

An exceptionally high diversity of hoverflies (Syrphidae) in the food of the reed warbler (*Acrocephalus scirpaceus*)

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Abstract: Despite being considered a classical example of protective Batesian mimicry hoverflies (Syrphidae) are known to be preyed upon by various passerines. The aim of the present study was to examine in detail food brought by reed warblers *Acrocephalus scirpaceus* to their nests to better understand the importance of hoverflies in the diet of small passerines. Using neck collars, 273 food samples containing 8,545 food items delivered to reed warbler and parasitic common cuckoo *Cuculus canorus* nestlings in warbler nests were recorded. The study was conducted during three breeding seasons in South Moravia, Czech Republic. An unusually high diversity of hoverflies was found – 27 species, including *Mesembrius peregrinus* (critically endangered species in the Czech Republic) and *Mallota cimbiciformis* (endangered species) – a new taxon to the Czech Republic. This indicates that nestling diet analyses may provide not only information on avian foraging behaviour but also important faunistic data. Thus, without the detailed identification to species level of material from foraging behaviour studies valuable scientific information may be lost. Overall dominance of Syrphidae was 3.7%, the most common species being *Episyrphus balteatus* (55.7%, $n = 318$). However, this number seriously underestimates the importance of hoverflies in the diet of reed warblers as hoverflies are one of the largest prey taken by warblers. Both larvae and pupae were rare, imagines strongly dominating (92.7%). Both specific wasp mimics (e.g., *Chrysotoxum verralii*) and bee mimics (e.g., *Eristalis* spp.) were not avoided by foraging reed warblers. The presence of a parasitic cuckoo chick did not affect host foraging behaviour with respect to overall dominance of hoverflies in the diet (warbler 3.3%, cuckoo 3.8%).

Key words: Batesian mimicry, faunistics, hoverfly, Syrphidae, predation, diet, foraging.

Introduction

Hoverflies (Syrphidae) are considered a good example of visual Batesian mimicry (STUBBS & FALK, 1983; RUXTON et al., 2004) and their similarity to various hymenopteran models also extends to behavioural mimicry (HOWART et al., 2004). In theory, Batesian mimicry should serve as an adaptation for avoiding the risk of predation (KREBS & DAVIES, 1993). However, hoverflies sometimes form an important part of the diet of various insectivorous avian species (KŘIŠTÍN, 1986, 1988, 1991, 1994).

During the study of interactions between the reed warbler *Acrocephalus scirpaceus* (Hermann, 1804) host and parasitic common cuckoo *Cuculus canorus* L., 1758 chicks a large sample of food delivered to both kinds of nestlings by warbler parents and fosterers respectively was obtained (GRIM & HONZA, 1996, 1997, 2001). Hoverflies were found frequently in the samples indicating they may form an important part of the warbler's diet.

The aim of the present study was to analyse hoverfly diversity in the diet of the model common species of insectivorous passerine – the reed warbler – in detail. Material analysed in the above mentioned papers

together with an additional 6,000 prey items of food predated by reed warblers during three breeding seasons at two sites were included. To my knowledge this is by far the largest sample of reed warbler and cuckoo nestlings diet collected so far. This should enable the importance of hoverflies in the food of this common insectivorous songbird to be determined.

Material and methods

The field work was carried out from May to mid-July in 1994, 1996 and 1997 field seasons on two fish pond systems near the villages of Lednice and Lužice in the SE part of the Czech Republic (47°40' N, 16°48' E), about 60 km SE of the city of Brno. Both pond systems are situated in a flat agricultural lowland landscape and are surrounded by deciduous woods and parkland. The distance between the areas is approximately 20 km. Reed warblers are known to build nests in various species of plants, however all the nests used in this study were placed in reed *Phragmites australis* vegetation. Both the Lednice and Lužice study plots have a relatively high parasitism rate of cuckoos in the nests of reed warblers (KLEVEN et al., 2004).

Among various methods for obtaining food samples from nestlings the neck-collar method enables the most ac-

curate analysis of the quantity of food allocated to nestlings and precise prey identification (JOHNSON et al., 1980). A plastic coated wire ligature placed around the nestling neck hinders the swallowing of food but is loose enough not to strangle the chick. Neck-collars were applied for one hour and food delivered by parents was removed every 20 min to prevent chicks from regurgitating food accumulated by the ligature. For more details on field procedures see GRIM & HONZA (2001).

For ecological analyses of hoverfly taxocenes found in food samples a simple ecological classification of hoverflies published by LÁSKA & MAZÁNEK (1998) was adopted.

In total, analyses included 2,131 prey items delivered to reed warbler nestlings ($n = 49$ chicks, 189 samples) and 6,414 food items found in the samples from cuckoo nestlings ($n = 32$ chicks, 84 samples). Sample sizes in particular analyses may differ due to the fact that some imagines and all larvae and pupae were not identified to species level.

Results

The overall number dominance of hoverflies was 3.7% ($n = 8,545$). Twenty-seven species (318 specimens) of hoverflies were found in food samples delivered to nestlings by reed warblers (Appendix 1). Most specimens were imagines (92.8%), the rest being both larvae (6.0%) and pupae (1.2%). The most frequent species was *Episyrphus balteatus* ($n = 177$), which formed 2.1% of all diet items and strongly dominated hoverfly taxocene in food samples ($D = 55.7\%$). Other hoverflies were much less common, e.g., *Eupeodes corollae* ($D = 7.9\%$), *Melanostoma mellinum* ($D = 5.3\%$), *Chalcosyrphus nemorum* ($D = 3.1\%$) and several species of the genus *Platycheirus* ($D = 5.0\%$). Large-sized species, such as *Eristalis tenax* or *Helophilus pendulus* were also taken. Both perfect (*Chrysotoxum verralii*) and putative (*Episyrphus balteatus*, *Sphaerophoria scripta*) wasp mimics and bee mimics (*Eristalis arbustorum*, *E. intricarius*, *E. tenax*) were preyed upon by reed warblers.

One specimen of *Mallota cimbiciformis* was found in the food brought to a cuckoo chick on 4 July, 1996 at Hlohovecký pond, Lednice. This is the first published record of the species in the Czech Republic (see HOLINKA et al., 1997).

Reed warblers showed a weak but non-significant tendency to prey more on hoverfly species in proportion to their abundance in the ecosystem (ranked according to LÁSKA & MAZÁNEK, 1998) ($r_s = 0.24$, $n = 26$, $P = 0.25$). There were 14 euryoecious, 7 mesophilous and 5 hygrophilous species of hoverflies in the food of reed warblers with dominances of 81.8%, 12.0% and 6.2%, respectively ($n = 291$ specimens). Samples contained hoverfly species that prefer woodland and parkland ecosystems (e.g., *Dasysyrphus albostrigatus*), open habitats like agricultural fields (*Sphaerophoria scripta*, *S. taeniata*) or wet meadows (e.g., *Mallota cimbiciformis*, *Melanostoma mellinum*, *Platycheirus clypeatus*) and several species showing strong association with endangered marsh habitats (*Eristalis intricarius*, *Chal-*

cosyrphus nemorum, *Mesembrius peregrinus*, *Neoascia interrupta*). However, most hoverfly species found in the food brought to warbler nests are not known to show any strong preferences for specific habitats.

In all three years of study the dominance of hoverflies was slightly higher in cuckoo samples, however, pooled data from the three years showed that the difference was not significant (warbler 3.3%, cuckoo 3.8%; $\chi^2 = 1.40$, $P = 0.24$). Reed warbler nestling diet also showed lower species diversity of Syrphidae (11 species, 70 specimens) than that of cuckoo chicks (27 species, 248 specimens). This most probably reflects a higher sample size for the latter (2,131 vs. 6,414 prey items).

Overall dominance of hoverflies (warbler and cuckoo samples pooled) decreased from 11.9% in 1994 to 3.3% in 1996 and 1.1% in 1997. The decline is highly significant ($\chi^2 = 141.55$, $P < 0.0001$).

The Lednice area showed a significantly higher dominance of hoverflies than the Lužice area (4.5 vs. 1.8%; $\chi^2 = 42.32$, $P < 0.0001$). This is supported by a more robust comparison of samples from the same year (1996) and kind of nestling (cuckoo) (Lednice: 3.6%, Lužice: 2.3%; $\chi^2 = 5.74$, $P = 0.016$). Samples from Lednice contained 25 hoverfly species while samples from Lužice only 10 (eight species were found at both sites). This difference is probably wholly explained by a higher sample size from Lednice in comparison to Lužice (6,101 vs 2,444 prey items).

Discussion

Hoverflies (Syrphidae) are a classical example of Batesian mimicry. However, despite their similarity to stinging insects like bees, wasps and bumblebees, the hoverfly fauna in my samples was relatively very rich comprising 27 species with overall dominance 3.7%. In contrast, no bees, wasps or bumblebees were found in the food samples. The Order Hymenoptera was represented almost entirely by ants in the food brought by warblers (see also GRIM & HONZA, 1997).

With respect to the relatively high dominance of hoverflies in the diet of reed warblers it is important to realize that the similarity of hoverflies and stinging insects to the human eyes does not necessarily imply that bird predators perceive the two categories of insects as similar (e.g., DITTRICH et al., 1993). Birds show very different visual acuity in comparison to mammals (including humans) and may perceive hoverflies very differently. Moreover, birds may pay more attention to other cues (prey traits) than colour patterns (e.g., qualities of flight motion). Thus, a human observer may mistakenly judge a hoverfly as a mimic of a hymenopteran insect (e.g., GOLDING et al., 2005) when in fact there is no mimicry in the eye of the relevant beholder – the avian predator (for detailed discussion of other explanations for the maintenance of poor Batesian mimicry see EDMUNDS, 2000; RUXTON et al., 2004; GRIM, 2005).

The diet included two species very rare in the Czech Republic: *Mesembrius peregrinus* and *Mallota cimbiciformis*. These are considered as “critically endangered” and “endangered” respectively (LÁSKA & MAZÁNEK, 1998). Also data from other authors indicate that research on bird foraging behaviour may provide important information on extremely rare and/or by traditional entomological methods hardly detectable species (LAUTERER & BUREŠ, 1984) or even lead to discovery of new species for a particular country (BUREŠ & PECINA, 1993; this study). This shows that without detailed identification to species level of material from foraging behaviour studies important scientific information may be lost. Data from avian foraging studies provide a rich, but so far overlooked, source of important distribution data for macroecological, biogeographical and conservation studies (GRIM, 2006).

In a large scale study KRIŠTÍN (1991) found 15 species of hoverflies in the food of 13 songbird species ($n = 17,335$ food items). The dominances of hoverflies was only infrequently higher than 10% in the avian species studied. The most dominant species of Syrphidae in his study were *Syrphus ribesii*, *S. vitripennis* and *Episyrphus balteatus*. All three species were also present in samples obtained from reed warbler and cuckoo nestlings in the present study. However, *Episyrphus balteatus* was the most numerous species by far. Interestingly, larvae were much more frequent (76.3%) than imagines in the study by KRIŠTÍN (1991) while larvae were extremely rare in the food collected by reed warblers (present study). In general, dominance and frequency of aphidophagous hoverflies increased in several study species during rainy weather compared to sunny periods (KRIŠTÍN, 1988). Data from the present study cannot test a potential effect of weather on foraging by warblers on hoverflies as food samples were collected only during sunny weather.

KRIŠTÍN (1986) reported even higher dominance of hoverflies in the food of the magpie *Pica pica* nestlings (exclusively the species *Eristalis tenax*; 11.4% of all food items, $n = 2,537$). The highest dominance of hoverflies among songbird species studied by KRIŠTÍN (1991) was 23.0% in the food of the nuthatch *Sitta europaea* during a mass outbreak of aphids, which were preyed upon by hoverflies. However, one and two years after an outbreak the dominance of both aphids and hoverflies fell dramatically (hoverfly dominances in nuthatch diet were 0.4 and 2.6 in two years respectively). GRIM & HONZA (1997) reported even higher dominance (29.1%) in the food fed to cuckoo nestlings by reed warbler hosts, but this is most probably an artefact of small sample size ($n = 172$ prey items from one field season). After adding data from another two field seasons to material from that study the hoverfly dominance decreased to 3.7%.

The diet of the closely related great reed warbler *Acrocephalus arundinaceus* at the same site (Lednice) showed a low dominance of hoverflies (1.1%, n

= 440 prey items) (GRIM, 1999). Interestingly, despite the marginal occurrence of Syrphidae in the great reed warbler food their diversity was relatively high – four species (all the species were also present in the reed warbler food).

Non-significant correlation between the abundance of particular hoverfly species in food samples and their relative abundance in the ecosystem probably reflects the opportunistic foraging tactics of reed warblers. This species forages in all available substrates from reeds and shrubs to herbaceous vegetation, dry mud and even agricultural fields or water surface (GRIM & HONZA, 1996). Moreover, it is able to use very short-term food sources. This is indicated by a large variation in diet composition among particular nests (GRIM & HONZA, 1996). However, a correlation between the rough ordinal scale of abundance of particular hoverfly species (LÁSKA & MAZÁNEK, 1998) and their dominance in the diet is a poor test of warblers' foraging selectivity. Such a test is confounded by the microhabitat characteristics of particular nests sampled and also time during the breeding season. A quantitative comparison of actual supply of hoverflies in warbler foraging areas with composition of the diet delivered to nestlings would provide a much stronger test.

Overall number dominance of hoverflies was 3.7% ($n = 8,545$). However, this underestimates their importance in the diet of nestlings: one ca. 10 mm long hoverfly weighs 14.0 mg (dry weight) whereas the same sized chironomid weighs only 1.3 mg (own unpublished data). Importantly, Chironomidae are by far the most dominant part of the warbler diet (42.0%; GRIM & HONZA, 2001; own unpublished data). Thus, the difference in weights (and consequently nutritional and energetic importance) between Chironomidae and Syrphidae indicates that the latter could contribute to the nutrition of nestlings by an order of magnitude more than would be judged from their number dominance alone. This is also supported by the high number (but clearly not weight) dominance of tiny aphids in the diet of reed warbler nestlings (13.8%; GRIM & HONZA, 2001; own unpublished data). The dominance of small diet items and especially aphids was consistently higher in cuckoo diet across the three field seasons (ranges: 2.4–10.3% in warbler and 6.9–36.4% in cuckoo food) indicating that hoverflies may be even more important for the growth of young cuckoos than could be expected from their numerical dominance alone.

There was no effect of cuckoo parasitism on host foraging behaviour with respect to hoverflies. Interestingly, GRIM & HONZA (2001) reported that the presence of a cuckoo chick increases the dominance of aphids and other small food items in the diet brought by reed warblers. This is most likely explained by supernormal food demands of a cuckoo chick (GRIM & HONZA, 2001). Parasitic chicks require a longer nestling period than warbler chicks to develop properly and when the parasite is 8 days old or older it requires more food than

an average-sized host brood (GRIM et al., 2003). This supernormal food consumption by the parasite leads to increased intensity of host foraging behavior (GRIM & HONZA, 2001). Higher foraging effort is generally known to be accompanied by decreased selectivity of foraging behaviour (see references and discussion in GRIM & HONZA, 2001). This mechanism may explain the increase in the dominance of aphids and other small food items in the cuckoo diet (GRIM & HONZA, 2001). However, Syrphidae were equally common in food brought to the hosts own and parasitic chicks which is also in line with the relationship between foraging intensity and selectivity (see above). Hoverfly diversity was higher in the cuckoo than warbler diet (27 vs 11 species) but this probably reflects a higher sample size in the former species.

In summary, the high percentage of hoverflies in the food delivered by reed warbler adults indicates that putative mimicry does not provide sufficient protection against predation by songbirds at least in some hoverfly species. Hoverflies may be important for the diet of small insectivorous passerines in terms of weight dominance rather than number dominance. The finding of one new species for the Czech Republic indicates that diet analyses in insectivorous songbirds may also make an important contribution to faunistic entomological research (see GRIM, 2006).

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Appendix 1. List of hoverfly species found in the food of reed warbler/cuckoo nestlings.

Eristalis arbustorum (L., 1758) – 1/0, *Eristalis intricarius* (L., 1758) – 0/1, *Eristalis tenax* (L., 1758) – 1/4, *Helophilus pendulus* (L., 1758) – 0/2, *Mesembrius peregrinus* (Loew, 1846) – 0/2, *Mallota cimbiciformis* (Fallén, 1817) – 0/1, *Chalcosyrphus nemorum* (F., 1805) – 0/10, *Melanostoma mellinum* (L., 1758) – 0/17, *Platycheirus clypeatus* (Meigen, 1822) – 3/8, *Platycheirus peltatus* (Meigen, 1822) – 0/1, *Platycheirus scutatus* (Meigen, 1822) – 0/1, *Platycheirus* sp. – 1/2, *Scaeva pyrastris* (L., 1758) 0/2, *Meliscaeva auricollis* (Meigen, 1822) – 0/1, *Eupeodes corollae* (F., 1794) – 16/9, *Eupeodes latifasciatus* (Macquart, 1829) – 1/1, *Eupeodes luniger* (Meigen, 1822) – 2/3, *Syrphus ribesii* (L., 1758) – 0/2, *Syrphus torvus* Osten-Sacken, 1875 – 0/1, *Syrphus vitripennis* Meigen, 1822 – 1/4, *Meligramma triangulifera* (Zetterstedt, 1843) – 0/1, *Episyrphus balteatus* (De Geer, 1776) – 34/143, *Sphaerophoria scripta* (L., 1758) – 4/6, *Sphaerophoria taeniata* (Meigen, 1822) – 0/1, *Neoascia interrupta* (Meigen, 1822) – 0/2, *Dasysyrphus albostrigatus* (Fallén, 1817) – 0/2, *Chrysotoxum vernali* Collin, 1940 – 0/3, *Eumerus* sp. – 0/1, larvae indet. – 6/13, pupae indet. – 0/4.

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FAUNISTICAL NOTES

First records of *Resseliella theobaldi* (Diptera, Cecidomyiidae), an important pest of raspberry from Slovakia

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The raspberry cane midge, *Resseliella theobaldi* (Barnes, 1927) (Diptera, Cecidomyiidae), was first observed from SE England in 1920 and later became a serious pest of commercial raspberry plantations throughout Europe (WOODFORD & GORDON, 1978). Its occurrence is known from Germany (NOLTE, 1952), Sweden, Denmark (SYLVÉN, 1952), Belgium (NIJVELDT, 1954), Italy (GRASSI, 1993), Greece (VASILAKIS, 1995), Bulgaria (STOYANOV, 1963), Slovenia (MASTEN, 1958), Poland (REBANDEL, 1968), Russia (VERESHCHAGINA & KRITSKAIA, 1975), Hungary (AMBRUS, 1973) and Czech Republic (SKUHRÁVÁ, 1997). No information has been available about *R. theobaldi* in Slovakia, but its occurrence was expected.

Adults of raspberry cane midges are small (1.4–2.1 mm long), reddish brown, and because of their similarity to other midges, they are difficult (even impossible) to identify in the field (GORDON & WILLIAMSON, 1991). BARNES (1927) described adults, PITCHER (1952) presented a full description of single developmental stages and biology of the species. Larvae feed on the cortex of raspberry cane. First they are translucent, but they soon change to yellow or orange-pink. Fully grown larvae, measuring about 3.5 × 1.0 mm, fall to the soil surface to spin cocoons and pupate in the upper 1.0–4.0 cm layer (GORDON & WILLIAMSON, 1991). The direct damage caused by midge larval feeding to raspberry is superficial, but the feeding sites soon become infected by a range of fungi [e.g. *Leptosphaeria coniothyrium* (Fuckel)

Sacc., *Didymella applanata* (Niessl) Sacc.; WILLIAMSON & HARGREAVES, 1979], resulting in a disease called “midge blight”.

Although females of *R. theobaldi* lay eggs on raspberry (*Rubus ideaus* L.), blackberry (*Rubus fruticosus* L.), loganberry (*Rubus loganobaccus* L.), rose (*Rosa* sp.), apple (*Malus* sp.), Haworth (*Crataegus* sp.), plum (*Prunus domestica* L.) and quince (*Cydonia oblonga* Mill.) (BARNES, 1944), larvae develop only on raspberry, blackberry, loganberry and rose (PITCHER, 1952). Only raspberry (*R. ideaus*) was recorded as a host plant in Slovakia.

Material examined: Slovakia; larvae of *R. theobaldi* were found during July and August at 16 sites/host plant for each site was *R. ideaus* (col. = date of infested canes collection/larval collection; em. = date of adults emergence): Bardoňovo (48°07' N, 18°27' E, 205 m a.s.l.), 15.VIII.2005, 15 larvae; Bukovec (48°42' N, 17°29' E, 362 m a.s.l.), 1.VIII.2005, em. 24.VIII.2005, 1 ♂, 3 ♀♀; Demandice (48°07' N, 18°47' E, 143 m a.s.l.), 3.VIII.2005, 15 larvae; 27.VIII.2005, 57 larvae; Fabianka (48°19' N, 19°42' E, 190 m a.s.l.), 16.VIII.2005, 5 larvae; Imeľ (47°54' N, 18°08' E, 108 m a.s.l.), 14.VIII.2005, em. 27.VIII.2005, 11 ♂♂, 8 ♀♀; em. 1.IX.2005, 4 ♂♂, 8 ♀♀; em. 3.IX.2005, 1 ♂, 2 ♀♀; Kamenica nad Hronom (47°50' N, 18°44' E, 153 m a.s.l.), 24.VIII.2005, 3 larvae; Lok (48°12' N, 18°26' E, 200 m a.s.l.), 21.VIII.2005, 2 larvae; Martovce (47°52' N, 18°08'