

Research article

Interactions of common species of family Hippoboscidae in Slovakia with their avian and mammalian hosts: their diversity and potential for disease transmission

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Abstract: The hippoboscids play important roles in ecosystem functioning and can serve as indicators of biodiversity and ecosystem health. These bloodsucking ectoparasites are important from a public health perspective, as they can serve as vectors of various endoparasitic pathogens in animals and humans, although our understanding is still limited in this case. The current study provides information on the host species and distribution, which can contribute to the understanding of the ecology and epidemiology of these important arthropods with a potential impact on both animal and human health. We present an ecological parasite-host interaction network of louse flies and deer keds (Diptera: Hippoboscidae) collected from various sites in Slovakia

from this time. A total of 123 new samples of eight hippoboscid fly species were captured on 17 species, including 15 birds and two mammals. New host-parasite interactions were recorded for the first time. *Ornithomya biloba* (Dufour, 1827) with the *Acrocephalus arundinaceus* (Linnaeus, 1758) and *Lipoptena fortisetosa* (Maa, 1965) with the *Phylloscopus collybita* (Vieillot, 1817) are new although it is unlikely that these birds are the host for these ectoparasites. *Ornithoica turdi* (Latreille, 1811) with the *Lanius collurio* Linnaeus, 1758, *Ornithomya avicularia* (Linnaeus, 1758) with the *Motacilla alba* Linnaeus, 1758 and *Currucà communis* (Latham, 1787), and *Ornithomya fringillina* (Curtis, 1836) with the *C. communis* and *Erithacus rubecula* (Linnaeus, 1758) represent new parasite-host relations for Slovakia. *O. avicularia* was observed to attack humans, and *L. fortisetosa* was found on different bird hosts, creating a possible bridge for the transfer of avian and mammalian pathogens.

Keywords: birds, ectoparasites, hippoboscid, interaction network, mammals

Introduction

The family Hippoboscidae are obligate ectoparasites of birds (known as “louse flies”) and mammals (known as “deer keds”) with an interesting and complex biology and ecology (Theodor & Oldroyd, 1964; Maa, 1969; Bezerra-Santos & Otranto, 2020; Oboňa et al., 2022, 2023; Rekecki & Rajkovic, 2023). The hippoboscids are divided into the subfamilies Lipopteninae (tribe Lipoptenini, parasitising exclusively mammals), Ornithomyinae (tribes Olfersiini and Ornithomyini composed of species that mostly parasitise birds) and Hippoboscinae (tribe Hippoboscini with all species in Europe affecting mammals) (Dick, 2018; Reeves & Lloyd, 2019). They play important roles in ecosystem functioning and can also serve as indicators of biodiversity and ecosystem health, which makes them an important group to study in the context of conservation (Hudson et al., 2006; Frainer et al., 2018).

These bloodsucking insects are also important from a public health perspective, as they can serve as vectors of various endoparasitic pathogens in animals and humans including malaria, sleeping sickness, *Haemoproteus* infections, and possibly filarial onchocerciasis (Baker, 1967; Sychra et al., 2020; Werszko et al., 2020; Attia & Salem, 2022). Moreover, the impact of climate change on the distribution and abundance of Hippoboscidae species, as well as their potential to act as pathogens vectors, is a growing concern (McCabe et al., 2020; Andreani et al., 2021; Benedict & Barboza, 2022; Maślanko et al., 2022; Dibo et al., 2022). The economic impact of Hippoboscidae infestations on livestock production and welfare is also an important issue (Maślanko et al., 2022). Finally, Hippoboscidae contribute to the transmission of vector-borne pathogens, especially

those affecting wildlife populations (Dehio et al., 2004; Hornok et al., 2011; Sato et al., 2021).

For most louse flies species related to wild birds (subfamily Ornithomyinae), there is limited information on their competence as vectors of pathogens (Bezerra-Santos & Otranto, 2020). Species of the genus *Ornithomya* were identified as competent vectors of avian trypanosomes (Baker, 1956; Santolíková et al., 2022). Species of genus *Lipoptena* pose a threat to the health of their hosts as potential vectors of numerous pathogens such as *Megatrypanum* trypanosomes, *Trypanosoma* spp., *Bartonella schoenbuchensis*, *Bartonella* spp., *Anaplasma phagocytophilum*, *Borrelia burgdorferi*, *Theileria* spp., *Moraxella* spp., *Mycobacterium* spp. and *Rickettsia* spp. (Böse & Petersen, 1991; Dehio et al., 2004; Halos et al., 2004; Víchová et al., 2011; de Bruin et al., 2015; Buss et al., 2016; Szewczyk et al., 2017; Werszko et al., 2020, 2022; Dibo et al., 2022; Andreani et al., 2023; Tiawsirisup et al., 2023).

Although our understanding of the role of hippoboscids as vectors of human pathogens is still limited, certain zoonotic agents (e.g., *Bartonella* spp., *Rickettsia* spp., *Borrelia* sp., *Anaplasma* sp. and *Theileria* sp.) have been detected in some species of keds (Buss et al., 2016; Kosoy et al., 2016; Liu et al., 2016; Boularias et al., 2020; Zhao et al., 2020; Attia & Salem, 2022; Bjelková & Horák, 2022; Dibo et al., 2022; Nartshuk et al., 2022a, b; Maślanko et al., 2022; Tiawsirisup et al., 2023). These findings have drawn the attention of the scientific community towards the need for further investigations regarding the vector role and host interactions of these ectoparasites in public health (Bezerra-Santos & Otranto, 2020).

People entering natural habitats of hippoboscids can be exposed to their attacks and subsequent health consequences, such as erythema and inflammation of

the bitten skin, allergic rhinoconjunctivitis, or even anaphylactic reaction (Laukkonen et al., 2005; Quercia et al., 2005; Vidal et al., 2007; Decastello & Farkas, 2010; Matito et al., 2010; Maślanko et al., 2020). Notwithstanding it seems that the reproductive potential of some hippoboscids species (e.g., *H. equina*) parasitising occasional hosts has not been fully explored to date (Maślanko et al., 2022). It has been found that humans are attacked as hosts for species of the genus *Lipoptena* spp. accidentally, as the insects cannot reproduce on this host (Kortet et al., 2010; Hodžić et al., 2012). For this reason, this is even considered an ecological trap in some cases (Robertson & Hutto, 2006; Kaunisto et al., 2009), because when the fly *L. cervi* settles on the host (or other vertebrate mistakenly considered to be the host), it loses its wings.

Ecological systems, characterised by organisms interacting with each other, can be effectively represented through ecological interaction networks, specifically in the context of host-parasite relationships (Delmas et al., 2019; Poisot et al., 2021). While extensive research has been conducted on mutualistic and predatory interactions, less attention has been given to parasitic networks (Poisot et al., 2021). The interaction networks of the family Hippoboscidae have not been studied yet, but those of other families from superfamily Hippoboscoidea have been published, such as Streblidae (Pena et al., 2023; Poon et al., 2023) and Nycteribiidae (Mlynárová et al., 2023; Poon et al., 2023).

Ecological network research seeks to comprehend how nature's complexity persists and impacts ecosystem functioning. This is crucial for predicting and mitigating the effects of environmental disturbances, such as habitat loss, climate change, and invasions of exotic species. Additionally, knowing the distribution of symbiont communities holds benefits for both wildlife and human systems, providing valuable insight into host health and symbiont transmission dynamics, especially during the current zoonotic spillover crisis (Nuñez et al., 2020). Therefore, the study of the distribution and diversity of hippoboscids in a particular region can offer important information about the health status of local bird and mammal populations, as well as potential risks to public health.

In this study, we aim to provide an overview of the Hippoboscidae from Slovakia – all data published so far (see Published records section in the Faunistics)

and new data from the period 2021–2022. Additional data from neighbouring countries such as the Czech Republic and Poland were also included (see Appendix 1). The current study provides information on the host species and distribution of hippoboscids in the region of Slovakia, which can contribute to the understanding of the ecology and epidemiology of these important arthropods with potential impact on both animal and human health.

Material and methods

The collection of hippoboscids from bird hosts can be challenging due to their mobility and ability to escape, making bird ringing stations and bird nests ideal places for their research (Sychra et al., 2008; Oboňa et al., 2019a; Gaponov & Tewelde, 2020). Despite the difficulties in collecting hippoboscids, several studies have reported the presence of these arthropods in various bird and mammal species in Europe, with 21 species known to occur in Slovakia alone (Petersen, 2004; Le Guillou & Chapelin-Viscardi, 2022; Oboňa et al., 2019b, 2022).

The louse flies collected for the purpose of this study were caught by authors at various study sites (Appendix 1). The louse flies were collected by ornithologists (MF, SG, PK, JR) primarily in ornithological station Drienovec and Sabinov from avian hosts. The deer keds were collected by PB, BB, RC, ACs, KD, PM, DT, and JO directly from humans (see Faunistics).

Collected hippoboscids were placed in Eppendorf tubes, fixed in 96% ethanol, and subsequently identified using determination keys by Povolný & Rosický (1955), Theodor and Oldroyd (1964), and Oboňa et al. (2022). The material is deposited in ethanol collection in the Laboratory and Museum of Evolutionary Ecology, Department of Ecology, University of Prešov (LMEE PO).

To create the species interaction network, qualitative data on collected hippoboscid flies and associated birds and mammals, supplemented with all available literature data from Slovakia (see Faunistics), were analysed using Gephi network exploration and manipulation software, (<https://gephi.org/>). In addition to simple information about presence and absence, we also used quantitative data, expressing the number of publications mentioning individual parasite-host relationships published so far

for Slovakia. Developed modules can import, visualise, spatialise, filter, manipulate and export all types of networks. The visualisation module uses a special 3D rendering engine to render graphs in real time (Bastian et al., 2009). The typical dataset used in Gephi comprises nodes (entities or objects) and edges (connections or relationships) connecting these nodes. In Gephi, the network is visually represented as a graph, wherein nodes are depicted as discrete points or shapes, and edges are illustrated as lines that link the nodes. To convey the strength or weight of the relationship between nodes, it is possible to customise the edges by adjusting their thickness and colour. Thicker or darker edges can signify stronger connections, while thinner or lighter edges can indicate weaker connections.

Results

A total of 8 species (123 specimens) of the family Hippoboscidae were recorded on 17 host species (15 Aves and 2 Mammalia, see Table 1, Faunistics).

In this study, a total of 87 host-parasite interactions were recorded between the eight hippoboscid fly

species and 56 avian and eight mammalian host species. These interactions encompass both comprehensive published data from Slovakia and new unpublished data (see Faunistics). (Note: An admitted weakness of this research is that data from mammals are incomparable with data from bird species. Thus, the results of mammals in the sample are significantly overestimated, while those related to bird species are significantly underestimated when compared to each other).

Out of the eight fly species, *O. avicularia* showed the highest number of associations with different host species ($n = 41$), followed by *O. fringillina*, which was associated with 16 host species. Both species are unspecific, polyxenous avian parasites, which is consistent with the claims of other authors (Nartshuk et al., 2019; Bartos et al., 2020; Gaponov & Tewelde, 2020). *O. turdi* is also polyxenous avian parasite (Gaponov & Tewelde, 2020) but its known range is mainly restricted to the northern regions of Slovakia (Oboňa et al., 2019b) resulting in a comparatively lower number of recorded hosts. *L. fortiseta*, *L. cervi* and *H. equina* were identified as oligoxenous species, but they mainly parasitised mammals. On the other hand, *O. biloba* and *C. pallida* were found to be stenoxenous (see Fig. 1).

Table 1. The overview of recorded host species.

Aves	<i>Accipiter nisus</i> (Linnaeus, 1758)
	<i>Acrocephalus arundinaceus</i> (Linnaeus, 1758)
	<i>Apus apus</i> (Linnaeus, 1758)
	<i>Curruca communis</i> (Latham, 1787)
	<i>Cyanistes caeruleus</i> (Linnaeus, 1758)
	<i>Erythacus rubecula</i> (Linnaeus, 1758)
	<i>Hirundo rustica</i> Linnaeus, 1758
	<i>Lanius collurio</i> Linnaeus, 1758
	<i>Motacilla alba</i> Linnaeus, 1758
	<i>Parus major</i> Linnaeus, 1758
	<i>Passer montanus</i> (Linnaeus, 1758)
	<i>Phylloscopus collybita</i> (Vieillot, 1817)
	<i>Prunella modularis</i> (Linnaeus, 1758)
	<i>Riparia riparia</i> (Linnaeus, 1758)
	<i>Sturnus vulgaris</i> Linnaeus, 1758
Mammals	<i>Canis lupus f. familiaris</i> Linnaeus, 1758
	<i>Homo sapiens</i> Linnaeus, 1758

Faunistics

The examined species have been sorted based on the study sites, and then arranged chronologically according to the date of collection. For captured birds that have been ringed, the bird ring number is provided in parentheses after the species name to facilitate identification of individual birds. This arrangement enables a clear overview of the diversity and abundance of species across different study sites and time periods.

Family Hippoboscidae

Subfamily Ornithomyinae

Crataerina pallida (Latreille, 1812)

Published records: Povolný & Rosický (1955), Krištofík & Štefan (1980), Chalupský (1986), Straka (1981), Čepelák (1985), Krištofík (1998).

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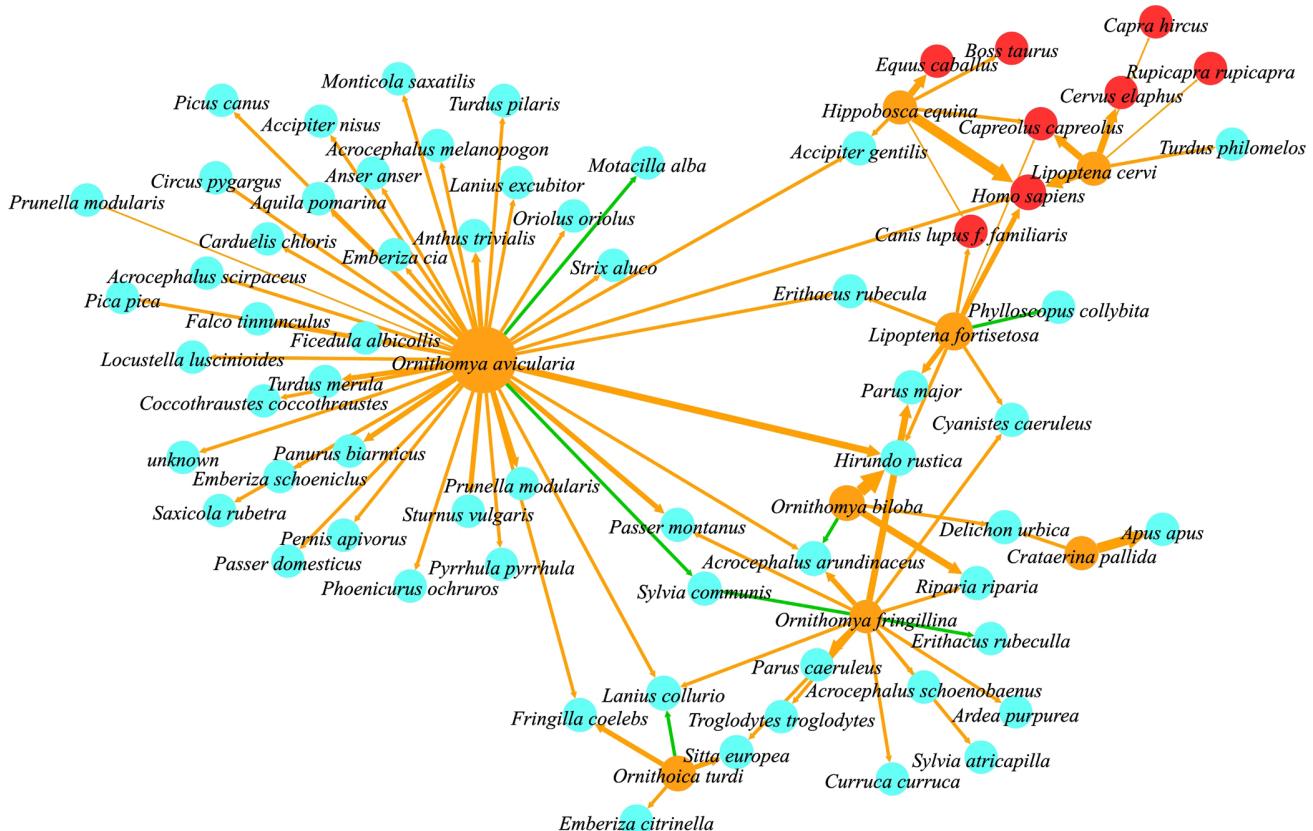


Fig. 1. Species interaction network of hippoboscid flies and associated hosts*.

* Orange dots represent hippoboscid parasites, blue dots represent avian hosts and red dots represent mammalian hosts. The green lines depict newly discovered host-parasite relationships for Slovakia, which were documented as part of this study and have not been published previously. The thickness of the lines represents the relative frequency of the interactions.



Fig. 2. The red-backed shrike *Lanius collurio* Linnaeus, 1758 (J. Repaský).

Material examined: Košice: 3 ind., host *A. apus*, 2.6.2022.

Comments: A common stenoxenous ectoparasite of *A. apus* and *Delichon urbicum* (Linnaeus, 1758).

Ornithoica turdi (Latreille, 1811)

Published records: Povolný & Rosický (1955), Chalupský & Povolný (1983), Chalupský (1986).

Material examined: Drienovec: 1 ind., host *L. collurio* (N24615), 23.8.2022.

Comments: Not native species of Central Europe, distributed in the Afrotropical region and southern Palaearctic. The red-backed shrike *L. collurio* (Fig. 2) is here recorded as new hosts of *O. turdi* in Slovakia.

Ornithomya avicularia (Linnaeus, 1758)

Published records: Povolný & Rosický (1955), Čepelák (1974, 1982), Krištofík & Štefan (1980), Chalupský & Povolný (1983), Chalupský (1986), Čepelák & Čepelák (1991), Roháček (1995), Krištofík (1998), Straka & Majzlán (2010), Oboňa et al. (2019a, b, 2021, 2022).



Fig. 3. The common whitethroat (*Curruca communis* (Latham, 1787)) (S. Greš).

Material examined: Boldigáň: 1 ind., host human, 2.8.2022; Červený Kláštor: 1 ind., host *M. alba* (S623731), 6.7.2022; Drienovec: 1 ind., host *P. modularis* (bird ring number: S640827), 10.10.2022; 1 ind., host *P. modularis* (S640982), 11.10.2022; Horné Seče: 1 ind., host human, 30.5.2022; Sabinov bird ringing station: 2 ind., host *H. rustica* (U95683, U87734), 28.7.2022; 1 ind., host *A. nisus*, 28.7.2022; Sabinov (garden): 1 ind., host human, 2.6.2022; Uzovský Šalgov: 1 ind., host *H. rustica* (U81920), 3.7.2022; 1 ind., host *H. rustica* (U82451), 7.7.2022; 1 ind., host *C. communis* (S618419), 7.7.2022; 2 ind., host *P. montanus* (S618420), 10.7.2022; 1 ind., host *H. rustica* (U95140), 10.7.2022; 1 ind., host *S. vulgaris* (L39194), 13.7.2022; 1 ind., host *H. sapiens*, 19.7.2022; 1 ind., host *H. rustica* (U82463), 24.7.2022; Zlaté Kopyto, valley Kopytovská dolina: 1 ind., host unknown, 3.8.2022.

Comments: A common polyxenous louse fly species in Slovakia. The white wagtail *M. alba* and common whitethroat *C. communis* (Fig. 3) are here recorded as new hosts of *O. avicularia* in Slovakia.

Ornithomya biloba (Dufour, 1827)

Published records: Brancsik (1910), Krištufík & Štefan (1980), Chalupský & Povolný (1983), Chalupský (1986), Krištufík (1998), Oboňa et al. (2019a, b, 2021, 2022).

Material examined: Drienovec: 1 ind., host *H. rustica* (U83391), 23.8.2022; 1 ind., host *H. rustica* (U83360), 21.8.2022; 1 ind., host *H. rustica* (U83371), 21.8.2022; 2 ind., host *H. rustica* (U83382), 23.8.2022; Hromoš, Poprad River: 1 ind., host *R. riparia*



Fig. 4. The great reed warbler (*Acrocephalus arundinaceus* (Linnaeus, 1758)) (S. Greš).

(U87058), 7.7.2022; Uzovský Šalgov: 1 ind., host *R. riparia*, 7.7.2022; 1 ind., host *A. arundinaceus* (N28106), 7.7.2022; 1 ind., host *H. rustica* (U95165), 15.7.2022; 3 ind., host *H. rustica* (U95332, U95332), 18.7.2022; 2 ind., host *H. rustica* (U95349, U98026), 19.7.2022; 2 ind., host *H. rustica* (U95401, U95401), 19.7.2022; 1 ind., host *H. rustica*, 9.8.2022; 1 ind., host *H. rustica*, 10.8.2022; 1 ind., host *H. rustica*, 13.8.2022; 1 ind., host *H. rustica* (U95967), 17.8.2022; 1 ind., host *H. rustica* (U83363), 21.8.2022; 2 ind., on *H. rustica* (U102147, U102060), 24.8.2022; 1 ind., host *H. rustica* (U82345), 24.8.2022; 1 ind., host *H. rustica* (U102143), 24.8.2022.

Comments: A common stenoxenous louse fly species in Central Europe, specialised mainly on *D. urbicum*, *H. rustica*, and *R. riparia*. The great reed warbler *A. arundinaceus* (Fig. 4) is here recorded as new host of *O. biloba* are also new, probably not published yet, but this bird species is unlikely to be the primary host for this ectoparasite.

Ornithomya fringillina (Curtis, 1836)

Published records: Krištufík & Štefan (1980), Chalupský & Povolný (1983), Chalupský (1986), Krištufík (1998), Straka (2005b), Straka & Majzlán (2008, 2014), Oboňa et al. (2019a, 2021, 2022).

Material examined: Červený Kláštor: 2 ind., on *C. communis* (S623741, S623740), 6.7.2022; Drienovec: 1 ind., host *E. rubecula* (S640571), 9.10.2022; Sabinov bird ringing station: 1 ind., host *P. montanus* (S602249), 28.7.2022; Tichý Potok: 1 ind., host *P. caeruleus*, 11.11.2021. Uzovský Šalgov: 1 ind., host *A. arundinaceus*, 7.7.2022.



Fig. 5. The European robin (*Erithacus rubecula* (Linnaeus, 1758)) (S. Greš).

Comments: A polyxenous louse fly species in Slovakia mainly of Passeriformes. The common whitethroat *C. communis* and European robin *E. rubecula* (Fig. 5) are here recorded as new hosts of *O. fringillina* in Slovakia.

Subfamily Hippoboscinae

Hippobosca equina (Linnaeus, 1758)

Published records: Thalhammer (1899), Brancsik (1910), Povolný & Rosický (1955), Krištofík & Štefan (1980), Chalupský & Povolný (1983), Čepelák (1986, 1992, 1993, 1994a), Chalupský (1986), Čepelák & Čepelák (1991), Krištofík (1998), Straka (2005a, 2016), Straka & Majzlán (2010, 2016), Oboňa et al. (2019b, 2022).

Material examined: Lakšárska Nová Ves, nr. Zelenka Nature Reserve, and Červený rybník Nature Reserve: 1 ind., host human, 25.8.2022; Plavecký Mikuláš, nr. Malacky: 1 ind., host human, 12.6.2022; Vanišovec Nature Reserve, nr. Šaštín: 1 ind., host human, 3.6.2022; 3 ind., host human, 23.6.2022.

Comments: Relatively large, not common deer ked species in Slovakia.

Subfamily Lipopteninae

Lipoptena cervi (Linnaeus, 1758)

Published records: Brancsik (1910), Povolný and Rosický (1955), Dyk & Schanzel (1964), Krištofík & Štefan (1980), Chalupský & Povolný (1983), Čepelák

(1986, 1987, 1988, 1992, 1994b), Chalupský (1986), Hubálek et al. (1988), Čepelák & Čepelák (1991), Krištofík (1998), Straka (2001, 2010, 2011), Roháček (2009), Straka & Majzlán (2014), Oboňa et al. (2019b, 2022).

Material examined: Beckov: 1 ind., host human, 7.10.2022; Bolešov: 1 ind., host human, 28.9.2022; Drienovec: 1 ind., host human, 3.11.2021; 1 ind., host human, 5.11.2021; 1 ind., host human, 10.10.2022; Chočské vrchy hills, path under Sokol: 1 ind., host human, 18.10.2022; Levočské vrchy mountains: 1 ind., host human, 15.10.2021; Prešov: 2 ind., host human, 7.2022; Rajtopíky, Branisko: 1 ind., host human, 12.10.2022; Rudník: 1 ind., host human, 23.10.2022; Sabinov – garden: 1 ind., host human, 9.2021; 1 ind., host human, 9.2021; Spiš Basin, Dreveník, yellow marked hiking trail, multiple locations: 1 ind., host human, 10.10.2022; Štiavnické vrchy mountains, Rudno nad Hronom railway station: 1 ind., host human, 29.10.2022; Vyšná Olšava: 1 ind., host human, 7.10.2022; Šranecké piesky: 1 ind., host human, 31.8.2022.

Additional data: Czech Republic: Přičovy, nr. Chlumečník hill: 1 ind., host human, 29.10.2022.

Comments: A frequent deer ked species in Slovakia.

Lipoptena fortisetosa (Maa, 1965) (Fig. 7 C)

Published records: Kočišová et al. (2007), Oboňa et al. (2019b, 2022).

Material examined: Bachureň: 1 ind., host human, 2.8.2022; Bikoš: 1 ind., host dog, 8.2022; Drienovec: 1 ind., host human, 23.8.2022; 2 ind., host human, 25.8.2022; 1 ind., host human, 27.8.2022; Chočské vrchy hills: 1 ind., host human, 19.7.2022; Lakšárska Nová Ves, nr. Zelenka Nature Reserve and Červený rybník Nature Reserve: 2 ind., host human, 25.8.2022; Lakšárska Nová Ves, Zelenka Nature Reserve: 1 ind., host human, 10.6.2022; Prešov: 1 ind., host human, 11.6.2022; 2 ind., host human, 7.2022; Rajtopíky, Branisko: 1 ind., host human, 12.10.2022; Rudník: 1 ind., host human, 28.5.2022; Ruská Nová Ves: 1 ind., host human, 8.2022; Sabinov bird ringing station: 2 ind., host *P. collybita*, 10.6.2022; 1 ind., host *P. major*, 11.6.2022; 1 ind., host *P. collybita*, 16.6.2022; 2 ind., host human, 29.6.2022; 1 ind., host human, 8.7.2022; 3 ind., host human, 28.7.2022; Sabinov: 1 ind., host human,



Fig. 6. The common chiffchaff (*Phylloscopus collybita* (Vieillot, 1817)) (S. Greš).

9.2021; Sedlo Zákruty saddle – above the valley Kopytovská dolina: 1 ind., host human, 4.8.2022; Studienka, nr. Malacky: 1 ind., host human, 31.8.2022; the Myjava hills, Holičov vrch hill: 1 ind., host human, 5.7.2022; the Slovak Karst, Plešivec, green marked hiking trail from the cave Gambasecká jaskyňa to Plešivec: 1 ind., host human, 9.9.2022; the Šalková, Zvolen Basin: 1 ind., host human, 15.7.2022; Vanišovec Nature Reserve, nr. Šaštín: 1 ind., host human, 3.6.2022; 1 ind., host human, 23.6.2022.

Additional data: Czech Republic: Kyselka: 1 ind., host human, 12.7.2022; Spáňov, nr. Domažlice forest: 5 ind., host human, 17.7.2022; the same, 4 ind., host human 2.7.2022. Poland: Beskid Żywiecki: 1 ind., host human, 14 – 17.7.2022.

Comments: A common and frequent not native deer ked in Slovakia. The common chiffchaff *P. collybita* (Fig. 6), probably not published yet, is a new host of *L. fortisetosa* in Slovakia, but as mentioned in Oboňa et al. (2021) birds are unlikely to be the primary host for this ectoparasite.

Discussion

Ecological networks serve as intricate representations of ecological interactions, providing a unique opportunity to study and predict the transmission of pathogens among different hosts and parasites (Runghen et al., 2021; Su et al., 2022). In this article, we focus on the potential role of Hippoboscidae species as vectors of various pathogens with the

possible use of ecological networks. In this context, we present several hypothetical scenarios where different species of hippoboscids could act as bridges for pathogen transmission between hosts.

Ornithomyia avicularia, exhibiting the highest number of interactions in our network (Fig. 1), represents a possible bridge for pathogen transmission between diverse avian hosts and mammals (Santolíková et al., 2022; Čisovská Bazsalovicsová et al., 2023). This fact could make it a possible link for the transfer of avian and mammalian pathogens. *Ornithomyia fringillina* represents a possible transmission of pathogens between our study's second most diverse range of avian hosts (see also Čisovská Bazsalovicsová et al., 2023). Likewise, *O. turdi*, a non-native species known to migrate with its hosts (Pfadt & Roberts, 1978), could facilitate the transmission of African (tropical and subtropical) and European avian pathogens. *O. biloba* and *Crataerina pallida* with a small number of interactions in the network, may contribute to transmission of pathogens among a smaller number of avian hosts.

We recorded two species of the genus *Lipoptena*: *L. fortisetosa* with eight interactions and *L. cervi* with six interactions. *L. fortisetosa*, a non-native species, can potentially serve as a possible bridge for the transmission of pathogens between a more restricted range of mammals, as well as between a more restricted range of avian hosts and mammals. Its trophic ecology is not fully understood, but it is a relatively aggressive species that attacks a wide range of hosts, including cattle and horses (Metelitsa & Veselkin, 1989; Dehio et al., 2004). *L. cervi*, together with *H. equina* represents a possible route of transmission for pathogens between a narrower range of mammalian hosts.

In addition to the previously mentioned interactions, we have also documented several new parasite-host relationships. The interaction between *O. turdi* and *L. collurio* is newly recorded only for Slovakia, since this relationship has already been detected in Hungary (Papp & Kaufman, 1989). *O. avicularia* with *M. alba* (Walter et al., 1990; Nartshuk et al., 2020) and with *C. communis* (Santolíková et al., 2022), *O. fringillina* with *C. communis* (Boyko et al., 1973; Doszhanov, 2003; Matyukhin et al., 2016; Labitzke & Jentzsch, 2019) and with *E. rubecula* (Boyko et al., 1973; Doszhanov, 2003; Matyukhin et al., 2016) has also been recorded. Furthermore, *O. biloba* with *A. arundinaceus* and *L. fortisetosa* with *P.*



Fig. 7. A: *Lipoptena cervi* (Linnaeus, 1758); B: *Hippobosca equina* (Linnaeus, 1758); C: *Lipoptena fortisetosa* (Maa, 1965) D: *Crataerina pallida* (Latreille, 1812) (G. Kunz).

collybita represent new, not yet published interactions not only for Slovakia but on a global scale. In view of the fact that *O. biloba* is specialised mainly on *D. urbiculum*, *H. rustica* and *R. riparia* (Krištofík, 1998), *A. arundinaceus* is unlikely to be the primary host for this louse fly. *A. arundinaceus* was collected on the same day at the same locality (Uzovský Šalgov, 7.7.2022) as *R. riparia*, so it is possible that this record is just a coincidence and caused by the authorshandling of these birds during ringing.

The interaction of *L. fortisetosa* with *P. collybita* is unexpected, as birds are not the primary hosts for this ectoparasite, which is known to infest cervids (Kowal et al., 2016; Oboňa et al., 2021). On the other hand, *L. fortisetosa* was found on two *P. collybita* examined on different days (10.6. and 16.6.2022). This is thus an accidental but apparently natural occurrence. In addition, there are other records of *L. fortisetosa* on *Parus major* and *Cyanistes caeruleus* in Fig. 1. (see also Oboňa et al. (2019b, 2022)).

In several cases of this study, flies were found on unexpected hosts. Like flies usually parasitising on birds were found on mammals and vice versa (e.g.: *L. fortisetosa* (Fig. 7 C) on the *P. collybita*). In other cases, flies were found on a host from the usual animal class, but on species they normally do not parasitise (e.g.: *O. biloba* on the *A. arundinaceus*).

Four species of hippoboscid flies – *Lipoptena fortisetosa*, *L. cervi*, *Hippobosca equina* and *Ornithomyia avicularia* – were collected on humans, underlining the potential of penetrating human skin as confirmed by several authors before (Maa, 1969; Borowiec, 1984; Quercia et al., 2005; Vidal et al., 2007; Matito et al., 2010; Decastello & Farkas, 2010; Buczek et al., 2020; Maślanko et al., 2020).

Given the potential impact of these parasites on human health, it is crucial to understand the networks that connect different species and how pathogens may spread through them (Proesmans et al., 2021; Runghen et al., 2021; Su et al., 2022). Therefore,

further research is needed to identify the specific host-parasite relationships and determine the potential risks to human and animal health.

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References

- Andreani A., Beltramo C., Ponzetta M.P., Belcari A., Sacchetti P., Acutis P.L., Peletto S. 2023 Analysis of the bacterial communities associated with pupae and winged or wingless adults of *Lipoptena fortisetosa* collected from cervids in Italy. Medical and veterinary entomology 7 (3): 472–482.
<https://doi.org/10.1111/mve.12644>
- Andreani A., Stancampiano L., Belcari A., Sacchetti P., Bozzi R., Ponzetta M.P. 2021 Distribution of Deer Keds (Diptera: Hippoboscidae) in Free-Living Cervids of the Tuscan-Emilian Apennines, Central Italy, and Establishment of the Allochthonous Ectoparasite *Lipoptena fortisetosa*. Animals 11: 2794.
<https://doi.org/10.3390/ani11102794>
- Attia M.M., Salem H.M. 2022 Morphological and molecular characterization of *Pseudolynchia canariensis* (Diptera: Hippoboscidae) infesting domestic pigeons. International journal of tropical insect science 42: 733–740.
<https://doi.org/10.1007/s42690-021-00597-2>
- Baker J.R. 1956 Studies on *Trypanosoma avium* Danilewsky 1885 II. Transmission by *Ornithomyia avicularia* L. Parasitology 46: 321–334.
<https://doi.org/10.1017/S0031182000026536>
- Baker J.R. 1967 A Review of the Role Played by the Hippoboscidae (Diptera) as Vectors of Endoparasites. The Journal of parasitology 53: 412–418.
<https://doi.org/10.2307/3276603>
- Bartos M., Włodarczyk R., Iciek T., Piasecka A., Janiszewski T., Minias P. 2020 Louse Flies of Charadrii and Scolopaci Shorebirds Migrating through Central Europe. Journal of wildlife diseases 56 (2): 414–418.
<https://doi.org/10.7589/2019-01-018>
- Bastian M., Heymann S., Jacomy M. 2009 Gephi: An Open Source Software for Exploring and Manipulating Networks. Proceedings of the International AAAI Conference on Web and Social Media 3 (1): 361–362.
- Benedict B.M., Barboza P.S. 2022 Adverse effects of Diptera flies on northern ungulates: *Rangifer*, *Alces*, and *Bison*. Mammal Review 52 (3): 425–437.
<https://doi.org/10.1111/mam.12287>
- Bezerra-Santos M.A., Otranto D. 2020 Keds, the enigmatic flies and their role as vectors of pathogens. Acta Tropica 209: 105521.
<https://doi.org/10.1016/j.actatropica.2020.105521>
- Bjelková K., Horák J. 2022 Finding a suitable coat: The ecology of the invasive deer ked (*Lipoptena cervi* (Linnaeus, 1758); Diptera: Hippoboscidae), an ectoparasite of large mammals in the Czech Republic. Medical and veterinary entomology 36: 480–485.
<https://doi.org/10.1111/mve.12592>
- Borowiec L. 1984 Muchówki-Diptera, Wpleszczo-wate-Hippoboscidae. Klucz do oznaczania owadów Polski. PWN, Poland.
- Böse R., Petersen K. 1991 *Lipoptena cervi* (Diptera), a potential vector of *Megatrypanum* trypanosomes of deer (Cervidae). Parasitology research 77: 723–725.
<https://doi.org/10.1007/BF00928691>
- Bouliarias G., Azzag N., Gandoi C., Bouillin C., Chomel B., Haddad N., Boulouis H.J. 2020 *Bartonella bovis* and *Bartonella chomelii* infection in dairy cattle and their ectoparasites in Algeria. Comparative immunology, microbiology and infectious diseases 70: 101450–6.
<https://doi.org/10.1016/j.cimid.2020.101450>
- Boyko A.V., Ayupov A.S., Ivliyev V.G. 1973 Krovososki (Diptera, Hippoboscidae) ptits v prirodnykh ochagakh kleshchevogo entsefalita lesostepnoy zony Srednego Povolzh'ya. Parazitologiya 6: 536–540. (In Russian)
- Brancsik K. 1910 A Trencsénvármegyeben talált Dipterák felsorolása. Trencs. Várm. Termész. Eg. Trencsén 31–33 (1908–1910): 127–158.

- Buczek W., Buczek A.M., Bartosik K., Buczek A. 2020 Comparison of Skin Lesions Caused by *Ixodes ricinus* Ticks and *Lipoptena cervi* Deer Keds Infesting Humans in the Natural Environment. International journal of environmental research and public health 17: 3316.
<https://doi.org/10.3390/ijerph17093316>
- Buss M., Case L., Kearney B., Coleman C., Henning J. 2016 Detection of Lyme Disease and Anaplasmosis Pathogens Via PCR in Pennsylvania Deer Ked. Journal of vector ecology 41: 292–294.
<https://doi.org/10.1111/jvec.12225>
- Čepelák J. 1974 Skupiny vyšších much (Diptera, Brachycera) z územia Súľovských skál. Súľovské skaly. Monografia vlastivedného zborníka Považia 1: 359–362.
- Čepelák J. 1982 Niektoré skupiny vyšších dvojkrídlovcov Malých Karpát (Diptera, Brachycera) II. Biológia, Bratislava 37: 599–607.
- Čepelák J. 1985 Prehľad nálezov dvojkrídlovcov (Diptera) z oblasti štátnej prírodnej rezervácie Suchý v Malej Fatre. Ochrana prírody 6: 163–187.
- Čepelák J. 1986 Vyššie dvojkrídlovce (Diptera, Brachycera) Štátnej prírodnej rezervácie Kováčovské kopce. Ochrana prírody 7: 127–148.
- Čepelák J. 1987 Vyššie dvojkrídlovce (Diptera, Cyclorrhapha, Schizophora) Hraškovej lúky a jej okolia. I. Rosalia 3 (1986): 193–209.
- Čepelák J. 1988 Ďalší príspevok k poznaniu vyšších dvojkrídlovcov (Dipt., Brachycera) ŠPR Hrdovická v CHKO Ponitrie. Rosalia 5: 153–164.
- Čepelák J. 1992 Vyššie dvojkrídlovce (Diptera, Cyclorrhapha) z oblasti Veľkého Lysca. Höhere Zweiflügler (Diptera, Cyclorrhapha) aus dem Gebiete Veľký Lysec. Rosalia 8: 191–198.
- Čepelák J. 1994b Blick and die Zusammensetzung der Fauna der höheren Zweiflüglern der Umgebung der Gemeinde Červený Kameň (Diptera, Brachycera). Dipterologica Bohemoslovaca 6: 25–32.
- Čepelák J., Čepelák S. 1991 Niektoré čeľade dvojkrídlovcov (Diptera) Zobora. Zobor 2: 245–278.
- Čepelák S. 1993 Výsledky orientačných zberov dvojkrídlovcov (Diptera) na vybraných lokalitách pohoria Tríbeč. Rosalia 9: 173–180.
- Čepelák S. 1994a Sammelergebnisse der Zweiflüglern (Diptera, Brachycera) an den Lokalitäten Štiavnické vrchy und Hronská pahorkatina. Dipterologica Bohemoslovaca 6: 33–37.
- Chalupský J. 1986 Hippoboscidae. In: Čepelák J. (ed.) Diptera Slovenska II., Veda, Bratislava, 201–202.
- Chalupský J., Povolný D. 1983 Additional notes to a list of Czechoslovak Hippoboscidae (Diptera). Acta Universitatis Agriculturae Brno, Facultas Agronomica 31: 137–141.
- Čisovská Bazsalovicsová E., Víchová B., Oboňa J., Radačovská A., Blažeková V., Králová-Hromadová I. 2023 Bird Louse Flies *Ornithomya* spp. (Diptera: Hippoboscidae) as Potential Vectors of Mammalian *Babesia* and Other Pathogens. Vector-Borne and Zoonotic Diseases 23: 275–283.
<https://doi.org/10.1089/vbz.2022.0088>
- de Bruin A., van Leeuwen A.D., Jahfari S., Takken W., Földvári M., Dremmel L., Sprong H., Földvári G. 2015 Vertical transmission of *Bartonella schoenbuchensis* in *Lipoptena cervi*. Parasites & vectors 8: 176.
<https://doi.org/10.1186/s13071-015-0764-y>
- Decastello A., Farkas R. 2010 Anaphylactic reaction following forest fly (*Hippobosca equina*) bite: A human case. Clinical and experimental medical journal 4: 193–198.
<https://doi.org/10.1556/CEMED.4.2010.1.19>
- Dehio C., Sauder U., Hiestand R. 2004 Isolation of *Bartonella schoenbuchensis* from *Lipoptena cervi*, a Blood-Sucking Arthropod Causing Deer Ked Dermatitis. Journal of Clinical Microbiology 42: 5320–5323.
<https://doi.org/10.1128/JCM.42.11.5320-5323.2004>
- Delmas E., Besson M., Brice M.-H., Burkle L.A., Dalla Riva G.V., Fortin M.-J., Gravel D., Guimarães P.R., Hembry D.H., Newman E.A., Olesen J.M., Pires M.M., Yeakel J.D., Poisot T. 2019 Analysing ecological networks of species interactions. Biological reviews of the Cambridge Philosophical Society 94: 16–36.
<https://doi.org/10.1111/brv.12433>
- Dibo N., Yang Y., Wu X., Meng F. 2022 A brief review on deer keds of the genus *Lipoptena* (Diptera: Hippoboscidae). Veterinary parasitology 313: 109850.
<https://doi.org/10.1016/j.vetpar.2022.109850>
- Dick C.W. 2018 Checklist of World Hippoboscidae (Diptera: Hippoboscoidea). Field Museum of Natural History, Chicago, 7 pp.

- Doszhanov T.N. 2003 Mukhi – krovososki (Diptera, Hippoboscidae) Palearktiki. Almaty, 280 pp. (In Russian)
- Dyk V., Schanzel H. 1964 Cudzopasníci jelenej zvery v Blatnickej doline (Veľká Fatra). Vlast. Zbor. Považia 6: 276–281. (In Slovakian)
- Frainer A., McKie B.G., Amundsen P.-A., Knudsen R., Lafferty K.D. 2018 Parasitism and the Biodiversity-Functioning Relationship. Trends in Ecology & Evolution 33: 260–268.
<https://doi.org/10.1016/j.tree.2018.01.011>
- Gaponov S.P., Tewelde R.T. 2020 Louse Flies (Diptera, Hippoboscidae) in Bird Nests in Voronezh Province. Entomological review 100: 763–767.
<https://doi.org/10.1134/S0013873820060044>
- Halos L., Jamal T., Maillard R., Girard B., Guillot J., Chomel B., Vayssier-Taussat M., Boulouis H.J. 2004 Role of Hippoboscidae flies as potential vectors of *Bartonella* spp. infecting wild and domestic ruminants. Applied and Environmental Microbiology 70: 6302–6305.
<https://doi.org/10.1128/AEM.70.10.6302-6305.2004>
- Hodžić A., Omeragić J., Alić A., Jažić A., Zuko A. 2012 *Lipoptena cervi* (Diptera: Hippoboscidae) in Roe deer (*Capreolus capreolus*). Veterinaria 61: 17–21.
- Hornok S., de la Fuente J., Biró N., Fernández de Mera I.G., Meli M.L., Elek V., Gönczi E., Meili T., Tánczos B., Farkas R., Lutz H., Hofmann-Lehmann R. 2011 First Molecular Evidence of *Anaplasma ovis* and *Rickettsia* spp. in Keds (Diptera: Hippoboscidae) of Sheep and Wild Ruminants. Vector borne and zoonotic diseases 11: 1319–1321.
<https://doi.org/10.1089/vbz.2011.0649>
- Hudson P.J., Dobson A.P., Lafferty K.D. 2006 Is a healthy ecosystem one that is rich in parasites? Trends in Ecology & Evolution 21: 381–385.
<https://doi.org/10.1016/j.tree.2006.04.007>
- Kaunisto S., Kortet R., Härkönen L., Härkönen S., Ylönen H., Laaksonen S. 2009 New bedding site examination-based method to analyse deer ked (*Lipoptena cervi*) infection in cervids. Parasitology research 104: 919–925.
<https://doi.org/10.1007/s00436-008-1273-0>
- Kočišová A., Lazar P., Letková V., Goldová M., Ciberej J., Čurlík J., Lukešová D. 2007 The species composition of the blood sucking Diptera (Tabanidae, Simuliidae) and Pupipara in deer breeding farm in East Slovakia. In: Book of Abstracts. 2nd International Symposium “Game and Ecology”, Plitvice Lakes National Park, October 17th to 20th October 2007. University of Zagreb, Faculty of Veterinary Medicine, Department for Game Biology, Pathology and Breeding, Zagreb (Croatia), pp. 21–22.
- Kortet R., Härkönen L., Hokkanen P., Härkönen S., Kaitala A., Kaunisto S., Laaksonen S., Kekäläinen J., Ylönen H. 2010 Experiments on the ectoparasitic deer ked that often attacks humans; preferences for body parts, colour and temperature. Bulletin of entomological research 100: 279–285.
<https://doi.org/10.1017/S0007485309990277>
- Kosoy M., Bai Y., Enscore R., Rizzo M.R., Bender S., Popov V., Albayrak L., Fofanov Y., Chomel B. 2016 *Bartonella melophagi* in blood of domestic sheep (*Ovis aries*) and sheep keds (*Melophagus ovinus*) from the southwestern US: Cultures, genetic characterization, and ecological connections. Veterinary microbiology 190: 43–49.
<https://doi.org/10.1016/j.vetmic.2016.05.009>
- Kowal J., Nosa P., Kornaś S., Wajdzik M., Matysek M., Basiaga M. 2016 Biodiversity and importance of hippoboscids infection in cervids. Medycyna Weterynaryjna 72: 745–749.
<https://doi.org/10.21521/mw.5602>
- Krištufík J. 1998 Louseflies (Diptera, Hippoboscidae) in the collections of František Balát. Acta Musei Moraviae, Scientiae biologicae 83: 211–216.
- Krištufík J., Štefan P. 1980 K poznaniu čelade Hippoboscidae (Diptera) na Slovensku. Biológia, Bratislava 35: 137–140.
- Labitzke V., Jentzsch M. 2019 Lausfliegenerfassungen während der Vogelberingung am Helmes-tausee Berga-Kelbra (Diptera, Hippoboscidae). Vogelwarte 57: 81–89.
- Laukkonen A., Ruoppi P., Mäkinen-Kiljunen S. 2005 Deer ked-induced occupational allergic rhinoconjunctivitis. Annals of Allergy, Asthma and Immunology 94 (5): 604–608.
[https://doi.org/10.1016/S1081-1206\(10\)61141-6](https://doi.org/10.1016/S1081-1206(10)61141-6)
- Le Guillou G., Chapelin-Viscardi J.-D. 2022 Découverte d'*Ornithomya comosa* (Austen, 1930) en Belgique et en France (Diptera Hippoboscidae). L'Entomologiste 78: 287–294.

- Liu D., Wang Y.-Z., Zhang H., Liu Z.-Q., Wureli H.-Z., Wang S.-W., Tu C.-C., Chen C.-F. 2016 First report of *Rickettsia raoultii* and *R. slovaca* in *Melophagus ovinus*, the sheep ked. Parasites & Vectors 9: 600.
<https://doi.org/10.1186/s13071-016-1885-7>
- Maa T.C. 1969 A revised checklist and concise host index of Hippoboscidae (Diptera). Pacific Insects Monograph 20: 261–299.
- Maślanko W., Bartosik K., Raszewska-Famielec M., Szwaj E., Asman M. 2020 Exposure of Humans to Attacks by Deer Keds and Consequences of Their Bites – A Case Report with Environmental Background. Insects 11: 859.
<https://doi.org/10.3390/insects11120859>
- Maślanko W., Szwaj E., Gazda M., Bartosik K. 2022 *Hippobosca equina* L. (Hippoboscidae: *Hippobosca*) – An Old Enemy as an Emerging Threat in the Palearctic Zone. International journal of environmental research and public health 19: 16978.
<https://doi.org/10.3390/ijerph192416978>
- Matito A., Bartolomé-Zavala B., Álvarez-Twose I., Sánchez-Matas I., Escrivano L. 2010 IgE-mediated anaphylaxis to *Hippobosca equina* in a patient with systemic mastocytosis. Allergy 65: 1058–1059.
<https://doi.org/10.1111/j.1398-9995.2009.02270.x>
- Matyukhin A.V., Zabashta A.V., Boyko E.A. 2016 *Ornithomya fringillina* (Diptera: Hippoboscidae) v Vostochnoy Yevrope. In: Skilsky I.V., Yuzik A.V. (eds) Regional Aspects of Floristic and Faunistic Research. Third International Scientific and Practical Conference, Chernivtsi (Ukraine), 13–14 May 2016. Druk Art, Chernivtsi, 266–269. (In Russian)
- McCabe R.A., Receveur J.P., Houtz J.L., Thomas K.L., Benbow M.E., Pechal J.L., Wallace J.R. 2020 Characterizing the microbiome of ectoparasitic louse flies feeding on migratory raptors. PloS one 15 (6): e0234050.
<https://doi.org/10.1371/journal.pone.0234050>
- Metelitsa A.K., Veselkin G.A. 1989 Parasitism of the louse fly *Lipoptena fortisetosa* on cattle. Parazitologija 23: 276–277.
<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2771435/>
- Mlynárová L., Korytár L., Manko P., Ondrejková A., Prokeš M., Smolák R., Oboňa J. 2023 Updated Taxonomic Key of European Nycteribiidae (Diptera), with a Host-Parasite Network. Diversity 15: 573.
<https://doi.org/10.3390/d15040573>
- Nartshuk E.P., Matyukhin A.V., Shapoval A.P., Markovets M.Y., Tolstenkov O.O. 2020 Louse Flies (Diptera, Hippoboscidae) on the Courish Spit (Kalinigrad Province, Russia). Entomological review 100 (2): 231–238.
<https://doi.org/10.1134/S0013873820020128>
- Nartshuk E.P., Matyukhin A.V., Shokhrin V.P. 2022a Parasitic Louse Flies (Diptera, Hippoboscidae) and Their Associations with Bird Hosts in the South of the Russian Far East. Entomological review 102: 367–376.
<https://doi.org/10.1134/S0013873822030083>
- Nartshuk E.P., Matyukhin A.V., Shokhrin V.P., Markovets M.Y. 2019 New records of ornithophilous louse-flies (Diptera: Hippoboscidae: Ornithomyinae) from the Russian Far East. Far Eastern entomologist 384: 15–20.
<https://doi.org/10.25221/fee.384.4>
- Nartshuk E.P., Yatsuk A.A., Matyukhin A.V., Shokhrin V.P. 2022b A new species of the genus *Ornithomya* (Diptera: Hippoboscidae) from the Far East. Zoosystematica rossica 31 (2): 190–194.
<https://doi.org/10.31610/zsr/2022.31.2.190>
- Nuñez M.A., Pauchard A., Ricciardi A. 2020 Invasion Science and the Global Spread of SARS-CoV-2. Trends in ecology & evolution 35 (8): 642–645.
<https://doi.org/10.1016/j.tree.2020.05.004>
- Oboňa J., Bazsalovicsová E.Č., Pintilioiae A.M., Dumitru V., Gavril O.C.V., Topală L.E., Manko P. 2023 Checklist of Hippoboscidae (Diptera) from Romania. Historia naturalis bulgarica 45: 229–238.
<https://doi.org/10.48027/hnb.45.092>
- Oboňa J., Fogašová K., Fulín M., Greš S., Manko P., Repaský J., Roháček J., Sychra O., Hromada M. 2022 Updated taxonomic keys of European Hippoboscidae (Diptera), with expansion in Central Europe of the bird louse fly *Ornithomya comosa* (Austen, 1930), first recorded from Slovakia. ZooKeys 1115: 81–101.
<https://doi.org/10.3897/zookeys.1115.80146>
- Oboňa J., Greš S., Krišovský P., Hromada M. 2021 Faunistic records and new parasite-host associations of Louse flies (Diptera: Hippoboscidae) from Sabinov, Slovakia. Biodiversity & Environment 13 (1): 74–79.

- Oboňa J., Krišovský P., Hromada M. 2019a Short-term faunistic sampling of Louse flies (Diptera: Hippoboscidae) from Drienovec Bird Ringing Station, Slovakia. *Biodiversity & Environment* 11 (2): 4–9.
- Oboňa J., Sychra O., Greš S., Heřman P., Manko P., Roháček J., Šestáková A., Šlapák J., Hromada M. 2019b A revised annotated checklist of louse flies (Diptera: Hippoboscidae) from Slovakia. *ZooKeys* 862: 129–152.
<https://doi.org/10.3897/zookeys.862.25992>
- Papp L., Kaufman G. 1989 Scatopsidae, Lauxaniidae, Diastatidae and Hippoboscidae (Diptera) of the Kiskunság National Park, Hungary. *Folia Entomologica Hungarica* 50: 111–117.
- Peña S.A., Alencastre-Santos A.B., da Silva J.B., Correia L.L., Urbieta G.L., Graciolli G., Palheta L.R., Vieira T.B. 2023 Bats (Mammalia, Chiroptera) and bat flies (Diptera, Streblidae) from the Cazumbá-Iracema and Chico Mendes Reserve, Western Brazilian Amazon. *Parasitology research* 122: 451–459.
<https://doi.org/10.1007/s00436-022-07741-y>
- Petersen F.T. 2004 Fauna Europaea: Hippoboscidae. In: Pape T. (ed.) *Fauna Europaea: Diptera, Brachycera*.
<http://www.faunaeur.org>
- Pfadt R.E., Roberts I.H. 1978 Louse flies (family Hippoboscidae). In: Bram R.A. (ed.) *Surveillance and collection of arthropods of veterinary importance*. Agriculture Handbook No. 518, U.S. Department of Agriculture, 60–71.
- Poisot T., Bergeron G., Cazelles K., Dallas T., Gravel D., MacDonald A., Mercier B., Violet C., Vissault S., Chapman D. 2021 Global knowledge gaps in species interaction networks data. *Journal of Biogeography* 48 (7): 1552–1563.
<https://doi.org/10.1111/jbi.14127>
- Poon E.S.K., Chen G., Tsang H.Y., Shek C.T., Tsui W.C., Zhao H., Guénard B., Sin S.Y.W. 2023 Species richness of bat flies and their associations with host bats in a subtropical East Asian region. *Parasites & vectors* 16: 37.
<https://doi.org/10.1186/s13071-023-05663-x>
- Povolný D., Rosický B. 1955 Faunisticko-bionomický nástín klošovitých (Hippoboscidae, Diptera) z území ČSR. *Zoologické a entomologické listy* 4: 5–20.
- Proesmans W., Albrecht M., Gajda A., Neumann P., Paxton R.J., Pioz M., Polzin C., Schweiger O., Settele J., Szentgyörgyi H., Thulke H.-H., Vanbergen A.J. 2021 Pathways for Novel Epidemiology: Plant–Pollinator–Pathogen Networks and Global Change. *Trends in Ecology & Evolution* 36: 623–636.
<https://doi.org/10.1016/j.tree.2021.03.006>
- Quercia O., Emiliani F., Foschi F.G., Stefanini G.F. 2005 Anaphylactic reaction after *Hippobosca equina* bite. *Alergología e inmunología clínica* 20: 31–33.
- Reeves W.K., Lloyd J.E. 2019 Louse flies, keds, and bat flies (Hippoboscoidea). *Medical and Veterinary Entomology* 20: 421–438.
<https://doi.org/10.1016/B978-0-12-814043-7.00020-0>
- Rekecki T., Rajkovic D. 2023 Diversity and prevalence of ornithophilic louse flies (Diptera: Hippoboscidae: Ornithomyinae) in Serbia. *Turkish Journal of Zoology* 47 (4): 261–267.
<https://doi.org/10.55730/1300-0179.3138>
- Robertson B.A., Hutto R.L. 2006 A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87: 1075–1085.
[https://doi.org/10.1890/0012-9658\(2006\)87\[1075:AFFUET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2)
- Roháček J. 1995 Hippoboscidae. In: Roháček J., Starý J., Martinovský J., Vála M. (eds) *Diptera Bukovských vrchov. SAŽP – Správa CHKO a BR Východné Karpaty*, Humenné, 193 pp.
- Roháček J. 2009 Hippoboscidae. In: Roháček J., Ševčík J. (eds) *Diptera of the Poľana Protected Landscape Area – Biosphere Reserve (Central Slovakia)*. SNC SR, Administration of the PLA – BR Poľana, Zvolen, 285 pp.
- Runghen R., Poulin R., Monlleó-Borrull C., Llopis-Belenguer C. 2021 Network Analysis: Ten Years Shining Light on Host–Parasite Interactions. *Trends in Parasitology* 37 (5): 445–455.
<https://doi.org/10.1016/j.pt.2021.01.005>
- Santolíková A., Brzoňová J., Čepička I., Svobodová M. 2022 Avian Louse Flies and Their Trypanosomes: New Vectors, New Lineages and Host–Parasite Associations. *Microorganisms* 10 (3): 584.
<https://doi.org/10.3390/microorganisms10030584>
- Sato S., Kabeya H., Ishiguro S., Shibasaki Y., Maruyama S. 2021 *Lipoptena fortisetaosa* as a vector of *Bartonella* bacteria in Japanese sika

- deer (*Cervus nippon*). Parasites & Vectors 14: 1–10.
<https://doi.org/10.1186/s13071-021-04585-w>
- Straka V. 1981 Entomologické zaujímavosti v zbierkach Turčianského múzea Andreja Kmet'a. Z minulosti a prítomnosti Turca 5: 177–179.
- Straka V. 2001 Dvojkrídlovce (Diptera) v Národnej prírodnej rezervácii Rozsutec v Národnom parku Malá Fatra. Naturaе tutela 6: 81–100.
- Straka V. 2005a Dvojkrídlovce (Diptera) Prírodnej pamiatky Krasín v Bielych Karpatoch. Naturaе tutela 9: 79–86.
- Straka V. 2005b Súčasné poznatky o faune dvojkrídleho hmyzu (Diptera) Veľkej Fatry. Zborník SNM. Prírodné vedy 51: 67–70.
- Straka V. 2010 The Flies (Diptera) of the Žalostiná massif in the Protected Landscape Area Biele Karpaty Mts (West Slovakia). Naturaе tutela 14 (1): 55–73.
- Straka V. 2011 K poznaniu dvojkrídlovcov (Diptera) širšieho okolia Vršateckých bradiel. Naturaе tutela 15 (1): 39–63.
- Straka V. 2016 Fauna dvojkrídleho hmyzu (Diptera) v oblasti Cerovej vrchoviny na Južnom Slovensku. Naturaе tutela 20 (2): 149–173.
- Straka V., Majzlán O. 2008 Dvojkrídlovce (Diptera) prírodnej rezervácie Ľutovský Drieňovec v južnej časti Strážovských vrchov. Rosalia 19: 183–202.
- Straka V., Majzlán O. 2010 Dynamics of the flies abundance (Diptera) in the National Nature Reserve Bábsky les near Nitra (South Slovakia). Rosalia 21: 167–184.
- Straka V., Majzlán O. 2014 Dvojkrídlovce (Diptera) Nitrických vrchov v južnej časti Strážovských vrchov. Naturaе tutela 18/1: 79–105.
- Straka V., Majzlán O. 2016 Dvojkrídlovce (Diptera) pohoria Burda. Ochrana prírody 27: 89–125.
- Su M., Jiang Z., Hui C. 2022 How Multiple Interaction Types Affect Disease Spread and Dilution in Ecological Networks. Frontiers in Ecology and Evolution 10: 466.
<https://doi.org/10.3389/fevo.2022.862986>
- Sychra O., Literák I., Podzemný P., Benedikt V. 2008 Insect ectoparasites from wild passerine birds in the Czech Republic. Parasite 15 (4): 599–604.
<https://doi.org/10.1051/parasite/2008154599>
- Sychra O., Symes C.T., Oschadleus H.D., Halajian A., Engelbrecht D., De Swardt D.H., Papousek I. 2020 Louse-flies (Diptera: Hippoboscidae) of birds from South Africa: prevalence and diversity. African Entomology 28 (2): 249–261.
<https://doi.org/10.4001/003.028.0249>
- Szewczyk T., Werszko J., Steiner-Bogdaszewska Ž., Jeżewski W., Laskowski Z., Karbowiak G. 2017 Molecular detection of *Bartonella* spp. in deer ked (*Lipoptena cervi*) in Poland. Parasites & Vectors 10: 487.
<https://doi.org/10.1186/s13071-017-2413-0>
- Thalhammer J. 1899 Ordo Diptera. Fauna regni Hungariae, III. Animalium Hungariae hucusque cognitorum enumeratio systematica. Edidit regia societas scientiarum naturalium Hungarica. Akadémiai Kiadó, Budapest, 76 pp.
- Theodor O., Oldroyd H. 1964 Hippoboscidae. In: Lindner E. (ed.) Die Fliegen der Palaearktischen Region 12: 1–70.
- Tiawsirisup S., Yurayart N., Thongmeesee K., Sri-In C., Akarapas C., Rittisornthanoo G., Bunphungbaramee N., Sipraya N., Maikaew U., Kongmakee P., Saedan A. 2023 Possible role of *Lipoptena fortisetosa* (Diptera: Hippoboscidae) as a potential vector for *Theileria* spp. in captive Eld's deer in Khao Kheow open zoo, Thailand. Acta Tropica 237: 106737.
<https://doi.org/10.1016/j.actatropica.2022.106737>
- Víchová B., Majláthová V., Nováková M., Majláth I., Čurlík J., Bona M., Komjáti-Nagyová M., Peťko B. 2011 PCR detection of re-emerging tick-borne pathogen, *Anaplasma phagocytophilum*, in deer ked (*Lipoptena cervi*) a blood-sucking ectoparasite of cervids. Biológia 66 (6): 1082–1086.
<https://doi.org/10.2478/s11756-011-0123-1>
- Vidal C., Armisén M., Bartolomé B., Rodriguez V., Luna I. 2007 Anaphylaxis to *Hippobosca equina* (louse fly). Annals of Allergy, Asthma & Immunology 99 (3): 284–286.
[https://doi.org/10.1016/S1081-1206\(10\)60666-7](https://doi.org/10.1016/S1081-1206(10)60666-7)
- Walter G., Kasparek M., Tschirnhaus M. 1990 Zur Lausfliegenfauna (Diptera, Hippoboscidae) der Vögel in der Bundesrepublik Deutschland. Ökol. Vögel 12: 73–83.
- Werszko J., Steiner-Bogdaszewska Ž., Jeżewski W., Szewczyk T., Kuryło G., Wołkowycki M., Wróblewski P., Karbowiak G. 2020 Molecular detection of *Trypanosoma* spp. in *Lipoptena cervi* and *Lipoptena fortisetosa* (Diptera: Hippoboscidae) from deer in Poland. Parasites & Vectors 13: 1–10.

- dae) and their potential role in the transmission of pathogens. *Parasitology* 147 (14): 1629–1635.
<https://doi.org/10.1017/S0031182020001584>
- Werszko J., Świsłocka M., Witecka J., Szewczyk T., Steiner-Bogdaszewska Ż., Wilamowski K., Asman M. 2022 The New Haplotypes of *Bartonella* spp. and *Borrelia burgdorferi* Sensu Lato Identified in *Lipoptena* spp. (Diptera: Hippoboscidae) Collected in the Areas of North-Eastern Poland. *Pathogens* 11 (10): 1111.
<https://doi.org/10.3390/pathogens11101111>
-
- Zhao L., Wang J., Ding Y., Li K., He B., Li F., Zhang L., Li X., Liu Y. 2020 *Theileria ovis* (Piroplasmida: Theileriidae) Detected in *Melophagus ovinus* (Diptera: Hippoboscoidea) and *Ornithodoros lahorensis* (Ixodida: Argasidae) Removed From Sheep in Xinjiang, China. *Journal of Medical Entomology* 57: 631–635.
<https://doi.org/10.1093/jme/tjz193>

Appendix 1

Study sites

Slovakia	
Bachureň	49°03'50.1"N 20°55'15.0"E
Beckov	48°46'35.7"N 17°54'32.3"E
Bikoš	49°01'26.1"N 21°13'13.6"E
Boldigáň	49°03'10.2"N 20°53'50.2"E
Bolešov	48°58'45.4"N 18°09'07.3"E
Červený Kláštor	49°23'15.3"N 20°23'49.2"E
Dreveník, yellow marked hiking trail, Spiš Basin	48°59'16.5"N 20°46'31.8"E
Drienovec	48°36'54.5"N 20°54'54.7"E
Holičov vrch hill, Myjava hills	48°44'05.0"N 17°32'57.1"E
Horné Seče	48°51'30.4"N 17°11'14.1"E
Hromoš, Poprad river	49°15'50.8"N 20°48'29.2"E
Chočské vrchy hills	49°07'07.7"N 19°22'01.7"E
Košice	48°43'14.5"N 21°15'20.9"E
Lakšárska Nová Ves, nr. Zelenka Nature Reserve and Červený rybník Nature Reserve	48°35'56.3"N 17°09'34.7"E
Levočské vrchy mountains	49°03'20.1"N 20°39'50.9"E
Plavecký Mikuláš, nr. Malacky	48°32'31.0"N 17°13'06.5"E
Prešov	48°59'58.0"N 21°13'04.0"E
Rajtopíky, Branisko	48°59'43.3"N 20°51'59.0"E
Rudník	48°43'09.9"N 21°00'34.8"E
Rudno nad Hronom railway station, the Štiavnica mountains	48°26'05.6"N 18°40'54.7"E
Ruská Nová Ves	48°58'13.1"N 21°19'23.8"E
Sabinov – garden	49°06'18.7"N 21°05'49.0"E
Sabinov Bird Ringing Station	49°06'02.5"N 21°04'27.4"E
Sedlo Zakruty saddle – above the valley Kopytovská dolina	49°03'36.0"N 20°54'12.0"E
Sokol (path under), Chočské vrchy hills	49°08'22.4"N 19°18'06.4"E
Studienka, nr. Malacky	48°32'48.3"N 17°12'41.5"E
Šalková, the Zvolen Basin	48°43'55.4"N 19°14'12.6"E
Šranecké piesky	48°32'48.3"N 17°12'41.5"E
The Slovak Karst, Plešivec, green marked hiking trail from the cave Gambasecká jaskyňa to Plešivec	49°03'24.2"N 20°55'00.3"E
Tichý Potok	49°08'22.8"N 20°48'30.5"E
Uzovský Šalgov	49°05'34.8"N 21°04'00.8"E
Vanišovec Nature Reserve, nr Šaštín	48°36'30.9"N 17°08'26.8"E
Vyšná Olšava	49°09'30.9"N 21°35'26.0"E
Zelenka Nature Reserve, nr Lakšárska Nová Ves	48°36'03.4"N 17°09'27.0"E
Zlaté Kopyto, valley Kopytovská dolina	49°03'27.3"N 20°54'56.1"E

Poland	
Beskid Źywiecki	49°41'31.0"N 19°22'45.1"E
Czech Republic	
Kyselka	50°15'31.6"N 12°59'40.8"E
Spáňov, nr. Domažlice les forest	49°25'25.8"N 12°58'06.5"E
Příčovy, nr. Chlumečník hill	49°40'23.6"N 14°22'29.9"E