DIFFERENCES IN PARENTAL CARE OF REED WARBLER (*ACROCEPHALUS SCIRPACEUS*) TO ITS OWN NESTLINGS AND PARASITIC CUCKOO (*CUCULUS CANORUS*) CHICKS

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A b s t r a c t

Differences were studied in the parental care of reed warbler (*Acrocephalus scirpaceus*) with its own nestlings and those of parasitic cuckoo (*Cuculus canorus*) chicks in its nest. The quantitative dominance of the most important prey groups (Diptera, Araneida, Sternorrhyncha) was very similar for both cuckoo and reed warbler nestlings. Results of weight dominance analysis for all orders of food showed the same proportions in both species. The most important orders in terms of biomass were Diptera, Araneida and Hymenoptera. The average length of prey delivered to reed warbler nestlings was 8.0 mm and to young cuckoo chicks 7.1 mm. The number of prey items delivered to one chick per hour was 4.3 for reed warbler nestlings and 7.5 for cuckoo chicks. Cuckoo chicks fostered by reed warbler hosts were fed with a quantity of food more than three times higher (69.3 $mg.h^{-1}$ dry mass) than the amount of food delivered to one reed warbler nestling (20.8 $mg.h^{-1}$). This result implies that a cuckoo chick is fed at the same feeding rate as an average sized brood (3.5 young) of the host's nestlings.

Key words: supernormal stimulus, feeding, diet, birds

Introduction

Brood parasitism is a form of breeding biology in which certain individuals, the parasites, receive parental care from unrelated individuals, the hosts. It is most prevalent in birds and some social insects. The European cuckoo (*Cuculus canorus*) is an obligate brood parasite, which uses a large group of hosts in Europe. The reed warbler (*Acrocephalus scirpaceus*) is one of the most frequently used hosts in the Czech Republic (H u d e c 1983), as well as elsewhere in Europe (M o k s n e s & R ø s k a f t 1995). The cuckoo chick usually hatches first, then ejects all the hosts eggs or nestlings and is raised alone in the nest.

During the course of co-evolution, a specific evolutionary response by host species has evolved (ejection of parasitic eggs from their nests, desertion or building over of nests (D a v i e s & B r o o k e 1988), but evolution of nestling rejection may be unlikely if parasitic nestlings induce supernormal stimuli for parental care due to their size or to some other feature (R o t h s t e i n 1990).

The commonly accepted idea of supernormal stimulus states that cuckoo nestlings provide hosts with a supernormal stimulus, which ensures that they are fed preferentially (Dawkins & Krebs 1979). The idea of supernormal stimulus implies that cuckoo chicks provide stronger stimuli for parental care than do host chicks. However, the results of Brooke & Davies (1989 a,b) and Davies & Brooke (1988) indicate that cuckoo nestlings provided no evidence for the supernormal stimulus hypothesis. However, Soler et al.'s (1995a) recalculation of Davies & Brooke's (1988) data suggests that European cuckoo chicks also provide hosts with a supernormal stimulus.

Another well studied brood parasite in Europe is the great spotted cuckoo (*Clamator glandarius*), which parasitizes the magpie (*Pica pica*). The great spotted cuckoo does not eject the hosts eggs or nestlings and is reared together with them. Great spotted cuckoo chick receives most of the food delivered to the nest, thereby drastically decreasing the breeding success of magpies. This is enabled by good chick mimicry (both visual and vocal) and a series of supernormal stimuli, including larger body size, coloration of gape and a greater intensity of begging (Soler et al. 1995a). The great spotted cuckoo exploits the obligatory reaction of magpies to feed all young that have been hatched in their nest (Soler et al. 1995b). In spite of this, magpies have the ability to discriminate against cuckoo chicks (ejection, attacks, no feeding), mainly when they are introduced at the end of the nestling period. However, natural ejection of the chicks has never been recorded, both in the great spotted cuckoo (Soler et al. 1995b) and the European cuckoo (Davies & Brooke 1988). Magpies cannot use their discriminatory ability because the great spotted cuckoo chick is born first and the foster parents learn to accept it as their own. With the european cuckoo, the newly born chick ejects all the eggs (or young) and remains as the only occupant of the hosts nest. Therefore, the hosts learn to accept the cuckoo chick as their own and feed it at a much higher rate than their own nestlings. This is probably caused by the colour of the gape and increased begging acting as supernormal stimulus.

The diet composition of the reed warbler young has previously been studied by Green & Davies (1972), Davies & Green (1976), Henry (1977,1978), Bussman (1979), Dyrcz (1979), Csörgő (1983), Bibby & Thomas (1985), Valius et al. (1986) and Grim & Honza (1996), however, composition of the food delivered to young cuckoos is still almost unknown. The only paper dealing with the diet of cuckoo nestlings was published by Brooke & Davies (1989). For some notes on the feeding of cuckoo nestlings see Cramp (ed.) (1985).

The aim of the present study was to determine the qualitative and quantitative composition of food brought to cuckoo chicks by reed warbler hosts. It was then tested whether reed warblers fed cuckoo chicks and their own young with a similar diet, size of prey and at the same feeding rate.

Study Site, Material and Methods

Field observations were carried out from 28 June to 15 July 1994 at the Mlýnský fishpond (107 ha) near the village of Lednice (47°48'N, 16°48'E) in the South-eastern part of the Czech Republic. Reed warbler nesting sites were situated in reed-beds (*Phragmites australis*). The pond was surrounded by arable land and separated from it by a zone of old parkland and oak forest. For a more detailed description of the study area see H u d e c (1975).

The observations of parental feeding visits used by B r o o k e & D a v i e s (1989) may not reflect the true consumption of food by nestlings (S o l e r et al. 1995a) because the number and size of prey items delivered is very variable (personal observations). Therefore, we used the neck collar method, which makes possible accurate prey identification, biomass calculation and analysis of the exact quantity of food allocated to nestlings per hour. The ligature (made of plastic coated wire) around the neck of the nestling is tight enough to hinder the swallowing of food and loose enough to let chicks to breathe (S o l e r et al. 1995).

All samples were taken from 05:50 to 21:00 (CET) under constant weather conditions. The neck collars were placed on nestlings (both reed warbler and cuckoo) within one hour. According to our experience, all chicks are usually fed during this time. This duration does not make the chicks vomit. Reed warblers started to feed the nestlings, both their own and parasites almost immediately (several minutes) after the neck collars were placed on all chicks in a nest.

All nests were situated in the same habitat at the same pond. The analysis was undertaken on 94 food samples of reed warbler nestlings from 16 unparasitized nests and 23 food samples of cuckoo chicks from 3 parasitized nests. The term food sample refers to the content of the crop of one nestling.

Prey items were determined, measured and then dried at room temperature to constant weight. All prey items were weighed on a precision balance (0.0001 g). The amount of food delivered to one chick was expressed as the number of prey items per hour and the mass of food as mg per hour ($mg.h^{-1}$). We did not regard chicks which were not fed.

Comparison of nestling diet was evaluated using the following criteria: abundance, dominance, frequency, feeding rate (expressed as prey items/hour/one nestling and mg of food/hour/one nestling). Differences between percentual values were assessed using the z-test (M a l ý 1962).

Results and Discussion

The diet of 51 reed warbler nestlings contained 708 prey items belonging to 16 orders of invertebrates (Table 1, Appendix 1). The most important dietary component was Diptera, especially Chironomidae (40.5%) and Syrphidae (7.8%). Other dominant orders of prey were Sternorrhyncha and Araneida. The most frequently observed orders were Diptera, Araneida and Sternorrhyncha. For more detailed information on food composition see G r i m & H o n z a (1996).

The food of three cuckoo nestlings contained 172 prey items belonging to 11 invertebrate orders (Table 1, Appendix 1). The most common prey delivered to the chicks were again Diptera, then Araneida and Sternorrhyncha. Every sample contained at least one specimen from the order of Diptera, other frequent orders were Araneida and Sternorrhyncha. In contrast to reed warbler diet, Chironomidae were not an important part of the food samples, forming only 4.7%. However, Syrphidae (29.1%) and other large flies were dominant.

A comparison of the weight dominance of all orders contained in samples (Fig. 1) revealed that both reed warbler nestlings and cuckoo chicks were fed

Table 1. The composition of food brought to reed warbler and cuckoo chicks (n = abundance, D = dominance, F = frequency).

Prey group	Reed Warbler			European Cuckoo		
	n (708)	D (%)	F (%)	n (172)	D (%)	F (%)
DIPTERA	471	66.5	98.9	83	48.3	100.0
Nematocera	310	43.8	58.5	10	5.8	13.0
Brachycera	147	20.7	83.0	71	41.3	91.3
Larvae	14	2.0	10.6	2	1.2	8.7
STERNORRHYNCHA	73	10.3	26.6	12	6.9	47.8
Aphidinea	67	9.5	22.3	9	5.2	21.7
Psyllinea	6	0.8	4.3	3	1.7	13.0
ARANEIDA	51	7.2	34.0	27	15.7	60.1
HYMENOPTERA	24	3.3	14.9	8	4.6	13.0
AUCHENORRHYNCHA	17	2.4	14.9	8	4.7	30.4
PSOCOPTERA	16	2.2	7.5	6	3.5	26.1
HETEROPTERA	15	2.1	12.8	10	5.8	39.1
PLANIPENNIA	12	1.7	10.6	1	0.6	4.3
Imagines	8	1.1	7.5	1	0.6	4.3
Larvae	4	0.6	3.2	-	-	-
COLEOPTERA	8	1.1	8.5	7	4.1	30.4
Imagines	2	0.3	2.1	5	2.9	21.7
Larvae	6	0.8	6.4	2	1.2	8.7
LEPIDOPTERA	8	1.1	7.5	-	-	-
Imagines	3	0.4	3.2	-	-	-
Larvae	5	0.7	5.3	-	-	-
GASTROPODA	7	1.0	5.3	9	5.2	30.4
TRICHOPTERA	2	2.1	2.1	-	-	-
OPILIONIDA	1	0.3	1.1	-	-	-
ONISCIDEA	1	0.2	1.1	-	-	-
DERMAPTERA	1	0.2	1.1	-	-	-
ENSIFERA	1	0.2	1.1	-	-	-
CAELIFERA	-	-	-	1	0.6	4.3

with the same proportion of Diptera ($z = 1.00$, N.S.), Araneida ($z = 0.34$, N.S.), Heteroptera ($z = 1.37$, N.S.), Auchenorrhyncha ($z = 0.00$, N.S.) and Coleoptera ($z = 0.00$, N.S.). Proportions of Hymenoptera ($z = 1.80$, $P<0.05$) and Gastropoda ($z = 6.55$, $P<0.001$) were significantly different.

The average length of prey delivered to reed warbler nestlings was 8.0 mm, ranging from 1.9 mm (Aphidoidea, Psocoptera, Araneida) to 21.0 mm (Geometridae larva; Fig. 2). The most frequent size categories were 2-4 mm (Aphidoidea, Araneida, Psocoptera, Auchenorrhyncha) and 10-12 mm (Chironomidae, Brachycera) (see also Grim & Honza 1996).

Cuckoo chicks received, paradoxically, smaller prey with an average length 7.1 mm. This situation was due to a high percentage of small prey items (Aphidoidea, Psocoptera, Psylloidea, Auchenorrhyncha in 2-4 mm and 4-6 mm categories; Fig. 2). The difference in length of prey was statistically significant ($t = 2.82$, $P<0.01$). This implies that the size of prey is not a very important factor for the comparison of feeding between cuckoo and reed warbler chicks because cuckoo chicks received a much greater amount of food than the host's own nestlings.

The number of prey items delivered to one chick per hour was 4.3 for reed warbler nestlings and 7.5 for the cuckoo chick (mean values). These values are interesting as the reed warbler parent often feeds nestlings (both its own and parasitic) with only one individual of prey (personal observation), but they

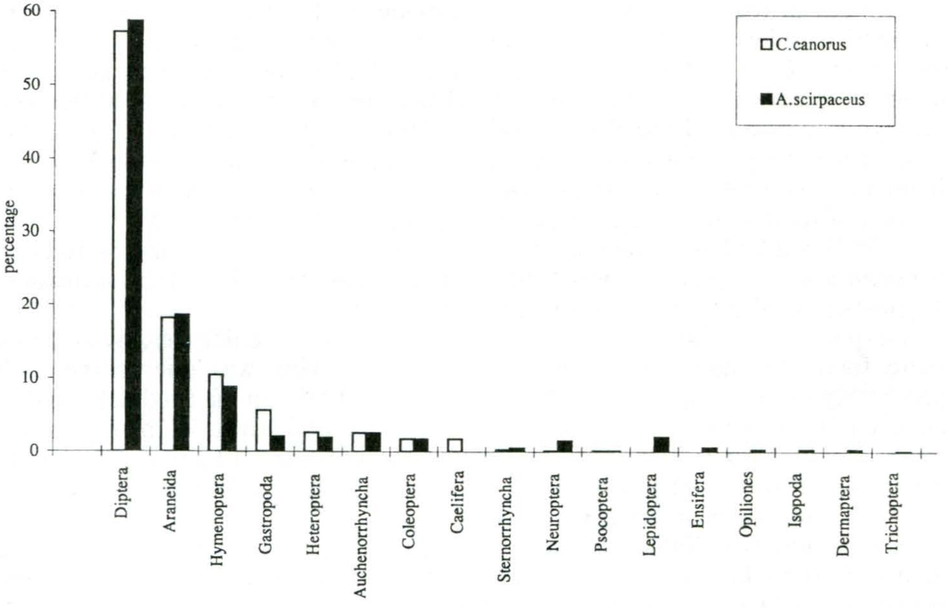

Fig. 1. Quantitative composition of food delivered to cuckoo and reed warbler nestlings.

cannot, however, reveal accurate differences in the feeding of parasitic and host nestlings due to the variable size and weight of prey items. One 10 mm long hoverfly (Syrphidae) weighted about 14.0 mg, but one specimen of Chironomidae of the same size) weighted only 1.3 mg (dry weight). Therefore, the feeding rate in mg food delivered to one nestling per hour provides the best information on

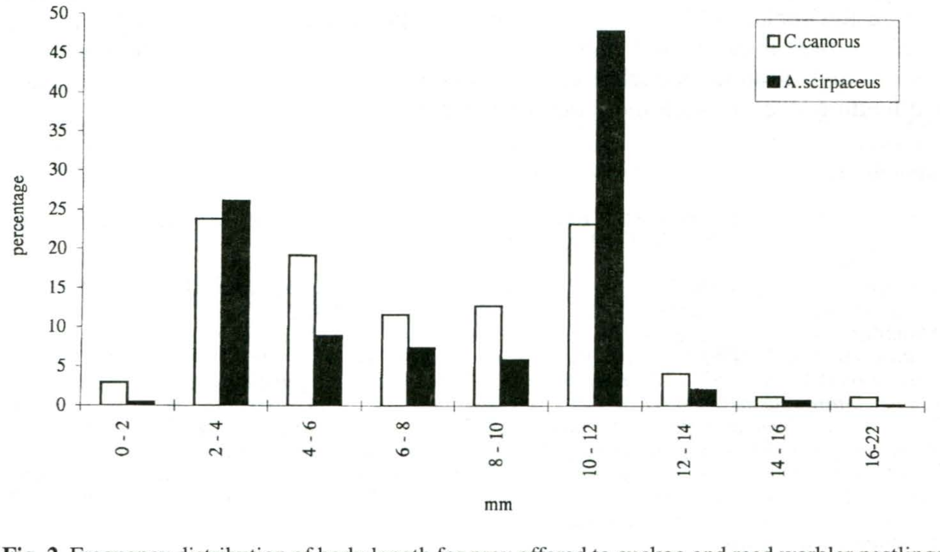

Fig. 2. Frequency distribution of body length for prey offered to cuckoo and reed warbler nestlings.

differences in feeding of nestlings. The amount of food carried to the nest by the reed warbler hosts to a parasitized nest containing one cuckoo chick was 69.3 $mg.h^{-1}$. One reed warbler nestling obtained 20.8 $mg.h^{-1}$. One cuckoo chick therefore received 3.33 times more food than one reed warbler nestling. The average size of a reed warbler's brood is 3.56 nestlings (H u d e c 1983), in the year of the study, the average number of nestlings in one nest on the Mlýnský fishpond was 3.19. This implies that one cuckoo chick was fed with the same amount of food as an average sized brood of reed warbler hosts. K h a y u t i n et al. (1982) studied the volume of food calls of cuckoo nestlings in redstart (*Phoenicurus phoenicurus*) nests and also found that the cuckoo chick stimulated the hosts to feed it at the same rate as the whole brood.

Despite the smaller average length of prey, cuckoo chicks received much more food (per hour) than hosts own nestlings. This was due to the high percentage of large flies, namely Syrphidae (D = 29.1%), in the food delivered to cuckoos in comparison to the amount of Syrphidae in the reed warbler nestlings food (D = 7.8%; z = 7.74, P<0.001). Particularly in the 10.12 mm prey length category, cuckoo nestlings received mainly large flies whereas reed warbler chicks obtained Chironomidae (D = 40.5%).

The qualitative (Table 1) and quantitative (Fig. 1) compositions of food delivered to cuckoo and reed warbler nestlings were found to be very similar. B r o o k e & D a v i e s (1989) studied the diet of reed warbler and cuckoo chicks using faecal analysis. They reported similar results on the qualitative composition of the diet. Using these data, and data on frequency of feeding, they concluded that the cuckoo did not provide hosts with a supernormal stimulus. S o l e r et al. (1995a) recalculated the data from D a v i e s & B r o o k e (1988) and found that cuckoo chicks received, on average, 4.5 feeds whilst reed warbler nestlings received only 3.5 feeds; during the experiment on responses of reed warbler to a simultaneous choice between feeding their own young or a cuckoo chick. Nestlings were presented in two nests tied side by side. S o l e r et al. (1995a) concluded that perhaps the cuckoo chick does indeed provide hosts with a supernormal stimulus, which ensures they are fed preferentially. Our results indicate that the theory of supernormal stimulus in cuckoos parasitising reed warbler nests could be accepted (see feeding rate), though more detailed research is still needed.

Appendix 1.

Review of Taxa Found in the Diet of Reed Warbler and Cuckoo Nestlings (Abundance in the Diet Brought to Young Reed Warbler/Cuckoo Chicks)

Gastropoda: *Succinea putris* (Linnaeus, 1758) - 5/4, *Perpolita hammonis* (Ström, 1765) - 0/1, *Arianta arbustorum* (Linnaeus, 1758) - 1/2, *Cepea hortensis* (Müller, 1774) - 1/2
Araneida: Theridiidae indet. - 1/0, *Theridion* sp. - 1/0, Linyphidae indet. - 6/7, *Oedothorax apicatus* (Blackwall, 1850) - 1/0, *Bathyphanthes nigrinus* (Westring, 1851) - 2/0, *Linyphia triangularis* (Clerck, 1757) - 1/0, *Linyphia* sp. - 3/0, *Microlinyphia pusilla* (Sundevall, 1829) - 0/7, *Neriene clathrata* (Sundevall, 1829) - 3/0, Tetragnathidae indet.-3/4, *Metellina segmentata* (Clerck, 1757) - 0/1, *Pachygnatha clercki* (Sundevall, 1823) - 0/1, *Tetragnatha extensa* (Linnaeus, 1758) - 1/0, Araneidae indet. - 3/0, *Araneus* sp. - 2/0, Clubionidae indet. - 4/2, *Clubiona* sp. - 5/0, Philodromidae indet. - 1/1, *Philodromus aureolus* (Clerck, 1757) - 1/0, *Philodromus rufus* (Walckenaer, 1826) - 2/1, *Tibellus maritimus* (Menge, 1875) - 1/0, Salticidae indet. - 1/0, Thomisidae indet. - 0/1, Araneida indet. - 9/2
Opilionida: indet. - 1/0
Oniscidea: *Armadillidium vulgare* (Latreille, 1804) - 1/0

Ensifera: *Metrioptera roeseli* (Hagenbach, 1822) - 1/0
Caelifera: *Chorthippus albomarginatus* (De Geer, 1773) - 0/1
Dermaptera: *Forficula* sp. - 1/0
Psocoptera: indet. - 16/6
Heteroptera: *Piesma capitatum* (Wolff, 1804) - 2/0, Miridae indet. - 3/2, *Deraeocoris ruber* (Linnaeus, 1758) - 0/1, *Lygus pratensis* (Linnaeus, 1758) - 1/1, *Lygus rugulipennis* (Poppius, 1911) - 2/1, *Orthops basalis* (Costa, 1852) - 1/1, *Stenodema calcaratum* (Fallén, 1807) - 3/2, *Stenodema* sp. - 0/1, *Orius minutus* (Linnaeus, 1758) - 2/0, *Himacerus apterus* (Fabricius, 1798) - 1/0, *Nabis ferus* (Linnaeus, 1758) - 0/1
Auchenorrhyncha: *Cixius nervosus* (Linnaeus, 1758) - 0/1, *Calligypona reyi* (Fieber, 1866) - 1/0, *Chloriona vasconica* (Ribaut, 1934) - 0/1, *Chloriona* sp. - 1/3, *Euides speciosa* (Bogeman, 1845) - 2/0, *Javesella pelucida* (Fabricius, 1794) - 1/0, *Laodelphax striatellus* (Fallén, 1826) - 2/0, *Deophax crassicornis* (Panzer, 1796) - 2/2, *Balclutha punctata* (Fabricius, 1775) - 1/0, *Cicadella viridis* (Linnaeus, 1758) - 1/0, *Empoasca solani* (Curtis, 1846) - 0/1, *Euopteryx atropunctata* (Goeze, 1778) - 1/0, *Macrosteles fieberi* (Edwards, 1891) - 1/0, *Macrosteles* sp. - 1/0, *Paralimnus phragmitis* (Boheman, 1847) - 1/0
Sternorrhyncha: *Livia juncorum* (Latreille, 1798) - 2/0, *Psylla alni* (Linnaeus, 1758) - 1/0, *Trioza urticae* (Linnaeus, 1758) - 3/3, *Hyalopterus pruni* (Geoffroy, 1762) - 40/0, Aphidinea indet. - 27/9
Planipennia: *Hemerobius* sp. - 7/1, *Chrysoperla carnea* (Stephens, 1836) - 2/0, *Chrysopa* sp. - 3/0
Trichoptera: *Oecetis ochracea* (Curtis, 1825) - 2/0
Lepidoptera: Geometridae indet. - 3/0, Tortricidae indet. - 1/0, Pyralidae indet. - 1/0, Noctuidae indet. - 2/0, *Caradrina* sp. - 1/0
Hymenoptera: Tenthredinidae indet. - 1/0, Braconidae indet. - 2/8, *Tetramesa* sp. - 2/0, Torimidae indet. - 1/0, *Eupelmus* sp. - 1/0, *Lasius brunneus* (Latreille, 1798) - 1/0, *Lasius flavus* (Fabricius, 1781) - 5/0, *Lasius* sp. - 11/0
Coleoptera: Cryptophagidae indet. - 1/0, Cucujidae indet. - 0/2, *Sitona* sp. - 0/5, Coccinellidae indet. - 6/0, *Adrastus* sp. - 1/0
Diptera: *Nephrotoma* sp. - 1/1, Limoniidae indet. - 1/0, Psychodidae indet. - 0/1, Culicidae indet. - 20/0, Chironomidae indet. - 287/8, Mycetophilidae indet. - 1/0, *Rhagio lineola* (Fabricius, 1794) - 2/1, *Chrysopilus auratus* (Fabricius, 1805) - 2/0, *Chrysopilus helvolus* (Meigen, 1820) - 12/6, *Chrysopilus splendidus* (Meigen, 1820) - 1/0, *Pachygaster atra* (Panzer, 1798) - 1/0, *Hybomitra* sp. - 1/0, *Haematopota pluvialis* (Linnaeus, 1758) - 1/0, *Leptogaster cylindrica* (De Geer, 1776) - 1/0, *Thereva plebeja* (Linnaeus, 1758) - 16/8, *Thereva praecox* (Egger, 1859) - 1/0, *Thereva* sp. - 3/0, *Platypalpus* sp. - 14/0, *Sciapus* sp. - 0/1, *Hercostomus* sp. - 1/0, *Eristalis arbustorum* (Linnaeus, 1758) - 1/0, *Eristalis tenax* (Linnaeus, 1758) - 1/3, *Melanostoma mellinum* (Linnaeus, 1758) - 0/8, *Platycheirus clypeatus* (Meigen, 1822) - 3/2, *Platycheirus* sp. - 1/1, *Scaeva pyrastri* (Linnaeus, 1758) - 0/1, *Metasyrphus corollae* (Fabricius, 1794) - 16/4, *Metasyrphus latifasciatus* (Macquart, 1829) - 1/0, *Metasyrphus luniger* (Meigen, 1822) - 2/2, *Syrphus vitripennis* (Meigen, 1822) - 1/0, *Episyrphus balteatus* (De Geer, 1776) - 19/26, *Sphaerophoria scripta* (Linnaeus, 1758) - 4/3, Syrphidae larvae - 6/0, *Myopa* sp. - 1/0, *Lyciella* sp. - 2/0, *Sapromyza* sp. - 1/0, *Micropeza corrigiolata* (Linnaeus, 1767) - 1/1, *Elachiptera cornuta* (Fallén, 1820) - 1/0, *Norellisoma spinimana* (Fallén, 1819) - 2/0, *Hylemya urbica* (v.d. Wulp, 1896) - 2/0, *Lispe* sp. - 1/0, *Coenosia agromyzina* (Fallén, 1825) - 1/0, *Lucilia silvarum* (Meigen, 1826) - 3/0, *Cynomya mortuorum* (Linnaeus, 1761) - 0/2, *Bellardia viarum* (Robineau-Desvoidy, 1830) - 2/0, *Pollenia rudis* (Fabricius, 1794) - 5/2, *Pollenia* sp. - 5/0, *Sarcophaga variegata* (Scopoli, 1763) - 1/1, *Sarcophaga* sp. - 2/0, *Loewia* sp. - 1/0, *Actia* sp. - 1/0, Diptera larvae indet. - 8/2.

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