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ORIGINAL ARTICLE

Does breeding habitat affect the amount of ants in the diet of European bee-eater nestlings?

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Abstract

European bee-eater (*Merops apiaster* Linnaeus, 1758; Coraciiformes: Meropidae) is known as a bee-predator, but its food spectrum is variable and depends on the current supply. This is the first study focused on the ants (Hymenoptera: Formicidae) as important prey in the diet of the European bee-eater. In 2017, 9,604 insect prey was obtained from pellets gained from two colonies breeding: (1) underground of a grazed sand dune (Radvaň nad Dunajom) and (2) in the sandy wall (Gabčíkovo) without pasture, both in southern Slovakia. Five ant taxa were identified, the list of ants in the bee-eater's diet was expanded by three taxa *Lasius* sp., *Camponotus vagus* (Scopoli, 1763) and *Liometopum microcephalum* (Panzer, 1798). In summary, ants represent the second most abundant family (12.35 %) of total prey. Compared to adults, nestlings (15.04 %) ate significantly more ants than adults (10.97 %). To study the ants' composition in the diet of bee-eater near to different types of habitats, the pellets of nestlings were chosen because they more accurately reflect the sources of insect during the breeding season. Differences in the feeding of the European bee-eater nestlings between the grazed and the non-grazed locality were confirmed, where *Lasius* sp. and *Tetramorium* sp. highly correlated with grazing site. Moreover, nestlings ate significantly more ants in the area, where an open habitat was managed by grazing (6.55 vs. 15.04 %). The presented research indicates the importance of traditional pastures in the country for ants and also for bee-eaters. These ecosystem engineers are likely to find more microhabitats on the pastures, which has also been reflected in the diet of the nestlings breeding on the grazed site.

Keywords Diet ecology · Formicidae · Grazing · *Merops apiaster* · Pellet · Slovakia

Introduction

Most insect species fly to seek new habitats and additional food sources, search for a mate or evade predators (Dudley 2000). Their dispersal activity is followed by other animal species exploiting them as prey from just above the ground up to hundreds of metres skywards (Hardy and Milne 1938). Because all flying animals land, terrestrial and aerial food webs are linked together (Helms et al. 2016).

Bee-eaters (family Meropidae) are undoubtedly one of the most supreme predators of flying insects. This taxonomic group contains three genera and twenty-seven species, of which a single species occurs in Central Europe – the European bee-eater (*Merops apiaster* Linnaeus, 1758).

The expansion of the European bee-eater to Central Europe closely correlated with climatic factors. As the distribution of this species is well documented in historical sources, it may be used as a historical bioindicator of climate changes (Kinzelbach et al. 1997; Stiels et al. 2021). Moreover, analysing of pellets of the insectivorous birds may serve as a non-invasive monitoring method for insect fauna research in nature conservation areas.

Many studies were provided to investigate its prey content (e.g., Ursprung 1979; Fry 1983, 1984; Matoušek 1951; Mařan 1958; Krebs and Avery 1984, 1985; Inglisa et al. 1993; Krištín 1994; Avery et al. 1998; Massa and Concetta Rizzo 2002; Krištín and Kaňuch 2005; Fuisz et al. 2013; Gyurácz et al. 2013; Arbeiter et al. 2014; Ullmann et al. 2017; Krüger 2018), mostly by examining its pellet-,

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nest- and gizzard-contents. According to current knowledge, the European bee-eater preys almost exclusively on medium-sized flying insects caught during the flight, with a preference for Hymenoptera (52 – 91 %). Odonata (0.3 – 60 %) and Coleoptera (0.48 – 35 %) are the other two most consumed groups of insects, followed by less frequent Lepidoptera, Diptera, Orthoptera, Dermaptera, Mantodea, Isoptera, Heteroptera and Homoptera. Diet composition of adults and nestling is different (e.g., Fry 1984; Krebs and Avery 1985; Inglisa et al. 1993; Krištín 1994; Arbeiter et al. 2014; Costa et al. 2016; Ullmann et al. 2017). In general, nestlings are fed more hymenopteran (e.g., Fry 1984; Ullmann et al. 2017) and larger insect species, i.e. bumblebees and dragonflies (Arbeiter et al. 2014). A study from Slovakia also confirmed that adults eat more beetles than nestlings (Krištín 1994). In general, nestlings grow best when they are fed by a mixed diet than just large species such as bees or dragonflies (Arbeiter et al. 2014; Costa et al. 2016). In fact, the food spectrum of bee-eater depends on the current supply. For example, the main part of their diet near clover crops are bumble-bees (Inglisa et al. 1993); dragonflies may be dominant near a water source (Marniche et al. 2007). Generally, they occur on open grasslands rich in spontaneous plants, where pollinators, particularly bees are concentrated (Massa and La Mantia 2007). High diversity of their food spectrum was evidenced in the area of a very old grassland continuously used as pastures surrounded by a marsh landscape which is intensively farmed in Lower Saxony, Germany. Due to the large variety of plant species, the old dikes are very rich in insects and represent hotspots of biodiversity. Here, bees and bumblebees were captured mainly during days with heavy rainfalls (Krüger and Bergmann 2015).

The research focused on the most represented insect group (Hymenoptera), an estimated impact of this colourful predator on apiary (e.g., Fry 1983; Avery et al. 1998; Galeotti and Inglisa 2001; Massa and Concetta Rizzo 2002; Ali and Taha 2012) and detailed data about the influence on the other insect taxa are sparse. It also applies to ants, some of the most abundant insects in terrestrial ecosystems (Folgarait 1998). Ants play an important role in the environment. They turn and aerate the soil, allowing water and oxygen to reach plant roots and indirectly contribute to plant reproduction because they take seeds down into their tunnel to eat the nutritious elaiosomes, the part of the seed (Seifert 2018). Moreover, swarming ants serve as an ideal prey for insectivore birds (Helms 2018) as European bee-eater is (Fry 1984). Winged ant gynes and males fly to mate and disperse and serve as attractive targets for insect predators (Whitcomb et al. 1973; Hölldobler and Wilson 1990). Especially ant gynes create a dense aggregation of nutritious prey because 70 % of their body weight consists of abdominal fat reserves, proteins, and glycogen (Keller and Passera 1989; Hahn et al. 2004). Out of numerous published papers about bee-eater's diet presented above, ants are mentioned only in six of them: *Messor structor* (Latreille, 1798), *Tetramorium* Mayr, 1855; *Formica* Linnaeus, 1758; *Myrmica* Latreille, 1804 or near ally and *Camponotus* Mayr, 1861 were previously documented in the diet of *M. apiaster* in Europe (Fry 1983, 1984; Krištín and Kaňuch 2005). Moreover, Marniche et al. (2007) reported *Cataglyphis bicolour* (Fabricius, 1793), *Crematogaster scutellaris* (Olivier, 1792), *Messor barbarus* (Linnaeus, 1767) and *Tapinoma simrothi* Krausse, 1911 to serve as prey of *M. apiaster* in Tunisia. Herrera and Ramírez (1974) and Krištín (1994) identified Formicidae only to the family level.

In this paper, we focused on the importance of ants in the diet of the European bee-eater. This study aimed to answer the question, how the composition of the ants in the diet of bird nestlings diverges in areas with different landscape management, and which ant species are preferred in the diet of adults compared to nestlings.

Methods

Studied species

Merops apiaster Linnaeus, 1758. Like the other bee-eaters, it is a richly coloured, slender bird reaching a length of 27–29 cm including central tail feathers (Fry and Boesman 2020). Its major populations breed in southern Europe, in parts of North Africa and western Asia. It is strongly migratory and overwinters in tropical Africa. It has a special requirement for sandy-loam or loess soil, where it forms colonies, nesting in burrows tunnelled into vertical sandy banks or in the flat ground (Fry 1984) and may be from 70 to 150 cm deep. The deepening process takes 10 to 20 days (Fry and Boesman 2020). In Slovakia, they usually breed most frequently in loess/loam walls, sunken roads and artificial walls on secondary habitats (gravel-, sand- and clay-sand pits or surface mines, terraces in the orchards etc.) (Krištín 1994; Viktora 1994; Darolová and Slobodník 2002; Balla 2009), and burrows under surface of the ground have been rarely observed in eastern (Balla 2009; Darolová and Slobodník 2002) and southern Slovakia (Bohuš 2015). This way of nesting is common in the xeric area in south and east of their nesting area (Iberian Peninsula, Balkan Peninsula, central Asia; Glutz and Bauer 1994; Kossenko and Fry 1998; Cramp 1985) and the nearest report was evidenced south of Slovakia in the loess slopes of the Gödöllő Hills, Hungary (Kerényi and Ivók 2013).

Bee-eaters have bi-parental care, but occasional bigamy has been encountered (Fry 1984; Avery et al. 1998) and cooperative breeders with helpers are common (Fry 1984). From late May to early June, females lay four to ten eggs in two-days intervals, which are incubated by both parents for three or four weeks and nestlings are hatched asynchronously (Fry and Boesman 2020). During the breeding, a hunt is realised around one kilometre from the nests, but they may fly to a distance of 12 km (Fry 1984; Hudec and Šťastný 2005). Prey is brought to the nest by one individual and nestlings are fed until cca. 20 days after birth (Fry 1984).

Study area

The study was carried out during the breeding season 2017 near two colonies of the European bee-eater 70 km apart in southern Slovakia:

1) Grazed site: a colony site in a Special Protection Area Dolné Pohronie (a part of NATURA 2000 network) near a village Radvaň nad Dunajom (47°45’38.9” N; 18°20’13.2” E). A sand dune, a respectively open grassland, where controlled livestock grazing was set up on 12 hectares as an overgrowth management measure to support its high flora and fauna biodiversity value. Bee-eaters could hunt in surrounding crops and graveyards, there is an oak-hornbeam foliaceous forest near and the Danube River flows up to 2 km away. Cca. 37 bee-eater pairs were breeding on the horizontal surface of the dune.
2) Non-grazed site: a colony site is in a non-protected area near Special Protection Area Dunajské luhy (a part of NATURA 2000 network) near a village Gabčíkovo (47°52’4.6” N; 17°32’39.8” E). A vertical, gravelly-sand wall (ca. 10 high × 30 wide metres) as a part of ruderal habitat created from material excavated during the construction of the supply and drainage channels of the Gabčíkovo Dam on the Danube River. The vegetation consists of poplar cultivars and pioneer plants and grazing is not provided. Occasionally, the surface is disturbed by racing four-wheelers and an illegal landfill is located nearby. The Danube channel as another potential hunting habitat is in the immediate vicinity (less than 300 m). On this site, the nests are dug into the vertical wall by cca. 10 bee-eater pairs.

Pellet collection and a diet analysis

Remains of the pellets from eight nests were obtained (four per locality) after the birds had left them. Moreover, 100 regurgitated pellets of adults were randomly obtained from the surface of the sand dune in Radvaň nad Dunajom during June and July 2017. Pellets were gathered separately by the spoon. Pulled material from nests was taken by the following methods: (1) excavation from sand dune (Radvaň nad Dunajom); (2) vacuuming by adapted handheld vacuum from sandy wall (Gabčíkovo). The material was stored in marked plastic zipper bags. Pellets and nest material were analysed under a stereomicroscope Zeiss Stemi DV4. The digestion process left damage on the structures crucial for the species-level identification, such as the loss of antenna, setae, or mouthparts. Other body segments were usually fragmented into single sclerites. The insect remains were identified to insect orders based on their head capsules preserved in their pellets. Selected ant heads were identified to the lowest possible taxon level using the keys of Czechowski et al. (2012) and Seifert (2018). In most cases only genus-level identification was possible. Ant heads (Fig. 1a-j) were photographed under a Zeiss Axio-Zoom V-16 stereomicroscope using diffuse LED lighting and attached Canon 5D Mark IV camera, under 17 times or 40 times magnification. The high-resolution pictures were stacked using Zerene Stacker 1.04 software and graphically edited in Adobe Photoshop CS5 Extended version 12.1. Material is deposited in KGBS—Katarína Goffová collection, Bratislava, Slovakia available at the Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava. Additional photo documentation of feeding was provided by Nikon D700 camera with objective Nikon 28-105mm f/3.5-4.5D AF Nikkor in 17th July 2017 from 11:30 to 16:00 (nestlings were min. 14 days old) and 29th July 2017 from 13:00 to 16:00 (nestlings were min. 25 days old). The shooting time was limited by the weather and orientation of the burrows due to the optimal position of the sun (avoiding the backlight). Pictures are archived in a personal photo album of Mirko Bohuš.

Statistical analysis

Six ant taxa were defined as ant types with following abbreviations: *Camponotus vagus* (CamV), *Formica* sp. (Form), *Lasius* sp. (Lasi), *Liometopum microcephalum* (LioM) and *Tetramorium* sp. (Tetr), the last group - Formicidae males - was omitted from analyses, because it was not possible to identify them to genus or species level and probably overlaps defined types. To test the differences in the nestling’s diet between grazed and non-grazed habitat, a chi-squared test (χ^2) was used with absolute values. Dependencies between ant types in the diet of nestlings and landscape management on the two studied sites (grazed and non-grazed) were analysed using spatial modelling with the multivariate redundancy analysis (RDA).

Before testing the difference between the diet of adults and nestlings on grazed site, the normality data distribution of the number of individuals was tested by the Shapiro-Wilks W test ($p = 0.001$) and then the Mann-Whitney U test was used.

A Shapiro-Wilks W test (distribution normality) and Mann-Whitney U test were performed in Statistica Cz. Ver. 7.0 software (Statsoft, inc. 2004). RDA analysis was tested

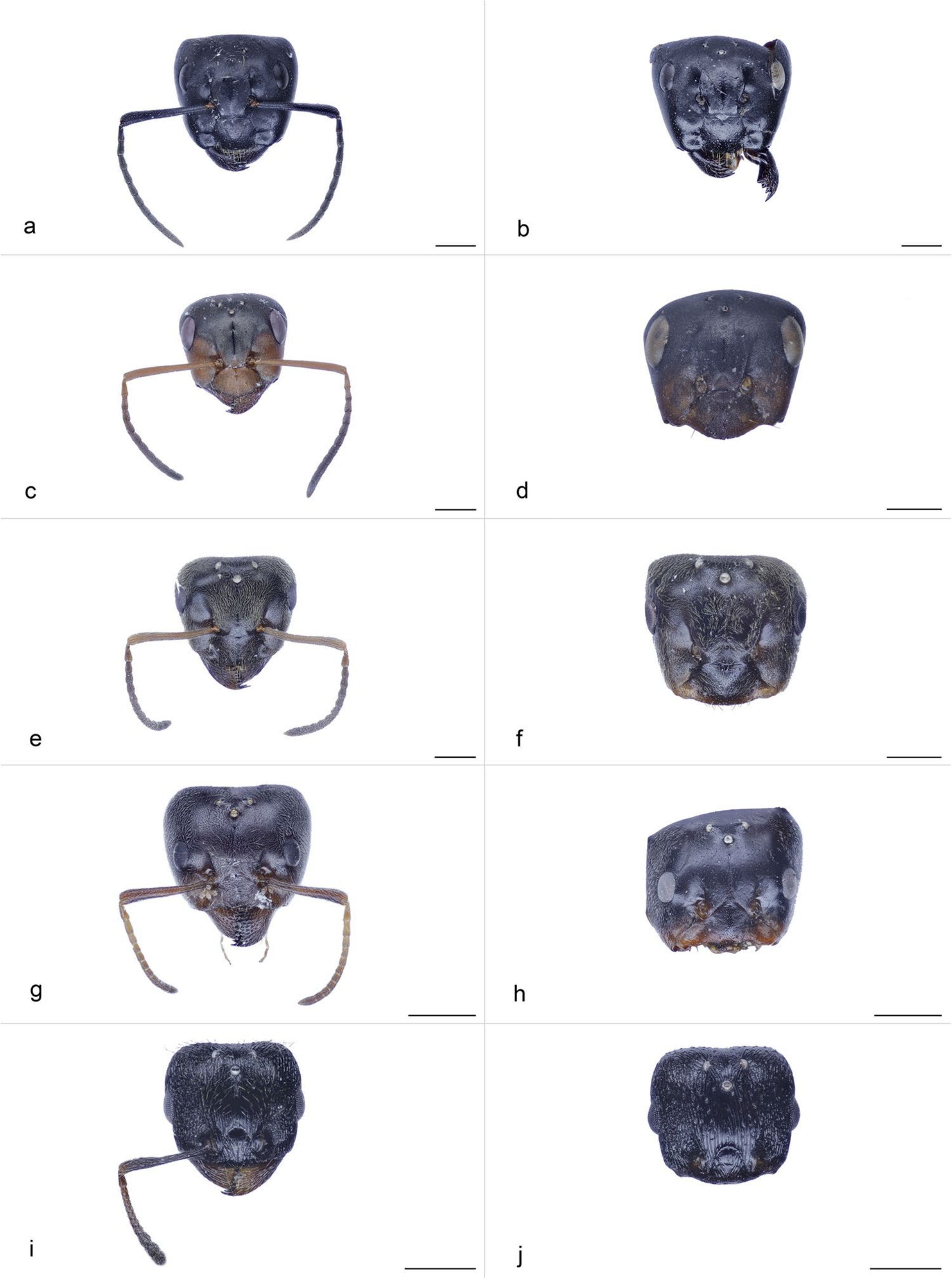

Fig. 1 Comparison of undamaged heads (left column) of ants recorded in Radvaň nad Dunajom with heads from pellets (right column); scales = 1mm: **a** Undamaged head of *Camponotus vagus*, gyne. **b** Head of *C. vagus*, gyne from pellet. **c** Undamaged head of *Formica* sp., gyne. **d** Head of *Formica* sp., gyne from pellet. **e** Undamaged head of *Lasius* sp., gyne. **f** Head of *Lasius* sp., gyne from pellet. **g** Undamaged head of *Liometopum microcephalum*, gyne. **h** Head of *L. microcephalum*, gyne from pellet. **i** Undamaged head of *Tetramorium* sp., gyne. **j** Head of *Tetramorium* sp., gyne from pellet; photo: Selnekovič D and Krčmárik S

by Monte Carlo permutation test in the Canoco 5 software (Braak and Šmilauer 2012).

Results

In total, 9,604 insect prey was obtained from material gained from both sites. Nestlings and adults are evaluated separately. Out of 8,227 insect specimens obtained from eight bee-eater's nests, 82.37 % of individuals belonged to Hymenoptera, followed by Coleoptera (12.34 %) and Heteroptera (4.63 %). Diptera, Odonata, Orthoptera, Neuroptera and Dermaptera were represented by less than 1 %. The most abundant species was *Apis mellifera* Linnaeus, 1758 (38.66 %), followed by *Bombus* spp. (17.79 %). Among the hymenopterans, the main bulk consisted of specimens from families Apidae (70.13 %) and Formicidae (15.27 %), followed by the other unclassified groups (14.59 %). Out of 1,377 insect specimens obtained from 100 pellets of adult birds, 934 individuals (67.83 %) belonged to Hymenoptera and 151 (10.97 %) were identified as ants (Table 1).

Altogether, two ant species and five genera were identified among the samples – *Camponotus vagus* (Scopoli, 1763), *Liometopum microcephalum* (Panzer, 1798), *Formica* sp.,

Table 1 Overview of the number of insect prey and ant taxa detected in the diet of *Merops apiaster* in southern Slovakia (Gabčíkovo and Radvaň nad Dunajom) in 2017

	Summary		Gabčíkovo_nestlings		Radvaň_nestlings		Radvaň_adults	
	n	%	n	%	n	%	n	%
Summary	9604	100	2382	100.00	5845	100.00	1377	100.00
NEUROPTERA	8	0.08	8	0.34	0	0.00	0	0.00
ODONATA	33	0.34	7	0.29	12	0.21	14	1.02
DERMAPTERA	1	0.01	0	0.00	0	0.00	1	0.07
DIPTERA	37	0.39	0	0.00	4	0.07	33	2.40
ORTHOPTERA	24	0.25	4	0.17	18	0.31	2	0.15
HETEROPTERA	411	4.28	107	4.49	274	4.69	30	2.18
COLEOPTERA	1379	14.36	129	5.42	887	15.18	363	26.36
HYMENOPTERA	7711	80.29	2127	89.29	4650	79.56	934	67.83
Apidae	5349	55.70	1779	74.69	2974	50.88	596	43.28
Apis mellifera	3577	37.24	1355	56.88	1826	31.24	396	28.76
Bombus sp.	1637	17.04	416	17.46	1048	17.93	173	12.56
Formicidae	1186	12.35	156	6.55	879	15.04	151	10.97
Camponotus vagus	4	0.04	1	0.04	1	0.02	2	0.15
Formica sp.	125	1.30	14	0.59	108	1.85	3	0.22
Lasius sp.	480	5.00	85	3.57	391	6.69	4	0.29
Liometopum microcephalum	34	0.35	2	0.08	31	0.53	1	0.07
Tetramorium sp.	477	4.97	52	2.18	304	5.20	121	8.79
Formicidae males	66	0.69	2	0.08	44	0.75	20	1.45

Lasius sp. and *Tetramorium* sp. Due to difficulties in identification, all ant males were classified as the family Formicidae. The same ant taxa were recorded in the bee-eater's diet on both study sites (Table 1; Fig. 1a-j). The most abundant ant taxon in the diet of bee-eaters was *Lasius* sp. (5 %). The largest evidenced species (*C. vagus*) was caught the least (0.04 %) (Table 1). According to the photo documentation of 30 feedings by ants, the bee-eater fed its nestlings always by a single alate ant specimen probably captured in air (Fig. 2).

A multivariate redundancy analysis (RDA) of site management and the ants in the bee-eater's diet (Fig. 3) provided the following results: The values of the explained variability of species data are 64.1 % on the 1st ordination axis (SD = 1.09 on the 1st ordination axis) and 22.5 % on

Fig. 2 *Merops apiaster* with detail on a caught alate ant; photo: Bohuš M

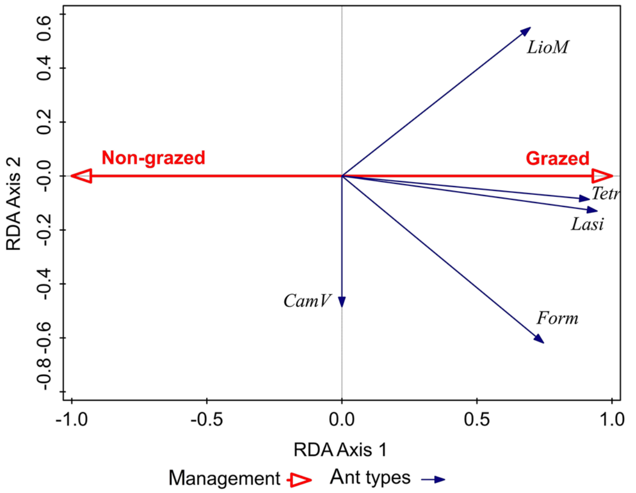

Fig. 3 RDA analysis. Composition of ant taxa detected in the diet of nestlings on grazed or non-grazed habitat with a high correlation of *Lasius* sp. and *Tetramorium* sp. with grazed habitat. Abbreviations – *Camponotus vagus* (CamV), *Formica* sp. (Form), *Lasius* sp. (Lasi), *Liometopum microcephalum* (LioM), *Tetramorium* sp. (Tetr)

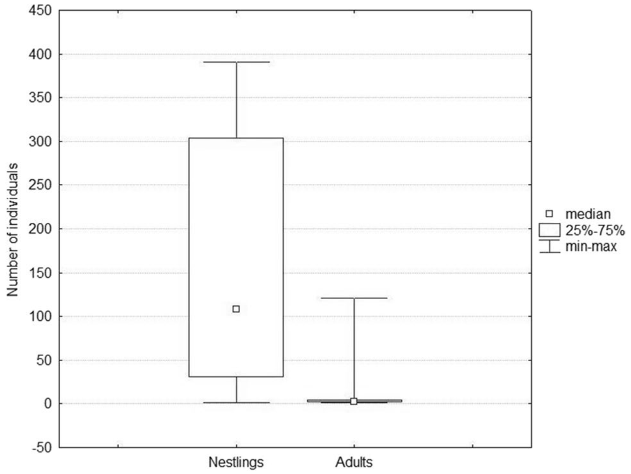

Fig. 4 Difference between amount of ant specimens in the diet of nestlings and adults

the 2nd ordination axis. The variability of the species set explained by environment variables is represented in the 1st ordination axis 94.6 % and in the 2nd axis 3.5 %. Monte Carlo permutation test identified a statistically significant effect of Non-grazed ($p = 0.041$), Grazed ($p = 0.026$), for the species composition of ants in the diet of the bee-eater in localities under examination. The selected environment variables were not mutually correlated with the maximum value of the inflation factor = 1.4529. The significance test of all axes is $p = 0.020$. All ant taxa but *C. vagus* formed one cluster in the ordination graph (biplot) and were strongly correlated with the environmental factor "grazed" (Fig. 3). *Camponotus vagus* showed no correlation with the evaluated environmental variables. The chi-squared test ($\chi^2 = 89.0446$; $p < 0.001$) also confirmed the difference between ant spectrum in the diet of nestling on grazed and non-grazed sites.

A nonparametric Mann-Whitney U test showed a statistically significant difference ($p = 0.0222$) of the number of ant individuals in the diet between nestlings (15.04 %) and adults (10.97 %). Nestlings ate significantly more ants than adult birds (Fig. 4) on the grazed site.

Discussion

In the analysed material of the bee-eaters, only two taxa were possible to identify to species level (*C. vagus*, *L. microcephalum*) and three were identified to genus level (*Formica*, *Lasius* and *Tetramorium*). Among the evidenced ant taxa, bee-eaters preyed mostly on smaller-sized species as *Lasius* sp. and *Tetramorium* sp. which perform high numerous swarms. The large-sized species as *L. microcephalum* and *C. vagus* were not so often preyed on by them. The main reason could be amount of these species. While larger species are K-strategists, *Lasius* sp. and *Tetramorium* sp. are generalists (Seifert 2018) and highly dominate in the number of colonies on the studied sites. In the present study, we confirmed the presence of the ant genera *Camponotus*, *Formica* and *Tetramorium* in the European bee-eater's diet, which was already known (Fry 1984). The ant species *C. vagus*, *L. microcephalum* and the genus *Lasius* were recorded as part of the bee-eater's diet for the first time.

The ant composition in the bee-eater's diet follows the sessional nuptial flight period of detected ant species. Most species of the genera *Camponotus*, *Formica*, *Lasius*, *Liometopum* and *Tetramorium* inhabiting the Central European lowlands swarm from May to the end of July (Czechowski et al. 2012; Seifert 2018). Among all massively swarming ant species recorded on the sand dune in Radvaň nad Dunajom (Purkart et al. 2019), the only species undetected in the bee-eater's diet was *Solenopsis fugax* (Latreille, 1798). A simple reason is that the swarming period for this species usually takes place in September or early October (Czechowski et al. 2012) when the birds are already on their migration flight to Africa (Fry 1984). This phenomenon can be an interesting adaptation for the avoidance of insectivorous birds. From the potential 24 ant species evidenced in Radvaň nad Dunajom (Purkart et al. 2019), bee-eaters were herein able to catch less than half (41.66 %) of ant genera.

Important is the finding of *L. microcephalum*, which is threatened in Central Europe due to its dependence on very old trees with hollows (Seifert 2018), with the density of its colonies being usually rather low (Schlaghamerský and Omelková 2007). It is also the only ant species in Slovakia protected by law. In our study area in Radvaň nad Dunajom, *L. microcephalum* specimens were not sampled by any of the three exposited Malaise traps, but it was detected in bird's pellets. Although European bee-eaters can fly for prey even more than 10 km, they hunt mainly within a 1 km radius around the nest (Fry 1984). We didn´t expect the presence of this unique species nearby nests, but a colony of *L. microcephalum* was additionally revealed less than one hundred meters from the nests in an old willow (Purkart et al. 2019). Analysing the pellets of insectivorous birds seems to be an interesting non-invasive method for detection of *L. microcephalum* and probably also other flying insect species in nature conservation areas, or places with difficult access.

Following the results of statistical modelling, the portion of the ants in the diet of bird's nestlings was significantly higher in the open habitat managed by grazing than the ruderal habitat without cattle. We assume it might be the relation with much higher ant biomass achieved in xerothermic sandy grasslands, than in habitat shed by the vegetation, where colder soil temperatures and low plant diversity inhibits ant diversity (Seifert 2017). In general, the abundance of insects usually increases with the plant species richness and structural diversity of the habitat (Haddad et al. 2001; Grüebler et al. 2008). In the present study, the ratio of ants in bee-eater's diet was 15.04 % in grazed locality considered for the hotspot of biodiversity in the agricultural landscape and 6.55 % in non-grazed habitat with lower diversity of plants and insects. In other studies from Slovakia, different ratios were observed on several localities: 2.6 % near Poľana Mountain (Krištín and Kaňuch 2005) and up to 19 % in Záhorie xerothermic lowland region (Krištín 1994). While a similar spectrum of ant taxa would be expected in colonies bred in the Danube area, Krištín (1994) surprisingly presented 0 % of Formicidae in the bee-eater's diet in southern Slovakia. The difference could be caused by the type of survived habitats. While our sites are typical xerothermic habitats, Krištín (1994) took material from habitats as sandpits and sand-clay banks and cliffs beside brickyard; clay-sand banks at the edge of fields and forest-steppes; terrace banks in orchards and vineyards; clay wall of field lanes. Next, pellets were gathered under the nest holes and from the nest holes with a special rake not with a vacuum cleaner, so small ant heads could be lost. Moreover, the author took the pellets only in July and we analysed material for the whole breeding season.

The multivariate analysis showed the relationships between observed ant types and selected environmental variables. As seen in Fig. 4, the ants of genus *Lasius* and *Tetramorium* were mostly correlated with grazing as an environmental factor. Such results are consistent with those of the myrmecological survey by Purkart et al. (2019), in which *Lasius niger* (Linnaeus, 1758), *L. psammophilus* Seifert, 1992 and *Tetramorium* group of species were found to be the most abundant ant species inhabiting the studied sites. In our analysis, the correlation of genus *Formica* with the environmental factor "grazed" was weak, while genus *Formica* is common in sandy grasslands (Seifert 2018), it is also abundant in shaded habitats such as poplar stands (Gallé et al. 2016). *Liometopum microcephalum* was not found in the non-grazed site, but its presence in the bee-eater's diet reveals its occurrence in the Gabčíkovo region, probably in nearby floodplain forests in SPA Dunajské luhy.

Differences between adults and nestlings' diet have been already known in bee-eaters. Hymenopterans (especially *Bombus* spp. and *A. mellifera*) are predominantly found in the diet of nestlings (Fry 1984; Inglisa et al. 1993; Ullmann et al. 2017) and nestlings are fed by hymenopterans up to more than one-fifth (Fry 1984). Krebs and Avery (1985) assumed, that nestlings are fed more by bumblebees, beetles and in general by larger prey than adults. Arbeiter et al. (2014) also observed more bumblebees and dragonflies in the diet of the nestlings . Overall, bee-eaters purposely choose which prey to bring to the nests and which to consume what is known as the central place foraging model when adults select larger prey with increasing distance between the place of capture and the nest. It probably depends on the size and nutritional value of the prey as well as the energy efficiency of the return compared to the continuous hunt (Krebs and Avery 1985). Separate research of the nestlings and adults' diet by Arbeiter et al. (2014), Costa et al. (2016) and Krüger (2018) showed larger prey in the diet of nestlings but also confirmed, that nestlings prosper better due to considerable insect diversity in their diet. In Slovakia, only Krištín (1994) observed a higher proportion of beetles in the adults' diet, probably due to more efficient digestion of adults and nestlings were more fed by hymenopterans, lepidopterans, and flies. Our results of the nonparametric Mann-Whitney U test showed a large difference between adults and nestlings in a proportion of ant specimens in the diet. It is evident that adult birds preferred to offer sexual ants to their nestlings rather than to consume them. It is known that flying ant gynes often possess rich fat reserves and the abdomens of males are full of nutritious sperm (Helms 2018). According to our results, the bee-eater significantly preferred alate ants with a bigger abdomen (Fig. 2), which were probably caught in flight, but flightless *Formica* sp. was also evidenced in its pellets. The other flightless arthropods are very rarely preyed on by the European bee-eater, but some examples of beetles (*Lethrus* sp., *Blaps* sp., *Dorcadion* sp. and *Carabus* sp.) and harvestmen (Phalangiidae) are known (Fry 1984; Marniche et al. 2007). Individuals of *Formica* sp. were probably taken straight away from the ground, but combination hunting and anting is also possible.

In general, pasture constantly disrupts the surface of grassland and new microhabitats for insects are constantly emerging what is an ideal condition for r-strategists as *Tetramorium* spp. and *Lasius* spp. - potential prey for insectivore birds. Disruption of the sandy dune is available also for bee-eaters which prefer areas with low vegetation cover for nesting (Kerényi and Ivók 2013). According to IUCN European Red List of Bird, the European bee-eater is the least concern (BirdLife International 2021), but this species is among the public and often also among the beekeepers considered as a pest of the *A. mellifera* (e.g., Fry 1983; Avery et al. 1998; Galeotti and Inglisa 2001). Support for biodiversity in landscape, elimination of vegetation overgrowth by pasture and protection of vertical walls in the landscape are considered essential tools of species protection of the European bee-eater´s breeding (Krištín 1994; Viktora 1994; Darolová and Slobodník 2002). Preliminary data indicates grazed sand dune as a habitat rich in coprophagous beetles and a wide spectrum of other hymenopteran pollinators. The possible trend: “the higher insect diversity on the breeding habitat, the less honey-bee is caught by bee-eaters”, must be confirmed by a larger dataset. To make matters worse, the general loss of insect biodiversity and natural habitats under the pressure of intensive agricultural practices poses an upscaling challenge for insectivore birds. Therefore, uncovering the unknown aspects of the bee-eater’s diet creates an important scientific basis for defending its conservation status in Europe.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and photo docummnetation were performed by Mirko Bohuš, Katarína Goffová, Samuel Krčmárik, Dávid Selnekovič and Adrián Purkart. Statistical analyses were performed by Vladimír Langraf, Katarína Goffová and Samuel Krčmárik. The first draft of the manuscript was written by Katarína Goffová and Adrián Purkart and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Material is deposited in KGBS—Katarína Goffová collection, Bratislava, Slovakia available at the Department of Zoology, Faculty of Natural Sciences, Comenius University in Bratislava as described in the Methods.

Code availability Not applicable.

Declarations

Conflicts of interest/Competing interests On behalf of all authors, the corresponding author states that there is no conflict of interest.

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