundance using MNI (minimum number of individuals), a taphonomical unit. This study is the first to examine the diet of the little owl in the Peloponnese (southern Greece). After examining 3,691 isolated skeletal and exoskeletal remains from the processed pellets, a total of 78 and 108 prey items were recorded for the two consecutive years. This study, in congruence with previous research, showed that in both years the little owl favoured primarily small mammals and arthropods, with a clear predominance of Thomas's pine vole (*Microtus thomasi*) and arthropods from the class Diplopoda. Finally, a redundancy discriminant analysis (RDA) was applied to our two-year results, along with those from similar studies in the Mediterranean region, to examine the relationship between habitat types and prey taxa, which supported the little owl's opportunistic feeding behaviour, depending on variation of ecological factors.

Abstrakt: Kuvik obyčajný (*Athene noctua*) je bežný dravec stredomorských biotopov. S cieľom získania ďalších poznatkov o potrave druhu, sme determinovali kraniálny a postkraniálny materiál so 70 vývržkov, zozbieraných v hniezdnom období v rokoch 2016 a 2017. Materiál bol kvantifikovaný do relatívneho množstva koristi pomocou metódy MNI (minimálny počet jedincov) a tafonomickej jednotky. Táto štúdia je prvou, ktorá skúma potravu kuvika obyčajného na Peloponéze (južné Grécko). Vo vývržkoch z dvoch po sebe nasledujúcich rokov bolo zaznamenaných 3691 kostrových a exoskeletálnych pozostatkov so 78 a 108 zložiek koristi. Táto štúdia v zhode s predchádzajúcim výskumom ukázala, že kuvik v oboch rokoch uprednostňoval drobné cicavce a článkonožce, s jasnou prevahou *Microtus thomasi* a článkonožcov z triedy Diplopoda. Následne boli naše výsledky a výsledky z podobných štúdií v oblasti Stredozemného mora analyzované vo vzťahu k typom biotopu. Výsledná Redundantná diskriminačná analýza (RDA) podporuje teóriu oportunistického získavanie potravy kuvika v závislosti od variability ekologických faktorov.

Key words: owl prey, owl pellets, Rodentia, Insecta, mainland Greece

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Introduction

Information on the diet of any owl species can be inferred from the contents of its pellets (Marti et al. 2007). Nonetheless, the study of pellets can also provide important information on the preying habits of a certain species and the group of animals it feeds upon in a particular area. Two elements accentuate the usefulness of pellets in such studies: (a) prey remains in pellets are usually well-preserved, which means that even the most delicate skeletal remains can be isolated from them; and (b) owls can swallow small vertebrates whole, minimising the chances of bone fractures during feeding and digestion.

The little owl (*Athene noctua*) has a wide geographical distribution, extending to Central and Southern Europe and Asia, and northwestern Africa. Besides urban areas (BirdLife International 2022), the species has a wide range that covers different habitats, such as orchards, cultivated fields, steppes and semi-desert, rocky regions (Mikkola 1983). It is considered an important predator for controlling small mammal populations, such as voles. The main threats for the studied species are habitat and nesting site loss due to industrialisation and intensified farming, the use of pesticides and even colliding with traffic (Tucker & Heath 1994, Holt et al. 2014).

The present study attempts to enrich existing knowledge on the feeding behaviour of the species in the Eastern Mediterranean (Al-Melhim et al. 1997, Charter et al. 2006, Paspali et al. 2015, Kayahan & Tabur 2016) and specifically in Greece, where, despite its widespread distribution, data on its diet and hunting behaviour are relatively scarce, with only a handful of published studies to date (Angelici et al. 1997, Goutner & Alivizatos 2003, Alivizatos et al. 2005, 2006). Ours is the first report on the little owl's diet from southern Greece and the first pellet study from a mainland habitat not associated with major wetlands, as had been the case until now (Goutner & Alivizatos 2003, Alivizatos et al. 2005, 2006). It is also the first such study from Greece that uses both cranial and post-cranial skeletal elements to identify and quantify every taxon of the prey retrieved from studied pellets. Although far more laborious, this approach was chosen in order to achieve the most accurate estimates possible concerning the number of prey individuals and, subsequently, biomass consumption, since the inclusion of post-cranial data minimises the probability of underrepresenting species, whose cranial elements are often absent from pellets, in contrast to post-cranial ones, like snake vertebrae. Finally, the data collected during the present study were compared to previous research on the little owl's diet to explore possible trends emerging from the different habitat types where pellets have been collected (e.g. wetlands, farmlands and phryganic habitats, both from insular and mainland areas) and seasons.

Material and methods

Study area

Our study took place in a rural area of northwestern Peloponnese, southern Greece, specifically Platanovrisi, a village located 18 kilometres south of the city of Patras at the foot of the southwestern extensions of Mt. Panachaiko (elevation 450 metres; Fig. 1). The study area can be described as an agricultural mosaic consisting of olive groves, pastures, cultivated fields, as well as shrub and forest patches dominated by Kermes oaks (*Quercus coccifera*) and Aleppo pines (*Pinus halepensis*).

Pellet sampling and preparation

To examine the little owl feeding habits in the area, 70 pellets were collected between February and May of 2016 and 2017 (35 pellets per year) from a pair of little owls that had been nesting underneath a tree trunk's cavity in an open estate. Our field observations showed the pair to have used the nest only during the breeding season, while throughout the rest of the year they were observed in the surrounding area. The size and density of the studied pellets indicated that it was the adult birds which produced them.

The pellets were initially processed by hand and the remaining hairs were removed after the collected skeletal elements had been soaked in a water bath for 24 hours. One pellet, consisting of a virtually complete house sparrow skeleton with only the skull missing, was placed in a 10% hydrogen peroxide solution to dissolve the remaining tissue without damaging the bones. The extracted skeletal material was identified according to Chinery 1986, Brunet-Lecomte & Nadachowski 1994, Macholán 1996, Venczel 2000, Kryštufek & Vohralík 2001, Leraut 2003, and Olsen 2004.

Material identification and data analysis

The minimum number of individuals (MNI), a standard zooarchaeological unit (Lyman 1994, 2008) was tallied and used to interpret the faunal representation and assess relative species abundance (Lyman 1994). In addition to skulls, mandibles and teeth, which are used in most owl pellet studies (for the little owl: Zerunian et al. 1982, Al-Melhim et al. 1997, Angelici et al. 1997, Hounsome

Fig 1. Map showing the study area (NW Peloponnese), and Platanovrisi village (red dot) where the pellets were collected.
Obr. 1: Mapa skúmaného územia (SZ Peloponéz) a obec Platanovrisi (červený bod), miesto zebu vývržov.

et al. 2004, Pocora et al. 2012), species were also identified from post-cranial skeletal elements and they were accordingly included in the calculation of the MNI. These values were calculated per pellet and then summed for the year. The skeletal elements of all major limb bones of rodents and birds were identified through direct comparison with reference skeletons in the collection of the Laboratory of Palaeontology and Stratigraphy at the University of Patras. Phalanges, metapodials and vertebrae (except reptilian) could not be attributed to a specific taxon beyond the order/family level and, thus, were not included in the data analysis.

Data analysis

Biomass calculations for each species were performed according to Marti et al. (2007), and for each pellet according to Pezzo & Morimando (1995). Prey weight information was taken from micromammal (Niethammer & Krapp 1978, 1982) and bird (Hume 2002) references and from the weight of juvenile snakes measured at a nearby location in the northern Peloponnese and recorded by the Laboratory of Zoology, Department of Biology, University of Patras. In the case of arthropods, the methodology by Zerunian et al. (1982) was followed to calculate the weight of specimens that could not be identified at the species level. The insects were separated into four distinct categories according to their estimated body-size range, with each category matched to a specific weight value. Categories and their respective weight values were likewise adopted from Zerunian et al. (1982). The weights of Diplopoda taxa and *Scolopendra* sp. were approximated from specimens in the collections of the Natural History Museum of Crete.

The average prey weight per pellet was calculated by multiplying the MNI of each prey in a pellet by its average weight, adding the values produced for each taxon and dividing the sum by the total number of prey items in each pellet. The average food intake per pellet was calculated by multiplying the MNI of each prey in a pellet by its average weight, adding the values produced for each taxon and dividing the sum by the total number of pellets. Once the calculations had been made, MNI and prey weight values for each pellet were statistically compared for the two sampling years (2016 and 2017), using the non-parametric Mann-Whitney test separately for vertebrate and invertebrate prey taxa.

To examine the relationship between habitat types and prey taxa, a redundancy discriminant analysis (RDA) of prey biomass percentages was performed among the different Mediterranean sites referenced and where little owls' prey biomass percentages were available (Appendix 1). The use of biomass, in lieu of the MNI contribution of the consumed prey, gives a more realistic representation of the little owl's diet when examined under the scope of different habitat types. Thus, we preferred biomass percentages, instead of numerical values, to eliminate the differences in the number of pellet samples collected in each study as a factor that could affect the analysis. In this comparative analysis, data from a total of seven different studies were used, which correspond to pellets collected from 13 sites across different habitat types (e.g. rural areas, cultivated farmland and wetlands) in Greece, Algeria, Israel, Italy and Spain (Appendix 1). Some of these sites were sampled and studied more than once. Type 2 Scaling was used to visualise better the data points during the plot's construction. Consequently, the distances between the points corresponding to prey taxa should not be interpreted as Euclidean distances, even though the points corresponding to the sites were unaffected. One-way PERMANOVA was used in order to investigate the statistical significance of potential differences between the referenced habitats (Appendix 1). Data analysis was carried out using PAST 4.11 (Hammer et al. 2001). Because the periods during which the comparative surveys in the references took place were either not clearly defined or varied notably, seasonality was not examined as a factor of prey selection and diet variance.

Results

A total of 3,691 skeletal and exoskeletal remains were isolated from the 70 processed pellets. Of these, 2,721 were identified up to species level when possible, while the remaining 970 could not be attributed to any specific taxon. The "unidentifiable elements" mostly corresponded to fragmented parts of the skeleton (phalanges, vertebrae, skull fragments, diaphyses) and they were considered insignificant in the calculation of the MNI index.

Prey size parameters examined for each year (Tab. 1) revealed an increase in both the number of taxa and the number of individuals consumed by the owls in 2017, thereby raising the average prey individuals (MNI, Mann-Whitney U test: U = 420, p = 0.020) consumed per pellet. The average food intake per pellet remained approximately the same for both years (ca 50 g) (Mann-Whitney U test: U = 524, p = 0.299), but the average prey weight per pellet decreased from 23.44 g in 2016 to 19.21 g in 2017 (Mann-Whitney U test: U = 426, p = 0.025). A shift in favour of the consumption of arthropods was observed, in particular during the second survey year, with regard to both the number of individuals and prey weight (Mann Whitney U test: U = 314 for MNI, U = 307, for prey weight, p < 0.001 in both cases) (Tab. 1 and 2). Thus in 2017, consumed vertebrates only equalled 74.29% of consumed biomass, represented by two mammalian species, whereas in 2016, the percentage was higher by ca 20%, involving four vertebrate taxa (Fig. 2, Tab. 2). The shift in diet was not found to be statistically significant, either in terms of individual consumption or biomass (Mann Whitney U test: U = 522, p= 0.248 and U = 524, p = 0.264, respectively).

Tab 1. Prey size parameters of the little owl for the sampling years 2016 and 2017.
Tab 1. Parametre potravy kuvika obyčajnéhov rokoch 2016 a 2017.

	2016	2017
Number of taxa	7	14
Total MNI	78	108
Average MNI per pellet	2.2	3.1
Median MNI per pellet	2	3
Min MNI per pellet	1	1
Max MNI per pellet	6	8
Average prey weight per pellet (g)	23.44	19.21
Average food intake per pellet (g)	49.08	50.72

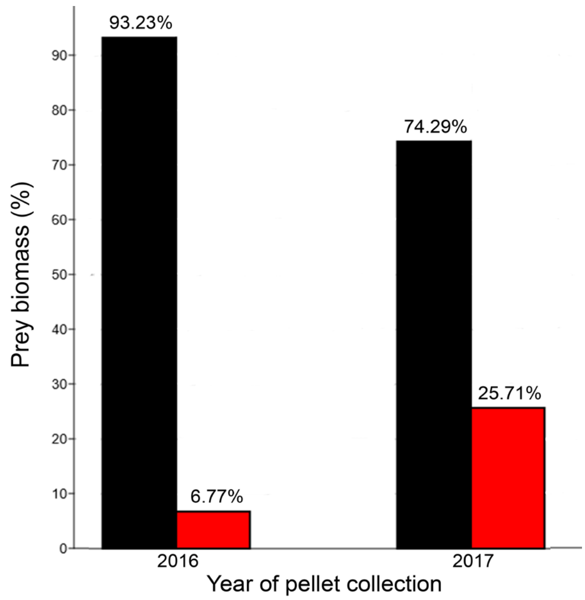

Fig 2. The proportion of biomass for vertebrates (black) and arthropods (red) extracted from the pellets of the little owl for the years 2016 and 2017.
Fig 2. Podiel biomasy pre stavovce (čierna) a článkonožce (červená) extrahovaná z peliet kuvika obyčajného za roky 2016 a 2017.

Among the identified taxa, the dominant prey for both years was Thomas's pine vole (*Microtus thomasi*), with a presence in 2016 and 2017 of 69.23% and 43.5% by numbers and 87.55% and 73.74% by biomass, respectively. Other taxa identified as prey in 2016 were the violet ground beetle (*Carabus violaceus*), Orthoptera (indetermined), Diplopoda (indetermined) and a few other vertebrates (juvenile snakes from the Colubridae family), the western house mouse (*Mus musculus domesticus*), and the house sparrow (*Passer domesticus*). These prey taxa and their numbers are shown in Table 2.

In 2017, the only vertebrate found in the little owls' diet was Thomas's pine vole, save for a single bicoloured white-toothed shrew (*Crocidura leucodon*). The undetermined Diplopoda taxa were the second most important biomass contributor (21.7%), followed by *Scolopendra* sp. (3.15%).

Tab 2. Prey taxa by numbers (MNI) and biomass (%) for 2016 and 2017.
Tab 2. Taxóny koristi kuvika obyčajného podľa počtu (MNI) a biomasy (%) za rok 2016 a 2017.

Year	2016		2017	
Taxon	MNI %	Biomass %	MNI %	Biomass %
VERTEBRATA				
Crocidura leucodon			0.93	0.55
Microtus thomasi	69.23	87.55	43.5	73.74
Mus musculus	3.85	3.19		
Passer domesticus	1.28	1.28		
Colubridae (juv.)	2.56	1.21		
ARTHROPODA				
Insecta - Coleoptera				
Carabus violaceus	12.82	1.47		
Copris hispanus			0.93	0.14
Melolontha melolontha			2.78	0.09
Poecilus cupreus			1.85	0.03
Tenebroides mauritanicus			0.93	<0.10
Tribolium confusum			2.78	0.01
Harpalus sp.			0.93	0.01
Insecta - Dermaptera				
Forficula auricularia			4.63	0.02
Insecta - Hymenoptera				
Camponotus lateralis			1.85	<0.10
Chilopoda- Scolopendromorpha				
Scolopendra sp.			7.41	3.15
Coleoptera (indet.)			12.03	0.18
Orthoptera (indet.)	6.41	0.06	7.41	0.1
Diplopoda (indet.)	3.85	5.24	12.04	21.97

indet. - indeterminate

The RDA plot of biomass percentage (Fig. 3, based on data in Appendix 1) indicated a significant relationship between habitat types and specific prey taxa ($F = 6.745$ and $p = 0.001$), explaining 40.28% of the constrained variance. A clear formation of sampling clusters emerged, according to the habitat where each study was conducted (Fig. 3). Four types of habitats stood out: wetlands/saltmarshes, farmlands near urban areas, phryganic areas in islands and cultivated areas (Fig. 3). This can also be inferred by PERMANOVA ($F = 9.037$, $p < 0.001$), since statistically significant differences between habitats (wetland vs urban farmland and insular phryganic) can be observed (Table 3).

Discussion

Our study provides evidence on the prey of the little owl in Southern Greece that confirms its strong tendency towards vertebrates – particularly rodents – as prey items, when they are available. Thomas's pine vole, represented in each pellet by at least one individual, was the dominant prey in both survey years, making it the primary food source for the little owls in our study area. This finding contradicts the general impression that the little owl feeds mainly on insects, especially around the Mediterranean region (Herrera & Hiraldo 1976, Mikkola 1983). However, according to several studies, the little owl may, in fact, base its diet on vertebrates as described, for instance, in Jordan (Al-Melhim et al. 1997), Evros and Axios Delta in Greece (Goutner & Alivizatos 2003, Alivizatos et al. 2005), Bulgaria (Georgiev 2005) and Albania (Paspali et al. 2015). The predominance of vertebrates is even more clearly demonstrated in studies where prey species representation was examined in terms of biomass instead of just numerical abundance of individuals as, for instance, in Spain (Delibes et al. 1984), Italy (Capizzi & Luiselli 1995, Bon et al. 2001), Israel (Charter et al. 2006), Greece (Goutner & Alivizatos 2003, Alivizatos et al. 2006) and Algeria (Chenchouni 2014). Our results thus fall in line with these studies (Fig. 2, Tab. 2), indicating the little owl to be a generalist predator that may opt to prey upon small vertebrates (whenever abundant and therefore relatively easy to capture).

The larger presence and wide variety of arthropods found in the pellets from 2017 (12 out of the 14 identified taxa were arthropods), when vertebrates seemed to contribute less to the little owl's diet and be restricted almost exclusively to the overall dominant prey, i.e. Thomas's pine vole (MNI = 47) (Tab. 2), constitute the main observed differences in diet composition between the two study years. These differences correspond to an increase in the average MNI per pellet in 2017, coupled with a simultaneous drop in the average prey weight per pellet, while the average food intake per pellet remained virtually steady (Tab. 1). This simply shows that the nutritional needs of the little owls (ca 50 g per pellet, Tab. 1) will have to be anyway satisfied, in this

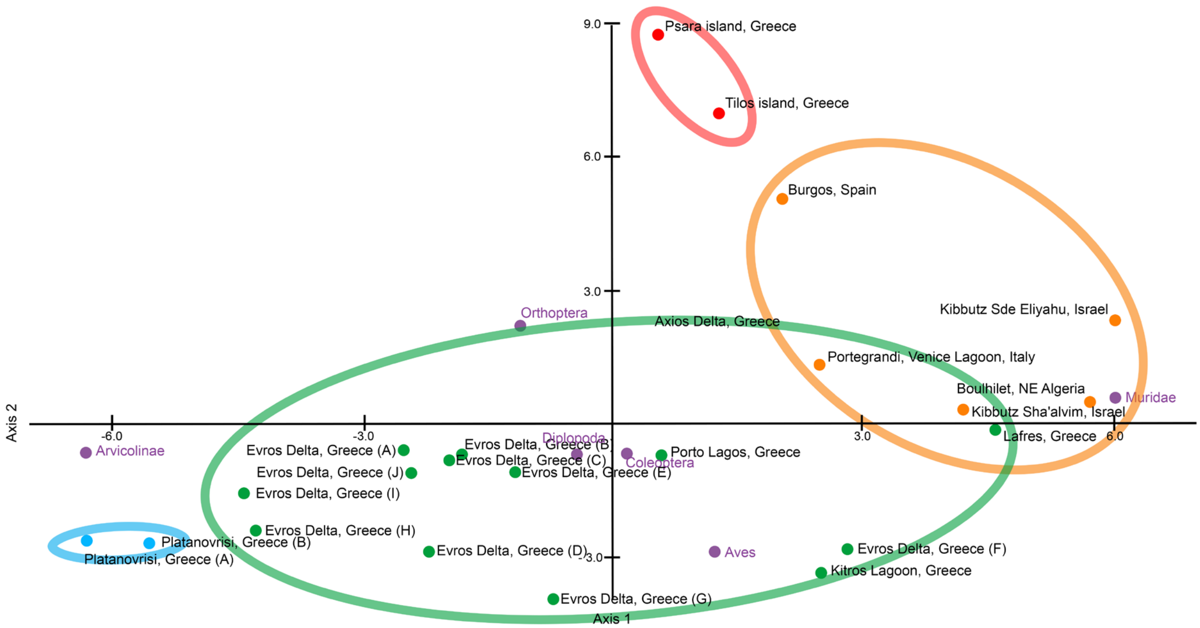

Fig. 3. Redundancy Discriminant Analysis (RDA) of the little owl's diet composition by biomass (%) of prey, identified from 23 different samplings from 13 different localities around the Mediterranean. The colors of each point (and the ellipses) represent the habitat type: green describes wetlands and saltmarshes, orange describes farmlands and crops near urban areas, red describes insular areas with phrygana and blue describes cultivated areas.

Fig. 3. Redundantná diskriminačná analýza (RDA) zloženia stravy sovy obyčajnej podľa biomasy (%) koristi, identifikovanej z 23 rôznych vzoriek z 13 rôznych lokalít okolo Stredozemného mora. Farby každého bodu (a elipsy) predstavujú typ biotopu: zelená - mokrade a slané močiare, oranžová - poľnohospodárska pôdu a plodiny v blízkosti mestských oblastí, červená - ostrovné oblasti s Garrigue vegetáciou a modrá - obhospodarované oblasti.

case by switching to prey with lower biomass values (i.e., arthropods) in comparison to micromammals and, consequently, consuming it in larger quantities.

The reduced representation of vertebrates in the little owl's diet in 2017 could have been linked to a potential decrease in the abundance of the dominant prey, Thomas's pine vole, in the study area that year. Even though not specifically examined during this study, such local abundance fluctuations over consecutive years appear rather commonly in this vole species (G. Mitsainas, pers. observation). It would also be worthwhile to examine whether other ecological factors could have been involved in the described differences in prey composition over the two years. For example, there ought to be research conducted into whether varying weather conditions might be related to variations in arthropod availability and abundance between different years, as has been previously suggested (Chenchouni 2014).

Concerning prey availability, all species found in the pellets are commonly present in the study area. Specifically, Thomas's pine voles are generally abundant around the estate whence the pellets were collected, based on the high density of their characteristic soil mounds (Ph. Katsiyiannis, pers. observation). Although considered a fossorial vole species, they have been occasionally observed to emerge from their burrows during the night and run across open spaces, such as fields or even roads (Mitsainas et al. 2009, Rovatsos et al. 2011), which makes them vulnerable to predators. Together with their common occurrence, this tendency probably explains the very strong representation of this vole species in the pellets. The taxon with the second highest biomass contribution to the diet of the little owl is Diplopoda, a class which includes nocturnal animals that are easy for a little owl to detect and capture.

On the other hand, the presence in the pellets of remains belonging to rather diurnal animals (e.g. *Passer domesticus*, juvenile snakes of the family Colubridae) confirms that the little owl may very well extend its hunting activity into daytime (Mikkola 1983). As prey of the little owl, snakes are of rather little interest since, from the recorded values, they appear to have contribute only a small percentage to the owls' diet. For example, in Greece, only once have reptiles been recorded at a

Tab. 3. Pairwise comparisons of prey biomass % (one-way PERMANOVA) between groups corresponding to different habitats.
Tab.3. Párové porovnania biomasy (%) koristi (one-way PERMANOVA) medzi skupinami jednotlivých biotopov.

habitat	Terrestrial cultivated areas	Wetlands and saltmarshes	Farmlands and crops near urban areas	Insular areas with phrygana
	F	F	F	F
Terrestrial cultivated areas	-	4.536*	23.12*	47.08
Wetlands and saltmarshes	4.536*	-	8.462**	9.027**
Farmlands and crops near urban areas	23.12*	8.462**	-	12.02*
Insular areas with phrygana	47.08	9.027**	12.02*	-

*<0.05;**<0.01

higher contribution to prey biomass than the 1.21% of the present study for 2016: one individual of Colubridae recorded in a study from Axios Delta (Alivizatos et al 2005), corresponded to a 4.6% contribution to prey biomass. Additionally, Colubridae (MNI = 1) and *Natrix* sp. (MNI = 1) have been reported in a study conducted in Evros Delta (Alivizatos et al. 2005), contributing 1% to prey biomass. Other Reptilia consumed by little owls were either lizards or unidentified reptiles, both in Greece (Angelici et al. 1997, Goutner & Alivizatos 2003 and references therein, Alivizatos et al. 2005, 2006) and other Mediterranean regions (Herrera & Hiraldo 1976, Delibes et al. 1984, Al-Melhim et al. 1997, Bon et al. 2001, Goutner & Alivizatos 2003 and references therein, Charter et al. 2006).

Viewing the present results in a broader context, the presence of micromammals and arthropods in the little owls' diet is relatively common, yet the numerical dominance observed in this study of the former over the latter had not been frequently documented in other studies from Greece (Angelici et al. 1997, Goutner & Alivizatos 2003, Alivizatos et al. 2005, 2006 – see Appendix 1 for details). The only cases where mammals seem to prevail in the diet of the little owl in Greece concern birds of prey that hunt in terrestrial or semi-terrestrial ecosystems (Goutner & Alivizatos 2003, Alivizatos et al. 2005, this study). On islands and at/around lagoons, where salinity levels of the water and soil do not favour micromammals, insects are the primary source of prey for the little owl (Angelici et al. 1997, Goutner & Alivizatos 2003, Alivizatos et al. 2006). However, even in such areas, it will probably extend its hunting range to capture small-sized mammalian prey (e.g. rodents from genera *Microtus*, *Mus* and/or *Micromys*) that are readily available and relatively easy to capture, yet rewarding in terms of the biomass they provide (Goutner & Alivizatos 2003, Alivizatos et al. 2005, 2006).

Gradient and statistical analysis shows an obviously clear grouping of studied sites by habitat type (Fig. 3, Tab. 3). Specifically, insular and phryganic habitats (Alivizatos et al. 2005) are grouped, although they are distant from the mainland sites because of the dominance of Orthoptera and Muridae in the island pellets, with a biomass contribution greater than 50%. Wetland and farmland habitats are also separated, which reflects the difference between the dominant prey species in each habitat type: anthropophilic Muridae dominate in farmlands near urban areas where humans are active. Concurrently, Arvicolinae and birds are the main biomass components in wetlands and lagoons where these taxa are more abundant (Alivizatos et al. 2006). Both sampling years in our study area are grouped together because of the prevalence of Arvicolinae in the biomass of the little owls' diet (> 70%). This also explains why their group is located close to what comprises the wetlands and deltas in which the same taxon is also present with a high contribution (> 50%).

However, some exceptions were also observed. The Burgos site (Delibes et al. 1984) is located further away from its cluster, approaching the areas around Tilos and Psara, probably due to the high concentration of Orthoptera in the biomass of the little owls' diet (25.5%), thereby appearing closely correlated with the aforementioned island sites. Similarly, Lafres (Goutner & Alivizatos 2003) is associated with the farmland cluster, possibly because of the high contribution of Muridae that characterises the locality, as well as the group of urban and farmland areas.

This study highlights the importance of micromammals in the diet of the little owl, something too often overlooked in analyses that tend to be derived from the abundance of prey instead of their contribution to the biomass and frequently giving the false impression that the little owls mainly prey upon insects. The present study shows arthropods to be a supplementary food source in mainland localities and the dominant prey on islands, or possibly habitats sharing the same characteristics with the islands in the above comparison. However, this needs to be further studied.

Finally, all the considerations mentioned above suggest the little owls' hunting behaviour to be opportunistic, according to prey availability and Mediterranean habitat types. This can be seen both at a local scale, such as the observed shift from vertebrate to invertebrate consumption over our study's two consecutive years, as well as at a larger scale, when comparing, sites around the Mediterranean that differ to a varying degree in prey availability and habitat features. However, more work on the hunting and feeding behaviour of the little owl in different habitats and geographical regions needs to be done and so the present study serves as an additional source of information on this topic.

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Appendix 1. Table of parameters that correspond to each geographical site used in the RDA analysis (Fig. 3) including: site name, authors of the study, pellet collection period, dominant prey (per biomass %) and brief habitat description, according to each study. Sites in alphabetical order; study area of this work in bold.
Príloha 1. Tabuľka parametrov, pre použité lokality v RDA analýze (obr. 3) vrátane: názvu lokality, autorov štúdie, obdobia zberu peliet, dominantnej koristi (% biomasy) a stručného popisu biotopu podľa každej štúdii. Stránky v abecednom poradí; študijná oblasť tejto práce tučným písmom.

Site	Study period	Dominant prey	Habitat	Literature
Axios Delta, Greece	Dec 1997 - Aug 2001 (winter)	Arvicolinae, Muridae	wetland and saltmarshes, lagoons, reedbeds, tamarisk and riparian forest, marshes, cultivations	Alivizatos et al. 2005
Boulhilet, NE Algeria	Jan-Feb 2008, 2011	Muridae, Aves	large fields of crops with patchy landscapes of brackish and fresh wetlands, montane habitats, country towns	Chencouni 2014
Burgos, Spain	winter 1976, 1980	Muridae, Orthoptera, Arvicolinae	farmland	Delibes et al. 1984
Evros Delta, Greece (A)	winter 1987	Arvicolinae, Muridae	wetland, saltmarshes, salty grounds, sand dunes and sandy islands, reed beds, tamarisk and riverine forest, temporary and permanent freshwater marshes, extensive cultivation areas	Goutner & Alivizatos 2003
Evros Delta, Greece (B)	summer 1987	Arvicolinae, Muridae	wetland, saltmarshes, salty grounds, sand dunes and sandy islands, reed beds, tamarisk and riverine forest, temporary and permanent freshwater marshes, extensive cultivation areas	Goutner & Alivizatos 2003
Evros Delta, Greece (C)	Dec 1997 - Aug 2001 (winter)	Arvicolinae	wetland and saltmarshes, lagoons, reedbeds, tamarisk and riparian forest, marshes, cultivation	Alivizatos et al. 2005
Evros Delta, Greece (D)	spring 2003	Arvicolinae, Muridae, Aves	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006
Evros Delta, Greece (E)	summer 2003	Arvicolinae, Muridae, Aves	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006
Evros Delta, Greece (F)	autumn 2003	Muridae, Aves	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006
Evros Delta, Greece (G)	winter 2003 - 2004	Arvicolinae, Aves, Muridae	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006
Evros Delta, Greece (H)	spring 2004	Arvicolinae, Muridae	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006
Evros Delta, Greece (I)	summer 2004	Arvicolinae, Muridae	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006

Appendix 1. Continuation
Príloha 1. Pokračovanie

Evros Delta, Greece (J)	autumn 2004	Arvicolinae, Muridae	extensive saltmarshes, sand dunes, mudflats, lagoons, reedbeds, tamarisk and riparian forests, permanent and temporary freshwater marshes, extensive cultivations	Alivizatos et al. 2006
Kibbutz Sde Eliyahu, Israel	Oct 2001 - Nov, 2003	Muridae	quarry, surrounded by agricultural fields, orchards, plantations	Charter et al. 2006
Kibbutz Sha'alvim, Israel	Dec 2001 - Jun 2003	Muridae, Aves	pastureland for domesticated animals around farm buildings of a village	Charter et al. 2006
Kitros Lagoon, Greece	Dec 1997 - Aug 2001 (winter)	Coleoptera, Muridae, Aves	wetland and saltmarshes, lagoons, reedbeds, tamarisk and riparian forest, marshes, cultivations	Alivizatos et al. 2005
Lafres, Greece	summer 1987	Muridae, Aves	two coastal lagoons surrounded by rocky cliffs with extensive grasslands, saltmarshes, sandy beaches and cultivation areas to the north	Goutner & Alivizatos 2003
Platanovrisi, Greece (A)	**Feb - May 2016**	**Arvicolinae, Diplopoda**	**olive groves and cultivated fields**	**this study**
Platanovrisi, Greece (B)	**Feb - May 2017**	**Arvicolinae, Diplopoda**	**olive groves and cultivated fields**	**this study**
Portegrandi, Venice Lagoon, Italy	Spring 1990	Arvicolinae, Muridae	typical agricultural environment with maize and soybeans crops, landscape poor of arboreal-shrubby elements, the environments marginal to the cultivated fields more interesting, in particular some wet meadows that develop along the Sile flood plain	Bon et al. 2001
Porto Lagos, Greece	summer 1987	Aves, Muridae, Orthoptera	village within a wide wetland complex, brackish lake in the north, reed beds and forests remnants, extensive coastal lagoons with saltmarshes, sandy beaches and livestock grazing fields in the southwest	Goutner & Alivizatos 2003
Psara island, Greece	Dec 1997 - Aug 2001 (winter)	Orthoptera, Muridae	phrygana, farmland	Alivizatos et al. 2005
Tilos island, Greece	Dec 1997 -Aug 2001 (winter)	Orthoptera, Muridae	phrygana, farmland	Alivizatos et al. 2005