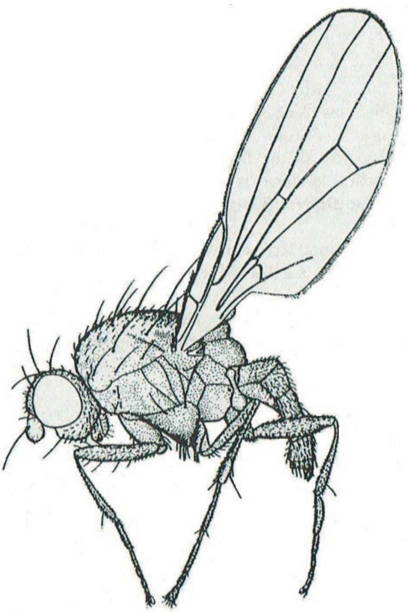
Dipterists Digest

2022 Vol. 29 No. 1

Cover illustration: *Brachyopa panzeri* Goffe, 1945 (Syrphidae) male, 16 May 2014, and (above) ovipositing female, 18 May 2014: Jaegersborg Hegn, Naerum north of Copenhagen, Denmark © Ruth Ahlburg. This species is the subject of the article by Leif Bloss Carstensen (pages 39-43).

Dipterists Digest



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Dipterists Digest is the journal of the **Dipterists Forum**. It is intended for amateur, semi-professional and professional field dipterists with interests in British and European flies. All notes and papers submitted to Dipterists Digest are refereed. Articles and notes for publication should be sent to the Editor at the above address, and should be submitted with a current postal and/or e-mail address, which the author agrees will be published with their paper. Articles must not have been accepted for publication elsewhere and should be written in clear and concise English. **Contributions should be supplied either as E-mail attachments or on CD in Word or compatible formats.**

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- records and assessments of rare or scarce species and those new to regions, countries etc.;
- local faunal accounts and field meeting results, especially if accompanied by ecological or natural history interpretation;
- descriptions of species new to science;
- notes on identification and deletions or amendments to standard key works and checklists.

Articles should be in A5 format with text in 9-point and Times New Roman font, title 12 point and author's name 10.5 point, with 1.27cm (narrow) side margins. Figures should be drawn in clear black ink, about 1.5 times their printed size and lettered clearly. Colour photographs will also be welcomed. Figures and photographs should be supplied separately as hard copy or as jpegs at 300dpi.

Style and format should follow articles published in recent issues. A short Summary (in the form of an Abstract) should be included at the beginning of each article. References to journals should give the title of the journal in full. **Scientific names should be italicised.** Authors of scientific names should be given in full and nomenclature should follow the most recent checklist, unless reflecting subsequent changes. Descriptions of new species should include a statement of the museum or institution in which type material is being deposited.

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Dipterists Digest 2022 **29,** 1-5

Phoretic mites on *Ula sylvatica* (Meigen) (Diptera, Pediciidae) show a preference for female craneflies

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Summary

A phoretic mite, *Zerconopsis* sp., was found to have a distinct preference for female *Ula sylvatica* (Meigen, 1818) craneflies emerging from the bracket fungus *Laetiporus sulphureus* (= *Grifola sulphurea*). It is concluded that this gives the mites an advantage in locating a new breeding site.

Introduction

Mites are regularly seen on Diptera, though records are relatively sparse, perhaps because the identification of mites is so difficult. One of the few reviews of mites on British Diptera is given by Ostoja-Starzewski (2010). Probably, most mites observed on Diptera are phoretic, though some mites are parasitic in their larval stages (e.g. water mites on mosquitoes: Medlock and Snow 2008, Bortolon *et al*. 2016). Phoresy is where one organism attaches to another for dispersal or more comprehensively "a phenomenon in which one organism (the phoretic or phoront) receives an ecological or evolutionary advantage by migrating from the natal habitat while superficially attached to a selected interspecific host for some portion of the individual phoretic's lifetime" (Houck and O'Connor 1991). Phoresy fits within a formal definition of 'migration' according to Binns (2008).

As part of a study on the Diptera developing in fungi, the pediciid cranefly *Ula sylvatica* (Meigen, 1818) was reared from the large bracket fungus *Laetiporus sulphureus* ('chicken of the woods'). It was noticed that some flies had mites attached (Fig. 1) and preliminary examination indicated that females had more mites than males. To test whether this was in fact the case, all subsequent *U. sylvatica* emerging from samples of the fungus were examined in detail for mites.

Ula is a common and widespread genus known to develop in fungi (Buxton 1960; Chandler 2010, p. 431), summarised in Kramer (2017).

Methods

Three pieces of the large fungus *Laetiporus sulphureus* (= *Grifola sulphurea*), weighing 126g, 99g and 98g, respectively, were collected from the base of a standing oak tree (*Quercus robur*) at Ashclyst Forest (SY001999), near Tiverton in Devon, UK on 20 June 2020. The pieces of fungus were kept separately in ventilated, 1 litre plastic containers on peat-free potting compost. The fungi were examined regularly for emerging flies over a period of 160 days. Flies emerging from day 44 onwards were collected individually with a large bore aspirator (7mm diameter) to minimise the impact of handling and each fly was transferred directly into individual vials of 70% ethanol. This ensured that any mites on an individual fly were captured in the alcohol (about 50% of the mites detached from their host and were found in the alcohol). Mites adhering to the fly as well as in the surrounding alcohol were then counted.

Craneflies were identified using an unpublished key to Pediciidae by John Kramer (based on a key by Alan Stubbs) and Kramer (2017). Genitalia preparations were made to confirm the identification.

Fig. 1. Female *Ula sylvatica* with phoretic mites (*Zerconopsis* sp.).

Results

The mites were identified as *Zerconopsis* sp. (Mesostigmata: Family Ascidae), probably *Z. remiger* (Kramer, 1876) by Jozef Ostoja-Starzewski. *Zerconopsis* species are characterised by specialised oar-shaped setae on the dorsal shield. A description of the mite and some British records is given by Evans and Hyatt (1960, pp 91-93). Species of *Zerconopsis* have been found on bracket fungi before and are thought to be 'general mycobionts' by Makarova (2004) rather than dendrobionts or litter dwellers, although they have been sporadically recorded from 'leaf litter, logs and soil'. Unidentified *Zerconopsis* deutonymphs have been found on Sphaeroceridae (Samsinak 1989) in Zaire. Several other members of the mite family Ascidae have been found on Diptera in Britain (Ostoja-Starzewski 2010). As the mites were adults, rather than immature stages, it is assumed that the relationship between the mites and their dipteran 'host' or vector is phoretic.

Craneflies started to emerge from day 29 to day 103 after the fungi samples were collected (examined until day 160) (Fig. 2). This gives a minimum development time of 30 days from egg to adult (the samples were not examined on collection for signs of *Ula* larvae). It is possible that the later emergence was an F1 generation from flies emerging early in the experiment because males and females copulated freely in the rearing containers. The peak male emergence preceded females, as has been seen often in other Diptera groups emerging from fungi (unpublished data).

A total of 25 males and 41 female *U. sylvatica* emerged from the three pieces of sporophore over the observation period. Of these, only 2 of the 25 males had mites, whereas 23 of the 41 females had mites, giving an infestation rate of 8% and 56% respectively. A total of only 4 mites was recovered from the 2 infested males but a remarkable total of 158 mites was recovered from the 23 infested females.

Table. Showing the distribution of mites between male and female *Ula sylvatica* emerging from samples of the fungus *Laetiporus sulphureus*.

Mites per fly	0	1	2	3	4	5	6	7	9	11	13	14	17	18	23
No. of males	23	1	0	1	0	0	0	0	0	0	0	0	0	0	0
No. of females	18	5	5	0	2	1	1	1	1	1	1	1	2	1	1

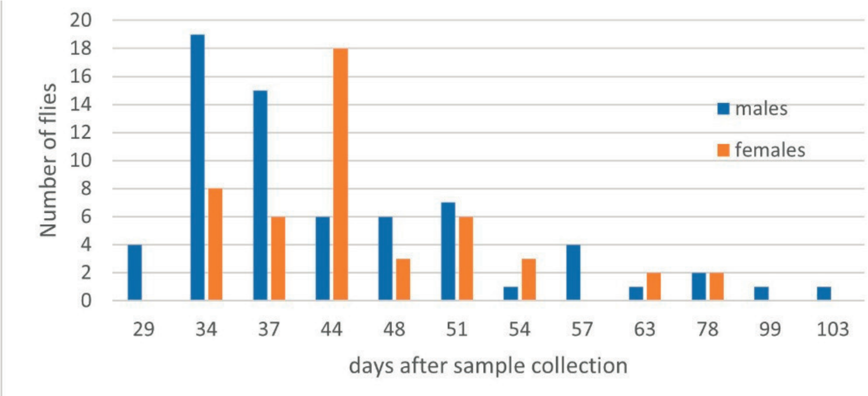

Fig. 2. Emergence of *Ula sylvatica* from samples of the fungus *Laetiporus sulphureus*.

The number of mites per female (= load) ranged from only 1 to a maximum of 23 and for males was 1 to a maximum of 3. The average load was 3.8 mites/fly for all females (n=41) and 0.16 mites/fly for all males (n=25).

Mites attached to hosts were always on the abdomen, not on the thorax or legs. Although not all mites were identified individually, it appeared that they were all the same species. A few immature mites (6-legged) were observed but could not be collected consistently for analysis.

Five ♂ and two ♀ *U. sylvatica* were also reared from the bracket fungus *Cerioporus* (= *Polyporus*) *squamosus* but only 1♀ had a mite (3 samples, various Devon localities). A few mites were seen in the alcohol into which a pool of other flies emerging from the *Laetiporus sulphureus* samples were collected, mainly Drosophilidae, indicating that *U. sylvatica* is not the only host for this mite species. In a pool of *Hirtodrosophila cameraria* (Haliday) (Drosophilidae) reared from *Amanita rubescens*, collected in Ausewell Woods, Devon, 8♀ had 1-5 attached mites per fly, 3♀ had no mites and the 3♂ did not have mites; 10 detached mites were found in the alcohol pool.

Discussion

There have been relatively few quantitative studies of phoretic mites on Diptera. McGarry and Baker (1997) found several mite species on *Stomoxys calcitrans* (Linnaeus) in Britain, with mean infestation rates for all mite species, over the entire sampling period of 31.6 ± 13.9% and 19.8 ± 3.6% for two sites respectively. During the peak abundance in July, 51% of flies found around cattle were infested with mites. More relevant to the present study, Navarro *et al.* (2019) examined the role played by phorids (*Megaselia halterata* (Wood)) and sciarids (*Lycoriella auripila* (Winnertz)) in the phoretic dispersal of a myceliophagous mite (*Microdispus lambi* (Krczal)) in commercial mushroom farms in Spain. They found that 19.6% of phorids and 4.4% of sciarids carried mites with a mean load of 3.4 and 1.9 mites/fly respectively. Both male and female phorids carried mites with only a very slight, but statistically significant, preference for females (1.86 mites/female versus 1.84 /male). This contrasts with the result here, where there was a marked difference in both the sexual preference for the host by the mites and the infestation rates.

When comparing infestation rates, it needs to be noted that Navarro *et al.* (2019) examined dead flies weekly from a light trap, where the mites could have left the fly corpses and therefore giving an underestimate of the true infestation rate, load and sexual preference (though the experimental bias might be similar for both males and females). In contrast, in the present study live individual flies were collected into separate tubes and the total number of mites found attached and in the surrounding alcohol were counted, making a more accurate measurement of infestation rates and load.

The impact of the mite loads on the flight ability of female *U. sylvatica*, especially the higher loads of 10 or more, was not specifically examined but the heavily infested individuals were noticeably less mobile in the small 1 litre rearing containers than other females. Beresford and Sutcliffe (2009) concluded that heavy mite infestations reduced the dispersal of *Stomoxys calcitrans*.

Navarro *et al.* (2019) found more mites on their phorid host later in the development of the mushroom crop than in the early stages, but it tapered off as the crop matured. In the present study there was a slight decrease in the number of mites on craneflies (data not presented), but numbers were too low to be reliably analysed.

How these results relate to the situation in the wild is difficult to estimate, as Buxton (1960) noted for his study on Diptera reared from a very wide range of fungi, although the sexual preference for females is very likely to be a real phenomenon. The finding of mites on female *Hirtodrosophila* reared from the *L. sulphureus* samples, gives an indication that the preference for female hosts might be a more common phenomenon for mites on fungivorous Diptera.

The advantage of mites attaching to females is presumably to maximise their chances of being transferred to a new breeding site, which the mites can colonise when the female cranefly locates a suitable fungus for oviposition. This ecological advantage is particularly important for temporary or transient habitats, such as carrion and dung, where mites have developed many life history adaptations (see Perotti and Braig 2009, p. 88). Many fungal sporophores clearly fall into this transient habitat category, including the soft tissue bracket fungi such as *L. sulphureus,* whereas the more robust and much longer lived bracket fungi might not. Navarro *et al.* (2019) considered the slight preference for females by the mites is simply because the male phorids were smaller than females rather than an adaptation to maximise dispersal and locate new breeding sites (fungi). Bortolon *et al.* (2016) however, considered that mites (trombidiformids) attached themselves preferentially to female mosquitoes to migrate to breeding sites.

These findings raise many further questions such as, when do mites attach to the females (as they emerge?) and how do they distinguish between male and female craneflies?

Acknowledgements

I am particularly grateful to Jozef Ostoja-Starzewski (Fera Science, York, UK) for undertaking the difficult task of identifying the mites. I also thank Nicola Bacciu (mycologist, Exeter) for identifying the fungus, Fiona Hailstone of the National Trust for permission to collect at Ashclyst Forest and Rob Wolton for arranging the Devon Fly Group meeting at Ashclyst when the original sample was collected.

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Calliphora uralensis **Villeneuve (Diptera, Calliphoridae) at the Bass Rock –** Murdo Macdonald reported the presence of *Calliphora uralensis* at the Bass Rock in 2018 (Macdonald, M. 2018. *Dipterists Digest* (*Second Series*) **25,** 143), following his record the previous year at nearby North Berwick (Macdonald, M. 2017. *Dipterists Digest* (*Second Series*) **24,** 164). On a recent trip by DS around the Bass Rock (NT600872, 22.vi.2021), well known for its large colonies of gannets (*Morus bassanus* (Linnaeus, 1758)), guillemots (*Uria aalge* (Pontoppidan, 1763)), razorbills (*Alca torda* Linnaeus, 1758), and kittiwakes (*Rissa tridactyla* Linnaeus, 1758), many flies appeared on board as the boat approached the island. Conspicuous among these flies were several orange-faced calliphorids, of which after many attempts, one was caught by hand, subdued and identified as a female *Calliphora uralensis* Villeneuve, 1922 (specimen donated to the Natural History Museum, London). Apart from a 1969 record from Ailsa Craig, this is the most southerly site for the species and it appears to be well-established **– DONALD SMITH,** Garden Cottage, Clerkington, Haddington EH41 4NJ, and **OLGA SIVELL,** 96 Hollybush Road, Luton LU2 9HQ

Dipterists Digest 2022 **29,** 6-8

Phytomyza paraciliata (Godfray) (Diptera, Agromyzidae) new to Italy

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Summary

The leaf mining fly *Phytomyza paraciliata* (Godfray, 1985) (Diptera, Agromyzidae) is reported as a species new to Italy, based upon a single male within Malaise trap material.

Introduction

During early 2020, I was sent several vials [by Dutch dipterist Ruud van der Weele] of unidentified Agromyzidae specimens from Malaise traps operated in Italy and the Netherlands. Upon examination of the Italian material, one male was noticeable owing to the distinct pubescence on the third antennal segment. Using the keys of Spencer (1972, 1976) and Papp and Černý (2019), no species agree with the male discussed here.

Dissection and examination of the genitalia placed the specimen in the *Phytomyza robustella*-group in which it was included by von Tschirnhaus (2021), owing to the typical structures of the phallus, first depicted by Griffiths (1964). Comparison of the phallus with all other known Palaearctic species of the *robustella*-group [*P. achilleaececis* Süss, 1984; *P. araciocecis* Hering, 1957; *P. buhriella* Spencer, 1969; *P. cecidonomia* Hering, 1937; *P. ciliata* Hendel, 1935; *P. cinerea* Hendel, 1920; *P. continua* Hendel, 1920; *P. farfarae* Hendel, 1935; *P. ferina* Spencer, 1971; *P. flaviventris* Zetterstedt, 1848; *P. gilva* Spencer, 1971; *P. hasegawai* Sasakawa, 1981; *P. hedingi* Rydén, 1953; *P. meridionalis* Spencer, 1972; *P. paraciliata* Godfray, 1985; *P. penicilla* Hendel, 1935; *P. picridocecis* Hering, 1957; *P. rhabdophora* Griffiths, 1964; *P. robustella* Hendel, 1936; *P. rufescens* von Roser, 1840; *P. wahlgreni* Rydén, 1944] suggested *P. paraciliata* (Godfray, 1985); when compared to reared *P. paraciliata* material within my private collection, the phallus and external morphology were conspecific with the Italian specimen, therefore confirming the species as *P. paraciliata*. This record represents the first known occurrence of the species in Italy.

Identification

Described by Godfray (1985) on the basis of adults reared from larval leaf mines on *Leucanthemum vulgare*. A medium-sized *Phytomyza* species, wing length 2.3mm-2.5mm. Two *ors*, two *ori* [lower weaker] usually present, third antennal segment with distinct pubescence, all antennal segments dark. Frons and orbits yellow, face and palps grey with all antennal segments dark grey. Mesonotum with 3+1 *dc*, *acr* in two rows. All legs dark, with all knees yellowish. Male genitalia (Fig. 1) with hypophallus poorly sclerotised, sclerites of basiphallus thickened in middle. Distiphallus with paired tubules well developed but the right one masked in lateral view.

Biology

Egg is laid on lower surface of the leaf, larva forming a long, linear corridor, which often crosses itself, initially lower surface then mostly upper surface. Frass in discrete, widely spaced, grains. The mine is identical to those created by *Chromatomyia horticola* (Goureau, 1851) and *C. syngenesiae* Hardy, 1849. Pupariation occurs within the mine; puparium whitish, posterior spiracles with c7 minute bulbs.

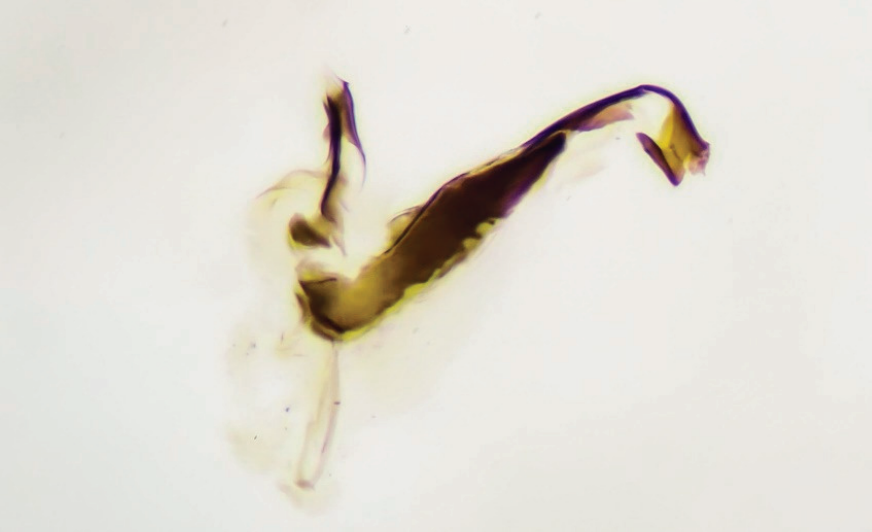

Fig. 1. ***Phytomyza paraciliata*** **(Godfray, 1985) phallus in left lateral view.**

Fig. 2. Collection site; Pantano di Montalto, Italy.

Distribution

Described from Southern England, *P. paraciliata* is also known from Serbia (von Tschirnhaus 2021), Spain and Switzerland (Černý and Bächli 2018). The male was obtained from a Malaise trap, situated in Pantano di Montalto [‘I. Calabria, Samo (RC), Pantano di Montalto – Bosco di Fagus, 06.vi.2018, 38°09'25.31"N, 15°54'55.95"E, alt. 1.812, leg. Castiglione, E. & Manti, F.’], a territory of the Aspromonte National Park, Reggio Calabria. The locality biotope is a marshy, grass area within a shrub and forest covered mountain plain, with a c30° slope (Fig. 2).

Acknowledgements

I would like to thank Elvira Castiglione for providing collection site details and permitting me to use her photograph (Fig. 2).

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Dipterists Digest 2022 **29,** 9-13

Two *Ophiomyia* Braschnikov (Diptera, Agromyzidae) species new to Germany, with a new larval host detected

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Summary

Two stem-mining agromyzids, *Ophiomyia spenceri* Černý*,* 1985 and *Ophiomyia ungarensis* Černý, 2015 (Diptera, Agromyzidae), are reported as species new to Germany based upon specimens reared from the stems of brown knapweed (*Centaurea jacea*) and teasel (*Dipsacus fullonum*) respectively. *Dipsacus* (Caprifoliaceae) is detected for the first time as the larval host plant genus of *O. ungarensis*.

Introduction

In November 2020, I was sent several reared Agromyzidae specimens for determination by F. Hannes Veihelmann, a student in Germany whose bachelor thesis is titled 'Diversity of hibernating insects in the stems and flower heads of selected herbaceous plants in Southwestern Germany'. In March and April 2020, Mr Veihelmann collected c. 5,000 stems of herbaceous plants [62 species in total]; all leaves were removed, sorted into species, wrapped in tubular film and placed in an unheated outbuilding. The resulting emergent insects were collected in August. Detailed examination of material reared from *Centaurea jacea* proved to be *Ophiomyia spenceri* Černý, 1985, with *Ophiomyia ungarensis* Černý, 2015 being successfully reared from the stems of *Dipsacus fullonum*, representing the first known record of each species in Germany.

Ophiomyia spenceri Černý, 1985

Introduction

Brown knapweed (*Centaurea jacea*) stems were collected, on 5 March 2020, from a small meadow between a country road and cycle lane (Fig. 2), adjacent to an agricultural field near Dettingen, on the 'Bodanrück' area near Lake Constance, 47.737329, 9.103140, south Germany. On 4 August 2020, all reared insects were collected from the bags containing *C. jacea* stems.

Upon initial examination of the reared material (2m, 1f), only one genus was present, *Ophiomyia* Braschnikov, a genus known chiefly as external stem miners. Using the key of Papp and Černý (2015), the males ran readily to couplet 35: *O. mohelensis* Černý, 1994 or *O. spenceri* Černý, 1985. Owing to the specimens possessing acrostichals [*acr*] in 8 rows and a flat facial keel, *O. spenceri* was the determination [confirmed by examination of male phallus, Fig. 1], representing the first known record for the species in Germany.

Identification

A relatively small species, wing length 1.8-2.0mm, male with vibrissal angle of 70°, long vibrissal fasciculus with gradually upcurved tip. Orbits not projecting above eye in profile, orbital setulae sparse, two *ors* and two *ori* [second weaker or sometimes absent on one side] usually present. Frons broad, 1.5-1.7x broader than eye. Antennae separated by a broad and arched facial keel, which possesses a distinct mid-groove in the upper third. Mesonotum finely shining, with two strong dorsocentrals [*dc*], the second shorter, *acr* in 8 rows to level of second *dc*. Wings normal, hyaline, costa ending at vein M_{1+2}, veins and base of wing brown. All legs dark brown.

Female lacking vibrissal horn, with only a simple vibrissal seta developed [typical for all female *Ophiomyia*]. All other features agree with male.

Male distiphallus (Fig. 1) distinctive, basiphallus v-shaped.

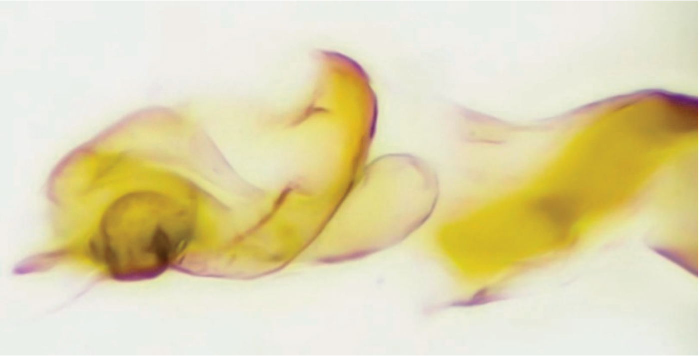

Fig. 1. ***Ophiomyia spenceri*** **Černý, 1985 distiphallus in left lateral view.**

Fig. 2. Collection site, near Dettingen; small meadow area where *Centaurea jacea* stems were obtained.

Biology

The larva forms an external stem mine, under the epidermis in the lower part of the stem, on *Achillea millefolium* and *Centaurea jacea* [Asteraceae]. Posterior spiracles on a short base, with 8-10 bulbs. Puparium black, with a metallic blue sheen, dorso-ventrally flattened. Length 2.5mm.

Distribution

Ophiomyia spenceri was described by Černý (1985) on the basis of adults reared from the stems of *C. jacea* in the Czech Republic. The species has subsequently been recorded from Hungary (Papp and Černý 2015), Lithuania (Pakalniškis 1994), Slovakia (Černý 2012) and Ukraine (Guglya 2012).

Additional comments

Centaurea jacea was the only plant sampled at the site near Dettingen; no other plants had remained through the winter, resulting in the area being rather ‘poor’. Along with *O. spenceri*, two parasitoid Chalcidoidea wasps were also successfully reared from *C. jacea* stems; an *Aprostocetus* sp. and a *Chrysocharis* sp. [both Eulophidae]. Unfortunately, it is not possible to ascertain if these parasitoids are directly associated with *O. spenceri* or incidental rearings.

Ophiomyia ungarensis Černý, 2015

Introduction

Stems of teasel (*Dipsacus fullonum,* Caprifoliaceae) were obtained from five localities: Dettingen [47.732472, 9.113157, a large ruderal meadow], Konstanz Petershausen [47.673348, 9.164164, construction wasteland] (Fig. 3), Erdmannhausen [48.927512, 9.293068, meadow strip], Erdmannhausen [48.932423, 9.287393, a flower strip since 2017, sown only once, then mown every spring without re-sowing] and Erdmannhausen [48.933515, 9.289574, a compensation area for ground breeders, ca. 5 years old] (Fig. 4).

Preliminary examination of the reared specimens proved they all belong to *Ophiomyia*, a genus not known to utilise *Dipsacus* as a host. Using the key in Papp and Černý (2015), the males run to couplet 38: *O. orientalis* Černý, 1994 or *O. ungarensis* Černý, 2015. The broad and flat facial keel between bases of the antennae suggests *O. ungarensis*; dissection and maceration of male genitalia (Fig. 5) confirms the imagines as *O. ungarensis*, a species previously not known from Germany.

Identification

Ophiomyia ungarensis is a relatively small species, wing length 1.8mm, with costa extending to vein M_{1+2}, ultimate section of M_{3+4} approx. 1.16x as long as penultimate. Orbits form a narrow ring in front of eye when viewed in profile. Orbital setulae all reclinate, sparse, with two slender *ori* and two *ors*. Vibrissal fasciculus short, broader at base and curving apically, vibrissal angle approximately 75°. Mesonotum with 2 *dc*, *acr* in 6-8 irregular rows. A mostly all dark species, wing slightly infuscate. Female (Fig. 6) previously unknown; essentially as in male, wing length 1.8-2.1mm, with simple vibrissal seta.

Fig. 3. *Dipsacus fullonum* on construction wasteland, Konstanz Petershausen.

Fig. 4. Erdmannhausen collection site, with *D. fullonum* present.

Distiphallus species-specific; (Fig. 5) slightly asymmetrical, mesophallus narrow and short with basiphallus possessing asymmetrical long arms. Ejaculatory apodeme with narrow blade.

Fig. 5. *Ophiomyia ungarensis* Černý, 2015 phallus viewed from below.

Biology
Previously larval host unknown [Warrington and Perry 2020 mentioned a possible association with *Cuscuta*] but can now be confirmed as *Dipsacus fullonum*. Although no detailed examination of the collected stems was undertaken, it is assumed the species is an external stem miner, typical of the genus.

Distribution
Ophiomyia ungarensis is currently only known from Great Britain (Warrington and Perry 2020),

Fig. 6. ***Ophiomyia ungarensis*** **Černý, 2015 female.**

Hungary (Papp and Černý 2015), Turkey (Černý 2019) and Ukraine (Guglya 2016).

Acknowledgements

I would like to thank F. Hannes Veihelmann (University of Konstanz, Germany) for providing collecting information and allowing me to use his photographs (Figs 2, 3 and 4) and Dr Michael von Tschirnhaus (University of Bielefeld, Germany) for providing additional references.

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Dipterists Digest 2022 **29,** 14-16

Cerodontha (Cerodontha) phragmitophila Hering (Diptera, Agromyzidae) new to the Netherlands

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Summary

Cerodontha (*Cerodontha*) *phragmitophila* Hering, 1935, a distinctive member of the subgenus *Cerodontha* Rondani, is reported as a species new to the Netherlands based upon a single male present within a Malaise trap sample. A description of the male is provided, along with an illustration of its phallus.

Introduction

In the autumn of 2020, I was sent several vials of unidentified Agromyzidae material obtained from Malaise traps used by Joop Prijs in the Netherlands. One sample, taken 16 July 2019, from a rough area (Fig. 1) containing abundant common reed (*Phragmites australis*), directly east of lake Markiezaatsmeer [51°27′26″N, 4°17′47″E], contained over 100 specimens; within the sample were two male *Cerodontha* species belonging to the subgenus *Cerodontha* [along with *Agromyza hendeli* Griffiths, 1963; *Agromyza reptans* Fallén, 1823; *Aulagromyza lucens* (de Meijere, 1924); *Cerodontha (Poemyza) atra* (Meigen, 1830); *Cerodontha (Poemyza) lateralis* (Macquart, 1835); *Cerodontha (Poemyza) muscina* (Meigen, 1830); *Cerodontha (Poemyza) phragmitidis* Nowakowski, 1967; *Chromatomyia milii* (Kaltenbach, 1864); *Liriomyza flaveola* (Fallén, 1823); *Liriomyza pusilla* (Meigen, 1830); *Liriomyza pusio* (Meigen, 1830); *Liriomyza taraxaci* Hering, 1927; *Napomyza carotae* Spencer, 1966; *Phytomyza chaerophylli* Kaltenbach, 1856; *Phytomyza cirsii* Hendel, 1923; *Phytomyza continua* Hendel, 1920; *Phytomyza conyzae* Hendel, 1920; *Phytomyza medicaginis* Hering, 1925; *Phytomyza pastinacae* Hendel, 1923].

The first specimen proved to be *Cerodontha* (*Cerodontha*) *fulvipes* (Meigen, 1830), a relatively common and widespread species throughout Europe. Using the key by Papp and Černý (2016), the second specimen, owing to it possessing *acr* in two rows, dark third antennal segment, yellow [centrally] scutellum and mesonotum broadly yellow adjoining scutellum, was determined as *Cerodontha (Cerodontha) phragmitophila* and not the similar *C.* (*C.*) *affinis* (Fallén, 1823) [mesonotum only narrowly yellow adjoining scutellum]; examination of the phallus confirmed the species as *C.* (*C.*) *phragmitophila*. This specimen represents the first known occurrence of the species in the Netherlands.

Identification

Wing length 1.8mm-2.7mm, usually one strong *ors*, two *ori*, with orbital setulae sparse, in a single row. Mesonotum with 0+3 *dc*, *acr* in two rows. Third antennal segment brownish-black with sharp spine at upper apical corner, first and second segments yellow. Scutellum broadly yellow centrally, mesonotum black with large yellow area centrally adjoining scutellum. Legs yellow, with tibiae and tarsi slightly darker. Male phallus (Fig. 1) distinctive, with paraphallus consisting of two sclerites situated posteriorly to the long hypophallus. Ejaculatory apodeme small, with narrow blade and long ‘stalk’ (Fig. 1).

Biology

The larva forms a corridor in the leaf sheath [very rarely in the leaf blade] of giant reed (*Arundo donax*) and common reed (*Phragmites australis*), often several mines together, sometimes merging into one larger mine. Puparium slender, posterior spiracles fist-shaped, with c15 irregularly arranged large bulbs. Anterior spiracles weakly bifid, with c10 bulbs.

Fig. 1. ***Cerodontha*** **(*****Cerodontha*****)** ***phragmitophila*** **Hering, 1935 phallus in left lateral view, with ejaculatory apodeme.**

Fig. 2. Malaise trap ***in situ*** **near lake Markiezaatsmeer, surrounded by abundant** ***Phragmites australis*****, a known host plant of** ***C.*** **(*****C.*****)** ***phragmitophila.***

Distribution

Within Europe, *C.* (*C.*) *phragmitophila* is known from Belgium, Bulgaria, Croatia, Corsica, Cyprus, Czech Republic, Finland, France, Georgia, Great Britain, Greece, Hungary, Italy, Madeira, Poland, Portugal, Russia, Slovenia, Spain, Switzerland and Turkey. Elsewhere, it is recorded from Egypt, Jordan, Israel, Kazakhstan, Pakistan, Sahara desert and Uzbekistan.

Acknowledgements

I would like to thank Joop Prijs for providing collection site information and permitting me to use his photograph (Fig. 2).

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Necrophagy in a phytophagous cyclorrhaphan larva (Diptera, Anthomyiidae) – On 1 August 2021 in Dumfriesshire, Scotland I was extracting larvae of the anthomyiid *Botanophila seneciella* (Meade) (Diptera, Anthomyiidae) from ragwort capitula, *Jacobaea vulgaris* (Asteraceae). *Botanophila seneciella* is an obligatory phytophage and feeds on flowers causing up to 75% seed loss per capitulum (Cameron A.E. 1935. A study of the natural control of ragwort (*Senecio jacobaea* L.) *Journal of Ecology* **23,** 265-322). Hence, the following observation was unexpected.

A 3rd (final) stage larva was killed accidentally and placed in a solid watch glass to extract the head skeleton. It was leaking body fluids. The next larva I extracted and placed in the same watch glass began feeding on the dead larva. On encountering the leaked body fluids, the larva pivoted its head skeleton up and down at a rapid rate. It fed more or less continuously for about 4 minutes and moved into the body of the dead larva (Fig. 1). After this time, it reversed out of the dead larva and rested.

Necrophagy in phytophagous larvae is apparently unusual. Certain predatory and saprophagous cyclorrhaphan larvae can feed in this way and will take conspecific larvae (Rotheray, G.E. 2019. Ecomorphology of Cyclorrhaphan Larvae (Diptera). *Zoological Monographs* **4**. Springer). Observations of necrophagy have led to misunderstanding and controversy about larval feeding modes in such families as the Lonchaeidae and Pallopteridae (Ferrar, P. 1987. A Guide to the Breeding Habits and Immature Stages of Diptera Cyclorrhapha. *Entomonograph* **8**). Necrophagy is, however, a source of nutrients and possibly a means of preventing contamination at development sites from dead and dying larvae (Vijendravarma, R.K. Narasimha, S. and Kawecki, T.J. 2013. Predatory cannibalism in *Drosophila melanogaster* larvae. *Nature Communications* DOI: 10.1038/ncomms2744).

In an attempt to investigate this further, over the next few days six pairs of live 3rd stage, *B. seneciella* larvae were placed together in watch glasses and their responses monitored for up to two hours. Larvae were slow-moving, but in each replicate they made contact with one another and although head skeletons pivoted, no piercing was observed and they eventually separated. It was not possible to determine whether on contact, larvae were attempting to disengage or being aggressive towards one another.

Fig. 1. A live 3rd stage larva of *Botanophila seneciella* (Diptera, Anthomyiidae), upper individual, just removed from a capitulum of *Jacobaea vulgaris* (Asteraceae) and placed in a watch glass, feeding with its head inside the body of the lower specimen accidentally killed and placed in the watch glass a few minutes earlier, 1.viii.2021, Dumfriesshire, Scotland.

Although ragwort capitula are usually infested with a single *B. seneciella* larva, Cameron (*loc. cit.*) sometimes recorded two. The observation reported here raises the possibility that if a larva dies or is wounded in a capitulum with two larvae, necrophagy may follow. Furthermore, contest competition is not ruled out with larvae fighting for sole occupancy.

Contest competition is apparently rare, but has been observed in the rose hip tephritid, *Rhagoletis alternata* (Fallén) (Diptera, Tephritidae) (Rotheray *loc. cit.*). In rose hips necrophagy of dead *R. alternata* larvae has also been observed, but not by *R. alternata* larvae. It was done by another rose hip occupant, larvae of the saprophage, *Drosophila subobscura* Collin in Gordon 1936 (Diptera, Drosophilidae) (author, unpublished observations). Clearly, studies of necrophagy in cyclorrhaphan larvae have a long way to go before being understood – **G. E. ROTHERAY**, 16 Bracken Wood, Gatehouse of Fleet, Dumfriesshire, DG7 2FA, grahamrotheray@gmail.com

Chamaepsila pectoralis (Meigen) (Diptera, Psilidae) new to the British Isles from Shetland – A fly photographed in Shetland was identified as a male of *Chamaepsila pectoralis* (Meigen, 1826), a species not previously recorded in the British Isles. The image was placed on the *Diptera.info* site and my identification was kindly confirmed by Paul Beuk.

This single individual (Fig. 1) was found on 6 June 2021 among a 1 metre clump of vegetation, mainly comprising wild angelica *Angelica sylvestris*, at the edge of Garths Voe Beach at Graven, Shetland (grid reference HU 40464 73318).

Fig. 1. _Chamaepsila pectoralis_ (Meigen) at Garths Voe Beach, Shetland.

This species may be identified using the recent key to the French species (Withers, P. and Claude, J. 2021. Les Psilidae de France (Diptera : Acalyptrata) : checklist et clés de détermination des genres et des espèces. *Naturae* **9,** 115-135. https://doi.org/10.5852/naturae2021a9). It is keyed by them as having one pair of scutellars, two pairs of dorsocentrals and three pairs of vertical bristles, and is distinguished from other species with these characters by its distinctive coloration as shown in Fig. 1. The thorax has the mesonotum mainly black, while the postpronotum (humerus) and most of the pleura are yellow, a dark patch being present on the katepisternum (sternopleuron).

This species is widespread in Europe, so finding it in Britain was not unexpected but that the first occurrence should be in Shetland was surprising. The distribution given by Withers and Claude (*op. cit.*) was France, Switzerland, Belgium, the Netherlands, Germany, Denmark, Finland, Lithuania, Poland, Czech Republic, Slovakia, Hungary and Romania – **ROGER THOMASON,** 24 Hamarsgarth, Mossbank, Shetland; thomasonre@gmail.com

Dipterists Digest 2022 **29,** 19-34

Swarming behaviour of male *Chrysopilus cristatus* (Fabricius) and *C. asiliformis* (Preyssler) (Diptera, Rhagionidae)

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Summary

Male *Chrysopilus cristatus* (Fabricius, 1775) formed large continuous swarms over an area of fen meadow in a rural garden. Swarming consisted of short bouts of swarming lasting about 15-30 seconds interspersed with similar periods when all the flies settled. The flies showed clear interaction, with one initiating a local swarm and others very quickly following. The swarm cascaded into neighbouring groups of flies and occasionally the entire area was covered in a single swarm. Swarming took place in the morning between about 8:30 and 11:00, after which males were difficult to find. In contrast to large numbers of males, females were rarely seen. Two mating pairs were followed from landing to separation, which took nearly 30 minutes. *Chrysopilus asiliformis* (Preyssler, 1791) males formed much smaller swarms over discrete markers but their flight closely resembled that of *C. cristatus*. Time in flight lasted about 10-30 seconds and resting for at least 25 seconds and as long as 190 seconds. The duration of each flight was correlated with the number of flies taking part. Swarming began in the morning and lasted about an hour; its onset was strongly correlated with temperature, unlike that of *C. cristatus* which did not vary much over the 69 days of observations. This type of swarm is rare among Diptera and does not align with the traditional concept of mating swarms centred on a swarm marker, but does fit with more recent work showing that interaction between swarming individuals is a normal but unrecorded part of nematoceran swarms, and helps to explain better the strongly interactive swarming in *Chrysopilus*.

Introduction

Flies that swarm almost invariably have zones of markedly larger eye facets (Oldroyd 1969) and this gives a clue in which species it may be expected when there is no previous record of swarming. Both types of eyes, with or without differently sized facets, are found in British rhagionids. *Rhagio* has simple eyes and, although *Rhagio scolopaceus* (Linnaeus) and *R. strigosus* (Meigen) often congregate in large numbers, they do not appear to interact much. However, Gruhl (1959) briefly described a swarm of *R. lineola* Fabricius in which a group used a small elder tree (*Sambucus*) as a swarm marker above which the males circled, with some hovering and looping. This continued for several minutes, although when the wind became strong they settled on the leaves. This appears to be the account that led Downes (1969) to say that some *Rhagio* species have a brief swarming flight, which alternates with longer periods at rest. In contrast, *Chrysopilus* and *Symphoromyia* have enlarged front facets. Swarming in several North American *Symphoromyia* species has been well described (Hoy and Anderson 1978, Shemanchuk and Weintraub 1961). Chvála (1994) knew that *Chrysopilus* form swarms as he obliquely refers to it when discussing the swarming of *Empis* (*Xanthempis*) *scutellata* Curtis (Empididae), whose behaviour is unusual in its subgenus as it swarms when the other species court on the ground, with the implication that swarming by *Chrysopilus* was aberrant in rhagionids. Kerr (2009) stated that the males of some *Chrysopilus* species are known to swarm.

A description of swarming in a British *Chrysopilus* was made by Alan Stubbs who saw five *C. asiliformis* (Preyssler) which “At intervals .... would rise into the air, causing the others to also rise and swirl around for a few seconds in a horizontal plane before settling again” (Stubbs and Drake 2014).

Here, I describe swarming in two common species, *Chrysopilus cristatus* (Fabricius) and *C. asiliformis*. I made the observation in my rural Devon garden where I had noted *C. cristatus* swarming in previous years. I first saw swarms in late May 2020, so started observations, not realising that I had embarked on two months of work until they ceased to swarm in early August. *Chrysopilus cristatus* is a good subject to study in the field, being large and easily identified. The sex can be determined from at least 2m away since the male's matt black and narrow tapered abdomen differs from the female's pale golden-dusted and stouter abdomen. They are not readily disturbed and I could walk past them slowly at about 50cm away without them taking flight. *Chrysopilus asiliformis* is smaller and dull pale grey so less easy to see, but was a good subject as its swarms were discrete, so allowed a different suite of observations.

Methods

My garden lies at the bottom of a small steep valley on shallow colluvium overlying Cretaceous Greensand (ST311060). The area where *C. cristatus* swarmed is a form of fen meadow that perhaps, under 20 years of relaxed management since I bought the property, is developing into a *Filipendula ulmaria – Angelica sylvestris* mire (M27) in the National Vegetation Classification (Rodwell 1991). In late May 2020, the dominant plants over which the flies swarmed were *Carex hirta* (hairy sedge), *Equisetum palustre* (marsh horsetail), *Angelica sylvestris* (angelica), *Dactylorhiza praetermissa* (southern marsh orchid), *Filipendula ulmaria* (meadow-sweet) and *Ranunculus acris* (meadow buttercup), with sparse grasses including *Phleum pratense* (timothy) and *Arrhenatherum elatius* (false oat). By midsummer, the plants were dominated in one part by tall flowering *F. ulmaria* and in another patch by *Pulicaria dysenterica* (fleabane) with dense *C. hirta*. Over the summer, the surface topography became increasingly complex as different plants poked up above the main sward, for example, *Cirsium palustre* (marsh thistle) and tall flowering grasses. Vegetation height varied widely owing to differences in my cutting regime and frequent browsing by roe deer (*Capreolus capreolus*), but in late May it was mainly about 30cm, and about 50cm over an extensive stand of *F. ulmaria*, rising to about 70cm at the end of observation in early August. Nearby were a tall hedge with trees, an outbuilding and a tall willow whose shadow drifted across the area during the course of the morning when observations were made. The ground over which swarms occurred was an approximately rectangular area of about 500m^2 (20x25m) although around this zone was more rough damp grassland that was rarely used by the flies.

The main area where *C. asiliformis* swarmed was a stand of *Eupatorium cannabinum* (hemp agrimony) about 2.5m in diameter and rising to 2.1m next to an outbuilding. Observations were made on another swarm over a stand of *Equisetum telmateia* (giant horsetail) close to the wall of our house. Both of these sites abutted the *C. cristatus* zone.

From late May to early August 2020, the weather was mostly warm and above the long-term average temperature and rainfall, but included some exceptionally hot days, for example, May 2020 was the sunniest and driest on record for England (Freeman 2020).

My observations were made opportunistically, so the timing of some events was approximate. Detailed timing of swarms of *C. cristatus* were made by sitting in one place so that the flies could be seen clearly against the dark backdrop of the hedge, in a 'corridor' about 5m wide by 10m long. The start and end times of each swarm event were measured to the nearest 5 seconds on the first three occasions and to the nearest 1 second thereafter using a stop-watch. Observations were made for about 30-35 minutes at 8:50–9:17 on 28 May, 9:09–9:37 on 29 May, 9:20– 9:55 on 9 June, and for about 2¼ hours at 8:37–10:46 on 30 May. It was clear from the first two days of observation that I had missed the start of swarming and that it continued after I had stopped, hence the long period on the third occasion.

I estimated the density of *C. cristatus* in a swarm using six crude 'quadrats' of dark string arranged in circles nominally 0.5m in diameter and with an area of 0.2m^2 (πr^2). Counts were made as the flies settled from a swarm, as they could be most easily located in this brief window before they became difficult to detect.

The time that an individual *C. cristatus* spent settled between participating in a swarm event was measured from the moment it landed from a swarm to when it took off again. Measurements were made on 7 June at 9:30–10:40 in sunny conditions but cooler than at the end of May, on 12 June at 9:05–9:25 in thinly clouded conditions at 14.5–15.5°C, and 13 June at 10:00–10:30 in breezy but sunny conditions at 14.5–16.1°C.

An attempt to find females within swarms was made by taking three sweeps with a sweep-net through a swarm when it was most active. This was not continued for long as it was considered too disruptive. An alternative measure of the relative abundance of males and females was started on 17 June based on the Butterfly Monitoring Scheme method (Pollard and Yates 1993). Two paths through the site were walked very slowly, counting the number of flies either side of the grass path within a 3m corridor; the path occupied about 0.5m and was discounted. Counts were made early in the morning before swarming started but after the flies had started 'perching' in preparation for swarming. Transects were 18m and 21m long, took about 9 minutes each to complete and were walked on 24 days between 17 June and 1 August.

As with *C. cristatus*, swarming of *C. asiliformis* was timed on four days in June: over *E. telmateia* at 9:30–10:18 on 12 July and 9:41–10:40 on 13 July; over *E. cannabinum* at 8:46–:33 on 20 July and 8:29–10:12 on 22 July. The swarms of *C. asiliformis* were small so the number of flies in each swarm event could be counted with moderate accuracy. However, it was difficult to catch the moment when a fly landed owing to their grey colour quickly blending with the background, so the time spent settled was not measured.

Casual observations were made on most of the 69 days between 27 May and 3 August, in particular the times when flies were first seen sitting on their perches, and their first and last swarm events. As observations were fitted in around normal life, there were gaps in coverage and inaccuracies in the times of the different activities, particularly the end of swarming. Temperature was measured in the shade of the adjacent outbuilding using an electronic thermometer reading to 0.1°C. I used non-parametric descriptors (median, interquartile ranges) as the observations were not statistically independent.

Results

Male C. cristatus *swarms*

At their peak of activity, swarming consisted of one fly, very quickly followed by others, rising up, flying rapidly and erratically to-and-fro and in small circles in an area about 1.5m across. Following the movement of an individual was not possible so the flight path may have been less or more than this, but not by much. Most flies remained within a shallow vertical zone about 15cm to 60cm above the vegetation, with occasional fast forays to about 1m and exceptionally to about 3m. In a gap between the tall willow and the outbuilding, over some tall *Anthriscus sylvestris* (cow parsley) and *Eupatorium cannabinum*, flies regularly rose to about 3m or more, so the vegetation's topography influenced their flight behaviour. Flies approaching within about 5-20cm of each other engaged in fleeting circling. After a few to many seconds they settled on prominent perches, usually with their dorsums facing the sun, where they remained perfectly still until the next swarm event a few to many seconds later. Swarming was therefore a series of bursts of synchronised activity with intervening periods of complete calm when usually no flies moved over the entire area.

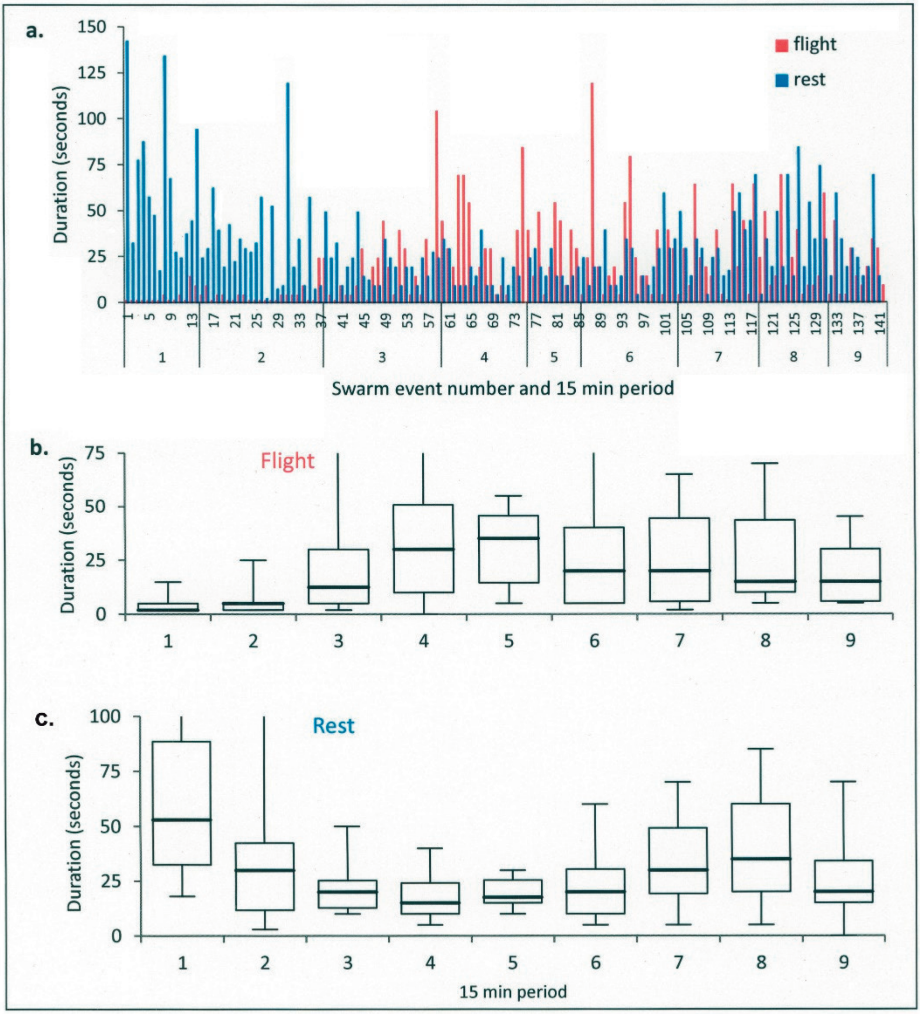

Fig. 1. Swarming of *Chrysopilus cristatus* males from 08:37 to 10:46 hours on 30 May 2020: a) Duration of each event comprising flight (red) followed by rest (blue). Summary of these values in 15 minute periods for b) flight and c) rest (medians with quartiles and range; high outliers have been curtailed but can be seen in the top histogram, a).

The pattern of flight and rest during swarming is shown for the 2¼ hour observation on 30 May (Fig. 1). In this period, 142 separate swarm events were timed (an 'event' was defined as flight followed by rest). Flights at the beginning were very short, consisting of a few flies making brief sorties lasting a few seconds. Gradually more flies joined in each flight, and it often appeared that flies in one local group stimulated those nearby in a cascade effect, so it was not possible to say exactly when an event started or finished, although complete quiescence marked the obvious end of an event. Later flights involved more flies and lasted longer than the periods of rest. At the peak of activity, the entire population appeared to take flight, conspicuously covering the entire plot. Grouping observations into 15 minute intervals makes this clearer (Fig. 1b, c) and also shows that, at the start of proceedings, there was greater variation in the time spent at rest than later in the morning. This was due to irregularity in the gaps between the ill-defined 'exploratory flights' that preceded the large swarms. On this day, swarming continued for a while after timed observations stopped.

Table 1. Duration of flight and rest of *Chrysopilus cristatus* and *C. asiliformis* for periods of 15 minutes (median and interquartile range, in seconds) on three days in 2020.

Date	Time	15 minute period	Flight	Rest
Chrysopilus cristatus				
28 May	8:51–9:17	1	33 (20–45)	33 (19–77)
		2	45 (19–56)	20 (15–33)
29 May	9:09–9:37	1	25 (15–65)	35 (25–45)
		2	30 (15–50)	15 (10–20)
9 June	9:20–9:56	1	14 (5–25)	28 (10–34)
		2	29 (16–56)	27 (12–41)
		3	19 (7–33)	12 (7–17)
Chrysopilus asiliformis				
12 July	9:30–10:18	1	32 (8-55)	49 (26-132)
		2	11 (11-20)	94 (53-132)
		3	10 (7-17)	45 (32-59)
		4	4 (2-12)	96 (53-145)
13 July	9:41–10:40	1	11 (6-38)	56 (26-68)
		2	31 (10-39)	24 (19-45)
		3	7 (5-47)	39 (29-62)
		4	8 (6-13)	188 (68-221)
20 July	8:46–9:33	1	16 (6-24)	150 (62-201)
		2	23 (7-42)	96 (61-129)
		3	22 (7-30)	36 (18-55)
		4	7 (6-7)	171 (86-257)

The three shorter (30-35mins) periods of timed observations were effectively snapshots of the middle of the 2¼ hour session. The median times in flight increased in the later part of each observation period as the time at rest decreased, matching values in Fig. 1 for about the third to fifth 15 minute intervals (Table 1). The time spent at rest by an individual between participating in swarms was measured on three days which differed in weather conditions. The first occasion was sunny with few clouds and windless; on the next two occasions the sun was weak owing to thin patchy cloud; the last day differed markedly in being much windier. Timing stopped after an atypically long period of inactivity when the sun disappeared. The median times spent resting differed significantly (Mann-Whitney test) so the three datasets could not be combined. The times (with lower and upper quartiles) differed on each of the days:

7 June	33 (7-67) seconds	(N=42, 66 mins recording)
12 June	15 (10-41) seconds	(N=23, 24 mins recording)
13 June	94 (61-153) seconds	(N=11, 31 mins recording)

Thus the time spent at rest varied, perhaps partly because the time of day differed so measurements were made in different sections of the changing pattern just described, but also because of sunniness and windiness. In more clement weather, half of the flies spent between about 15-30 seconds at rest before taking part in a swarm, and the short lower quartile showed that a quarter of them were settled for a very short time (7-10 seconds). Wind delayed swarming, so on the last day half of the flies sat doing nothing for up to about 90 seconds until a short break when the breeze subsided allowed them to swarm, which they did almost without delay. The pattern of time at rest was similar on the first two days (Fig. 2) and approximately followed a negative power curve whereas wind resulted in an erratic pattern. The resting times for the two non-windy days were very similar to the median times of resting measured for whole swarms (as given in Table 1 and Fig. 1).

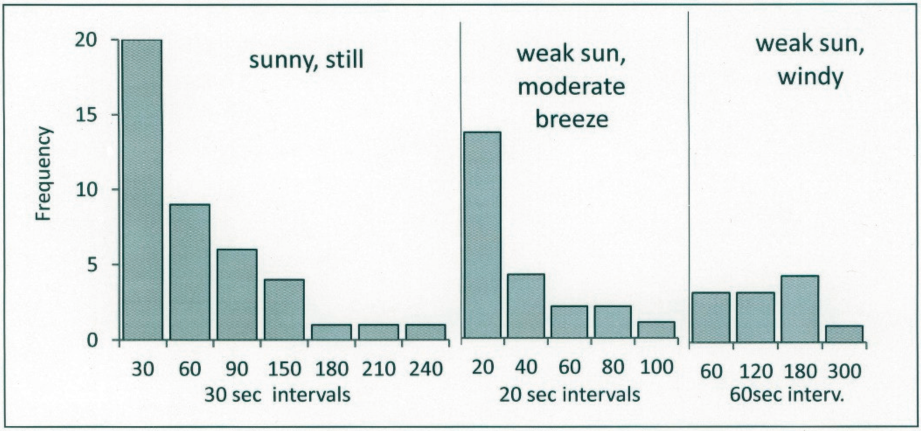

Fig. 2. Time that individual *Chrysopilus cristatus* males spent resting between swarm events on 7 June 2020 (N=42 observations), 12 June 2020 (N=23) and 13 June (N=11) in different weather conditions. Different time intervals are for convenience of presentation.

While watching single individuals, it was clear that they did not always participate in the local swarm taking place immediately above them. Some flies also appeared to land on or very close to a particular perch, suggesting one individual had its own ‘patch’, but this could not be confirmed. Resting males appeared to take no notice of others nearby, even when within two body-lengths of each other on the same leaf. Other insects flying nearby rarely disturbed them.

The daily routine remained constant over the period of nearly 70 days. To help describe their behaviour, the activity of males was classified into four phases: perching, which involved finding and then sitting still on a perch; exploratory flights that did not constitute a swarm although a few flies may have flown together; the first small swarms of 10-20 flies; the first big swarms that were extensive and contained many tens to hundreds of flies. This classification was only for convenience as the activities ran into one another as there were huge numbers of flies active over a large area. On most days perch-finding took place between about 8:00 and 9:00, the first large swarms started between 8:30 and 9:30, and swarming had finished between 10:00 and 11:00 (Fig. 3a).

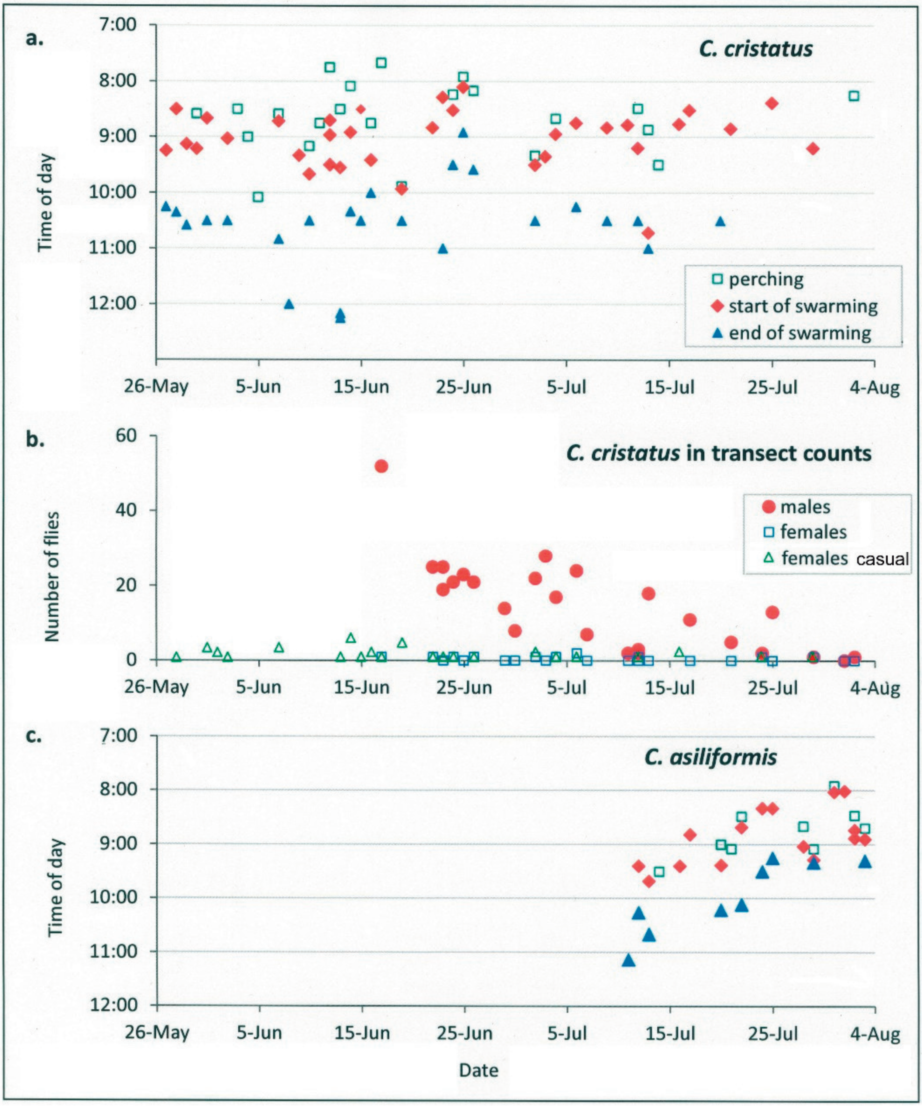

Fig. 3. Timing of daily activity from 27 May (day 1) to 3 August (day 69) for a) *Chrysopilus cristatus* and c) *C. asiliformis*; b) Transect counts for both sexes of *C. cristatus* from 17 June (day 22) and casual records for females starting 27 May.

Shortly after swarming stopped, flies were difficult to find, and they may have descended into the herbage or migrated to surrounding hedges. Only an approximate and probable overestimate of the duration of swarming is possible as I could not spend all morning for many weeks watching, so the time of the end of swarming was not always accurate. However, the median (with interquartile range) of duration for 21 days when the end time was probably within 10-15 minutes of the real value was 87 (59-111) minutes. There was no correlation with day number so the duration of swarms did not decline with time (r = -0.14, p>0.05).

Variation in these times depended only partly on the immediate weather conditions and temperature. It is likely that a threshold temperature had to be passed before activity could begin. Perch-finding and exploratory flights started when the shade temperature exceeded 13°C, or exceptionally as cool as 11°C or as warm as 17°C. Large swarms began when the temperature exceeded 13°C (exceptionally a little cooler). Immediate weather conditions probably also influenced starting times. For instance, the sun was showing on most days when the flies swarmed and, on the few overcast days when they swarmed, the starting time of swarming tended to be delayed until about 9:30. The appearance of the first large swarms or the early solo flights sometimes coincided with the sudden appearance of the sun as cloud moved away. However, providing that the air temperature was above about 13°C, they often swarmed when completely in the shade so perhaps bright conditions were sufficient stimulus. Warmth could not be the only factor to initiate swarming since there was no correlation between temperature measured in the shade and the onset of perching (r= -0.242, p>0.05, N=21 days) or swarming (r= -0.164, p>0.05, N=31). Similarly the end of swarming was not correlated with temperature (r= -0.348, p>0.05, N=18) although the day had warmed by that time. It is possible that hot conditions suppressed swarming as, in hot mornings, the flies were active only in the shade of the large willow, while those previously in the sun had either moved to join an on-going swarm in the shade or perhaps stopped all activity and withdrawn into the vegetation. On nearly all days, the temperature rarely exceeded 18°C at the close of activity. At the other extreme on cold wet days, there was no activity and sometimes no flies were seen all day.

No estimates of abundance were made until the transect counts were started on day 21 (17 June). The counts showed a gradual decline from then until the end of the period (Fig. 3b). By early August, flies had almost disappeared and were at a sufficiently low density that none were seen during the transect counts even though small swarms were sometimes seen later in the morning. None were seen at all after 6 August. Despite the decline in abundance, they did not change their daily routine although the area covered by swarms contracted.

The estimated density of flies in a swarm was provided by those landing in the ‘quadrats’ on 2 June at 9:00–10:15. The average density of 30 counts was almost 10 m^{-2} which was similar to visual estimates. The area of garden where swarms were seen was about 500m^2, giving an approximate upper count of 5000 males. This was almost certainly too high as the dense swarms over the quadrats did not extend to all parts of the plot. Another crude estimate of density of the population (not in the swarms) was made using the transect counts. These counts probably gave reasonably good estimates of relative abundance over time but clearly would underestimate actual abundance. In the fortnight starting 22 June, when the average daily numbers seen in 12 days was 20 flies, this gave an underestimated density in the combined transects (39x2.5m) of about 0.2 m^{-2}, and a total number in the 500m^2 plot of 100 flies, which was far too low. A best guess between these extremes was 1000-2000 males in early June.

It was not possible to tell whether flies that first appeared in their perching phase had been roosting low in the vegetation or migrated from adjacent hedges. However, on a number of occasions, slowly flying males were seen finding their perch in a slightly clumsy manner compared to their agility later in the morning, and females were also sometimes seen flying or crawling upwards from deeper vegetation to a perch. Late in the morning after swarming was over, males were sometimes seen flying downwards into the herbage. It seemed probable that both sexes roosted for much of the day in dense low vegetation.

Predation of males was seen four times. Two were caught and eaten by unidentified spiders in their webs, one was caught as it slowed to land by *Dioctria rufipes* (De Geer) (Asilidae) and another was prey to a female *Empis tessellata* (Fabricius) (Empididae).

Female **C. cristatus**

Females were rarely seen. In the entire period of observation during the mornings, one to five were seen on 22 days (Fig. 3b). If it is assumed that all sightings were of different individuals, these amounted to 38 flies. Most females merely sat on perches that were usually less prominent than those used by males but still had a clear view overhead. Compared to the motionless males, females tended to fidget, sometimes wash, and walk or occasionally fly from leaf to leaf, but in general remained in the same place for a long time, from 10 to 88 minutes for eight timed flies. Several sat unresponsively while small swarms took place overhead and within 20-30cm, while others did not respond to males landing within 10cm of them; in one case a male landed repeatedly between swarming on the same grass stem occupied by a female.

Females were marginally easier to find earlier in the morning before swarming began, and it was for this reason that the transect counts were undertaken in the pre-swarming phase. However, they were seen so sporadically and sometimes in areas where swarming males were rarely seen that no further analysis is sensible. Fig. 3b shows counts from the transects and these mirror casual observation. After midday, when male activity had usually stopped and they were difficult to find, occasional females were found elsewhere in the garden.

Interaction between females and males was seen a few times. On these occasions, a female (one walking, two taking off) was immediately followed by two or more males that had been sitting nearby; another that had been sitting for just over a minute took off, when a small swarm of about 20 males immediately formed, lasting for about 15 seconds. I could not follow whether the males successfully intercepted the females.

Four females were seen mating. These sightings were on two consecutive days at the beginning of the study, 31 May and 1 June; despite considerable time spent searching, no mating pairs were seen after this date. They mated end-to-end, with the female seeming to be in control of the orientation which was female uppermost; in one case the male hung freely from the female. Two pairs landed just in front of me although I did not see the prelude to their descent. They scrambled briefly until the female had a good grip of the leaf. One pair seen landing (so mating had just begun) separated after 26 minutes, when both parties walked a few centimetres apart, and the male flew to a nearby leaf after about 30 seconds, then had flown off after 2 minutes, leaving the female who moved just a few centimetres to another leaf. A second pair seen landing remained coupled for at least 28 minutes after which I lost track of them and do not know whether they had separated by then.

Male **C. asiliformis** *swarms*

Swarms were rarely found in the garden. Observations were restricted to two groups of flies, one being a small and short-lived group over *Equisetum telmateia* in the shade of our adjacent house, and the other a larger and longer-lasting group over *Eupatorium cannabinum*. The first swarm was noted on 11 July 2020, although earlier activity was probably missed. The last swarm was noted on 3 August. Two sets of timing were made for each of these two groups, as well as casual observations over the 24 days when they were present.

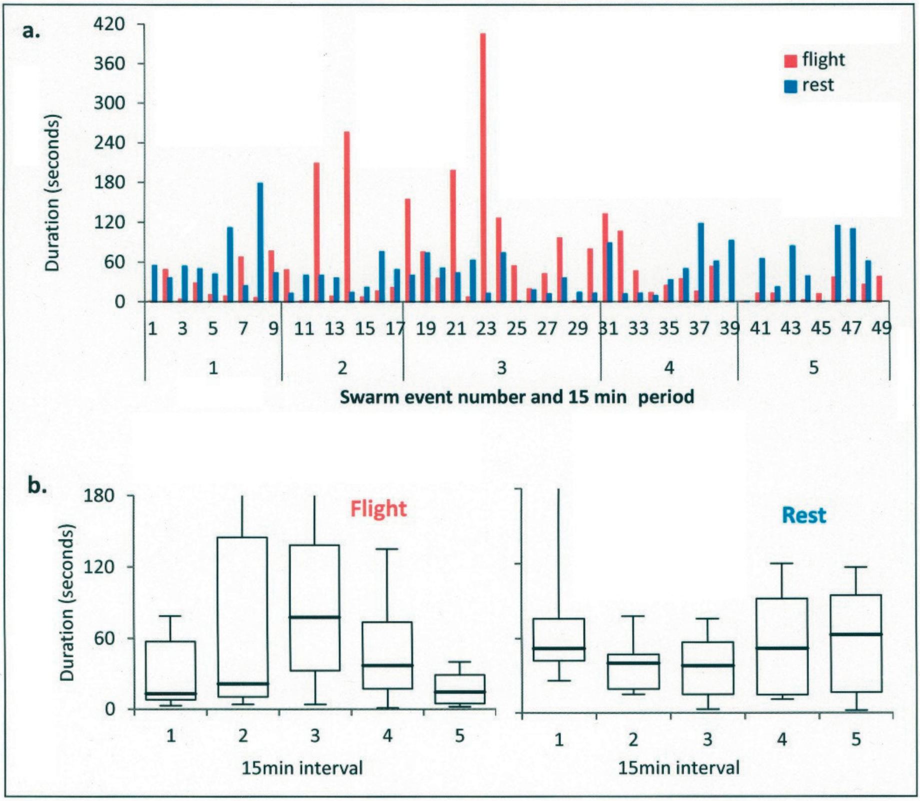

Fig. 4. Swarming of *Chrysopilus asiliformis* males, from 09:40 to 10:40 hours on 13 July 2020: a) Duration of each event comprising flight (red) followed by rest (blue); b) Summary of these values in 15 minute periods for flight and rest (medians with quartiles and range; high outliers have been curtailed but can be seen in the top histogram, a).

Swarming followed a predictable pattern. Fig. 4 shows the results for a swarm that lasted for nearly 1hr 15minutes on 22 July, comprising up to about 25 flies that used the flower-heads of *Eupatorium* as a swarm marker and landing stage. Table 1 summarises the other three days' events. Flies were first seen on the flower heads in prominent positions, although they were rarely seen arriving and it was presumed they flew up from roosting sites low in the herbage. On most occasions, one fly would make the first move and was usually quickly followed by a few more. Swarms consisted of up to a maximum of about 25 flies but usually only about ten individuals. Their flight was similar to that of *C. cristatus* but on a smaller scale. The volume occupied by ten flies was approximately a sphere about 50cm in diameter although with occasional dashes outside these bounds. The flight was rapid back-and-forth and circular movement, somewhat erratic and including much gyrating around each other. After a while, they settled one-at-a-time within a few seconds. The first swarm was usually short, but occasionally almost the first swarm event lasted for about a minute. Shortly after swarming started, events became longer; in the example shown in Fig. 4, the median flight time at the peak of swarming was over a minute, with some particularly long events lasting for many minutes. These very long times were the result of one fly concatenating two events by not landing, so making it difficult to decide when the flight stopped. This was exceptional: two days earlier, the same group of flies swarmed for a median time of 22 seconds, and the longest flight lasted 53 seconds, as was also reflected in the shorter overall median times spent aloft in the other three timed swarms (Table 2). As more time was spent in flight, less was spent settled on the flowers or leaves. After a while, flights became shorter and rests longer until eventually activity stopped altogether. After about 5 minutes of inactivity, it was extremely difficult to see any flies. Swarming lasted for about 45 to 75 minutes on the four days when they were timed, and casual observation on later days confirmed that swarming did not last longer than this (Fig. 3c). In the first few days of this period when more flies were present, they sometimes split into two groups operating almost independently, but when one swarm became particularly large, long-lasting and more vigorous, it would stimulate the neighbouring flies to join in, like the cascade effect noted often for *C. cristatus*. These flies appeared to remain separate and return to their 'home patch' about 50-75cm distant when they settled. On one occasion, 2-3 *C. cristatus* were briefly mixed with a *C. asiliformis* swarm, as the *Eupatorium* stand was at the boundary of the two species' areas, but I could not tell whether they responded to each other.

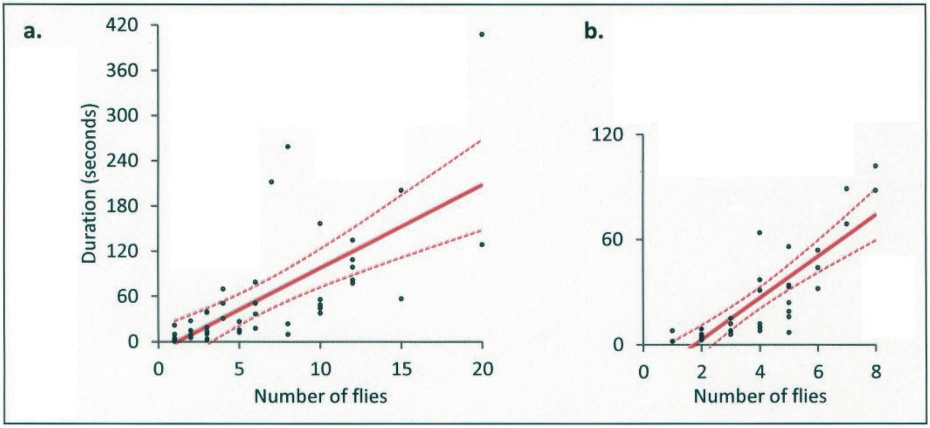

Fig. 5. Duration of swarm events of *Chrysopilus asiliformis* against the number of flies in each event, for two groups of flies, a) over *Eupatorium* 22 July 2020 and b) over *Equisetum telmateia* 13 July 2020. Fitted regression with 95% confidence limits. Scales of both axes differ in the two graphs.

Over the 24 days of observations of the flies using the *Eupatorium* flowers, perching and swarming took place between about 8:00 and 9:30, and swarming finished about an hour later than the first large swarm (Fig. 3c). These times became gradually earlier and this was difficult to explain. The onset of swarming showed a significant negative correlation with temperature for 14 dates between 12 July and 3 August ($r= -0.58$, 12d.f., $p<0.05$) and explained a moderate amount of the variation ($r^2=0.34$), suggesting that swarming started earlier when it was warmer. But temperature at the start of swarming did not change over the 24 day period. Observer error seems unlikely since the end of swarming also became earlier, and I am unlikely to have been consistently wrong in both sets of times. On only eight days were both the start and end times of swarming noted, and these gave a median (with interquartile range) of 55 (47–62) minutes.

The duration of each swarm event was plotted against the number of flies in each event for the four timed swarms. The regression was significant at $p<0.05$ for one swarm and at $p<0.001$ for three of the swarms; one example of each group of flies is shown in Fig. 5.

The only female seen was elsewhere in the garden 10 days after the end of swarming.

Discussion

This study showed that male *Chrysopilus cristatus* and *C. asiliformis* have a characteristic swarm behaviour of repeated bouts of synchronised flight when they interact strongly with each other, separated by periods when all the flies settle. Both species had a similar flight pattern although individual *C. cristatus* used a larger air-space than those of *C. asiliformis*. There was also a similar daily routine, beginning with flies finding a perch site with a good view overhead, followed by a few tentative flights or short swarms separated by long periods of rest, then building up to extended flights that lasted longer than the intervening rests, before tailing off at the end of swarming. Median times in flight measured in periods of 15 minutes were 15-45 seconds for *C. cristatus*, and 10-30 seconds, or exceptionally 80 seconds, for *C. asiliformis*, although with considerable variation. But whereas *C. cristatus* spent a similar time at rest as in flight, *C. asiliformis* was at rest for at least as long as the flight, and usually far longer. However, part of this difference may be an artefact of observation since the behaviour of the tiny swarms of *C. asiliformis* could be followed more accurately than the huge swarms of *C. cristatus*, and this was supported by the timed resting periods of individual *C. cristatus* which were more in line with those of *C. asiliformis*. *Chrysopilus cristatus* used no swarm marker but instead swarmed over a large area of heterogeneous vegetation. In contrast, *C. asiliformis* used a more conventional swarm marker.

Swarming was a morning activity. The main period of swarming of *C. cristatus* started at about 8:30–9:30 and ended at about 10:00–11.00, with a median duration (overestimated) of 87 minutes. Times for *C. asiliformis* were similar (8:00–9:30, median duration of 55 minutes). Temperature influenced the start of swarming. For both species, the threshold for swarming was just over 13°C and, at least for *C. asiliformis*, swarming started earlier on warmer mornings. Both species appeared to avoid strong sun, moving into shade or stopping altogether. For *C. cristatus* an upper threshold appeared to be 18°C. Swarms stopped, or never started, in rain, persistent drizzle and strong winds. The swarm ‘season’ was long for *C. cristatus*, starting at the end of May, although I probably missed the first events, and ending at the beginning of August. The first swarms of *C. asiliformis* were not noticed until mid-July, but they too had stopped within a day of *C. cristatus*.

Although this description appears to be moderately full, the flies’ behaviour raised some interesting issues. Firstly, where did females fit in? Only 38 individual female *C. cristatus* were seen in the 69 days over which observations were made, compared to a rough daily estimate of the male population in June of 1000-2000 individuals in the $500m^2$ plot (20,000-40,000 ha^{-1}), and perhaps several hundred males seen landing from swarms and just sitting on the vegetation during this period. Even on early morning transect counts, before males had started swarming, they far outnumbered females, yet similar numbers would have been expected as both sexes sought a perch with an open view of the sky. This disparity is not due to an imbalance in the sex ratio. By good fortune, Robert Wolton was running emergence traps in a wet woodland in North Devon concurrently with my study (1 June – 28 July). His counts of emerging *C. cristatus* were 40 males and 39 females, the males emerging throughout this period and females absent only in the first 10 days. Grootaert *et al.* (2020) recorded 63% males among 275 individuals collected by Malaise traps in Belgium. The scarcity of females in my garden may therefore have been because males moved to the meadow for courtship but larvae did not develop here but in the adjacent wet woodland, although only eight males and no females were recorded in a Malaise trap here in 2005

(Drake 2011). Although my numbers of *C. asiliformis* were far too small to provide an estimate of its sex ratio, Grootaert *et al*. (2020) had a ratio of 68% males in 671 individuals caught by Malaise trapping, and they quote a similar ratio (70%) recorded by Krizelj (1971, not seen).

Interactions between males and females were rarely seen. The scarcity of mating pairs is difficult to explain since two remained coupled for 26-28 minutes, so I would have expected to find more if they remained immobile on the vegetation for this duration. It is also odd that these pairs were seen only at the very start of the study. What, then, was the purpose of swarming for the bulk of the time? Although rare, these few male-female interactions dispel Chvála's (1983) suggestion, at least for *Chrysopilus*, that male-only swarms are 'relict swarms' (his term) that are a "relict form of behaviour on the part of species that originally mated in aerial aggregations but have subsequently transferred their mating activity to the ground."

Many studies show that females are relatively rare within Diptera swarms but this is usually because females, having been attracted to the swarm, are quickly removed by the males (several studies quoted by Downes 1969). A few studies have, like mine, recorded remarkably few matings and Downes (1969) suggested that swarming continues after the first females have been intercepted on the off-chance that more will appear. If this is the case in *Chrysopilus*, it represents a huge expense of energy for what seems to be almost no return. Downes also quotes Corbet (1964, not seen) who found that matings in mosquitoes were seen more frequently when steps had been taken to improve the methods of observation. This may be true for small mosquitoes but it seems most unlikely that inadequate observation was the reason for seeing so few females and even fewer male-female interactions in *C. cristatus* which is large and conspicuous. One would expect that a pair mating in mid-air would be most un-airworthy and drop conspicuously onto the vegetation and, as those seen appeared to remain paired for about 30 minutes in full sight, their scarcity was unlikely to be due to inadequate observation.

The second issue arising from this study is that the behaviour of *Chrysopilus* is unusual among swarming flies. Gruhl (1955) provided a classification of swarming behaviour in Diptera and, while it is probably discredited (it is rarely mentioned), it provides a useful label that can be applied to the behaviour of *Chrysopilus*. Among flies exhibiting some development of social structure in their swarms, thus excluding the apparently unordered swarms of many Nematocera, he speculated that the primitive condition was a single fly at a perch rising to intercept any passing insect as a possible mate, and the most advanced behaviour as the synchronised and complex swarms of either sex in which individuals remain aloft for very long periods (his synorchesium). Intermediate stages in this evolutionary advancement were for a single fly to remain aloft for a while, then land (monorchesium), and then for several flies to do this (polyorchesium). Chvála (1994) neatly summarised the polyorchesium as 'rhythmic dancing-perching-dancing'. Gruhl speculated that the driving force was to obtain a better view of potential mates by flying up from the perch, and that, as a species became a more proficient flier or hoverer, the resting phase between flights becomes shorter until eventually obsolete. Regardless of whether Gruhl's theory can be substantiated (for instance, Daugeron (1997) and Yuval (2006) presented the evolutionary path in the opposite direction), his classification is of use in the present case of *Chrysopilus* as its swarming behaviour fits his polyorchesium. Gruhl erected this category for the syrphid *Cheilosia proxima* (Zetterstedt) and the non-British empid *Empis* (*Anacrostichus*) *bistortae* (Meigen), and Chvála (1994) added the *Empis* subgenus *Kritempis* with his description of its swarming behaviour having similarities to that of *Chrysopilus*. Later, Gruhl (1959) observed *Rhagio lineola* swarming and alighting at intervals, although he proposed yet another behavioural class for this pattern and his descriptions suggests that it was windiness that caused the flies to alight frequently, which is different from the inherent behavioural pattern of *Chrysopilus* (*R. lineola* has simple eyes). Nagatomi (1962) described behaviour in Athericidae that fall into Gruhl's polyorchesium. I can add the muscid *Hebecnema nigricolor* (Fallén), based on observations in my garden. Here for six weeks (1 August to 15 September 2020) a group of seven individuals gathered in early morning on an unremarkable sprig of a hazel hedge, where the same ten leaves in permanent shade formed the focus of their activity. No other such groups were found despite the hundreds of opportunities of similar swarm markers in the garden. The flies swarmed with a flight-and-rest pattern rather like that of *Chrysopilus asiliformis* for about an hour, then disappeared for the rest of the day, only to reappear the next morning to repeat the performance. Their numbers slowly dwindled until only 1-2 flies were seen during the last 7 days, still swarming as before. This complex behaviour required these same individuals to remember for several weeks where their swarm marker was and respond to each other, much as *C. asiliformis* did. Polyorchesium is clearly an uncommon pattern of behaviour.

Within the Rhagionidae, the rapidly alternating flight and rest of *Chrysopilus* contrasts with long-lasting swarms in the closely related *Symphoromyia* as reported in two Canadian studies. Shemanchuk and Weintraub (1961) described the male swarm of *S. hirta* Johnson as up to 100 yards along pathways through trees and they imply that the swarm remained airborne from 7:30 in the morning until late afternoon, and males had an erratic flight. Hoy and Anderson (1978) described the swarms of *S. sackeni* Aldrich, which, although they were continuously aloft, had some aspects in common with those of *Chrysopilus*. Swarming in *S. sackeni* took place in the morning, sometimes lasting into early afternoon when cooler, and they suggested that high temperature was one factor that stopped swarming, as appeared to be the case in both *Chrysopilus* species. Initially, there were only a few flies per swarm but numbers increased at the peak of activity, then decreased again towards the end of the period. For one day, they quote numbers of 5-10 individuals at the beginning, rising to 25-35 individuals at the peak, although on other days the maximum was about 100 flies. These values are similar to those of *Chrysopilus* swarms although *C. cristatus* was far more abundant at peak-swarm, and *C. asiliformis* less numerous. They also noted how infrequent females were, those that had not been inseminated comprising 5% of their sample, and they saw only three mating pairs.

Flying continuously is presumably energy-intensive, so perhaps swarming for only part of the time saves energy while still advertising to females and being able to respond rapidly to a female. Although I could not measure the time that any individual remained in a swarm, since it was impossible to follow, I did measure the time that individual *C. cristatus* remained resting between flights. These times were similar to measurements of the entire population resting between swarms, which provided confidence in both measurements, and they are similar to the time spent in flight. This suggests that males on average remain settled for about half of the time. During the peak of the swarming period, resting time was shorter, presumably because no male wanted to ‘miss out’, although any individual was often seen resting when the next swarm was taking place overhead. Being able to respond very quickly as other males begin to swarm allows resting males to conserve energy without suffering too much loss of time in intercepting a female. I add this speculation as an evolutionary reason for polyorchesia.

Regardless of whether intermittent swarming is an energy saving mechanism, the flies presumably live for many days so would be expected to have to feed. Rhagionids are reported feeding by mopping-up material on leaves (e.g. Drake 2014), but only twice was a male *C. cristatus* seen to do this. Perhaps feeding is an activity for the afternoon when they were scarcely seen after about 11:00. Although they disappeared as mysteriously as they appeared on their perches, the few seen at the end of swarming appeared to move deep into the vegetation where, they perhaps roost and feed until the next morning, rather than migrate to nearby hedges.

It was unclear what initiated each swarm event. In both species, one individual took off of its own volition, and others very quickly followed within 1-2 seconds, but what prompted that first fly to take off was unclear. The time *C. cristatus* males spent at rest before re-joining a swarm followed a negative power curve which strongly suggests an intrinsic behaviour – how long shall I wait before taking off again? The prompt for the first males to take off therefore appeared to be internal, and following males were responding to this first fly. On rare occasions when a female was seen taking off, the males followed, so they were responding to a cue coming from below their perches since females nearly always perched lower down. If this is correct, then females do not respond to males, but males do respond to females that take flight. It is possible that the bright golden tergite hairing of females makes them more visible to the males. However, neither *Chrysopilus* was seen to respond to other passing insects, including several, such as the syrphids *Chrysotoxum*, *Episyrphus* and *Platycheirus*, with yellow patterns that might resemble the golden hairing of female *C. cristatus*. But females were very rare so could not be the stimulus for nearly all swarm events.

Downes (1969) had a clear notion that a swarm was "In essence .... a group of individuals responding independently to the one [swarm] marker, a preferred object of a relatively rare sort; it does not owe its existence to responses between the insects themselves." Downes dismissed interaction between individuals in forming the swarm and regarded any interaction and coherence as subsidiary phenomena. This view appeared to have been developed in the 1960s and was repeated by later workers (e.g. Sullivan 1981) but it seems an oversimplification for the tightly coordinated swarms of many flies where interaction between individuals clearly takes place, whether or not there is a discrete swarm marker. The synchronised pattern of taking-off and landing of *Chrysopilus* is not a mere subsidiary phenomenon but is closer to the complex behaviour associated with leks, but apparently without male aggression or defending a space. Furthermore, this behaviour appears to be more than an intermediate evolutionary step between Gruhl's monorchesia and synorchesia, but a distinct class of behaviour of perhaps greater complexity than either of these. Yuval (2006) suggested that the mating system of Rhagionidae may represent a link between the swarming behaviour of Nematocera and more recently evolved suborders, but this was based on the behaviour of *Symphoromyia* which does not resemble that of *Chrysopilus*.

More recent work has moved ideas forward from those of Downes in a way that embraces the apparently aberrant behaviour of *Chrysopilus*. Attanasi *et al*. (2014) investigated swarms of three tiny nematocerans, two chironomids and one ceratopogonid, with body lengths 1.2 – 2.4mm. Using techniques way beyond those available to me, they show that these flies respond not just to the swarm marker but also to the motion of both nearby individuals within a few body-lengths, and to those at a considerable distance of about 15 to 25cm, depending on the species, which is a huge distance for a tiny fly in a milling throng. They dispelled the notion that all individuals react only to the physical environment (the swarm marker) but instead act in a coordinated fashion. This is what *Chrysopilus* does in a manner far more obvious than seen in most nematoceran swarms. Several aspects of *Chrysopilus* swarms indicate considerable awareness and response to neighbouring flies. Most trivially is the rapid circling around one-another when they approached closely but this can be seen in the swarms of many flies. Their almost instantaneous take-off, the cascading of the swarm across the area and landing in synchrony were the strongest expressions of interaction. More flies in the air led to a longer event, seen most convincingly in *C. asiliformis*, which again suggests an awareness of the extent of the swarm. The mechanistic swarm-marker view of swarming promulgated by Downes needs re-assessing for many Diptera.

Acknowledgements

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Dipterists Digest 2022 **29,** 35-38

The early stages of *Pegomya cunicularia* (Rondani) (Diptera, Anthomyiidae)

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Summary

Adults of the leaf miner *Pegomya cunicularia* (Rondani, 1866) were reared from perpetual spinach (*Beta vulgaris*). The life history is discussed and illustrated.

Introduction

The *Pegomya hyoscyami* species complex contains four species that are morphologically distinct in both sexes: *Pegomya betae* (Curtis), *Pegomya cunicularia* (Rondani), *Pegomya exilis* (Meigen) and *Pegomya hyoscyami* (Panzer) (Michelsen 1980).

These are important economically as leaf miners of spinach and beet crops. In Britain *P. cunicularia* is known primarily as an uncommon coastal species, feeding on sea beet (*Beta vulgaris* subsp. *maritima*) (Ackland *et al*. 2018).

Pegomya cunicularia feeds on Chenopodiaceae such as *Atriplex glauca* (waxy saltbush), *Beta vulgaris* (beet), *Chenopodium album* (fat-hen), *Patellifolia procumbens* and *Spinacia oleracea* (spinach). An infestation of *P. cunicularia* can cause seedlings to die and mined leaves to wilt (Mehklif 1999).

On 31.v.2020, I found a couple of leaves of perpetual spinach (*Beta vulgaris*) with large blotch mines in my vegetable patch in the garden. The blotches were initially white, later with a greenish tinge, as the mine developed. I could not initially find any eggs on the undersides of the leaf, as one would expect for *Pegomya* miners on these leaves, and wondered if they were perhaps the mines of *Scaptomyza graminum* (Fallén, 1823) (Drosophilidae).

I sent photographs to Barry Warrington and Willem Ellis for their comments. WE did not think they were a *Scaptomyza* species and BW suggested that they were perhaps a *Pegomya* species. Closer examination of leaves proved this to be the case as a typical *Pegomyza* egg cluster (4 eggs) was found under a leaf. Adult flies were reared through (emerging from 15.vi.2020) and dissected to determine the identity of this miner.

Life history

Eggs are laid in batches of 3-8 (Plant Pests of the Middle East). My spinach had a small infestation and I found one leaf with four small white lozenge-shaped eggs under a leaf (Fig. 1), from which larvae had emerged to feed in the leaf. The eggs were laid on the lower leaf surface. Steyskal (1970) gave detailed descriptions of the larvae and puparia.

The large blotch mines formed were initially white (Fig. 2), but having a greenish tinge at the edges as they expanded (Fig. 3) through the leaf (presumably due to the colour of the underlying parenchyma in the thick perpetual spinach leaf). These mines discoloured as they aged to become a dirty purple/grey colour in this host (Fig. 4).

These mines were usually upper surface and could occupy the majority of the leaf but sometimes developed wholly on the lower surface.

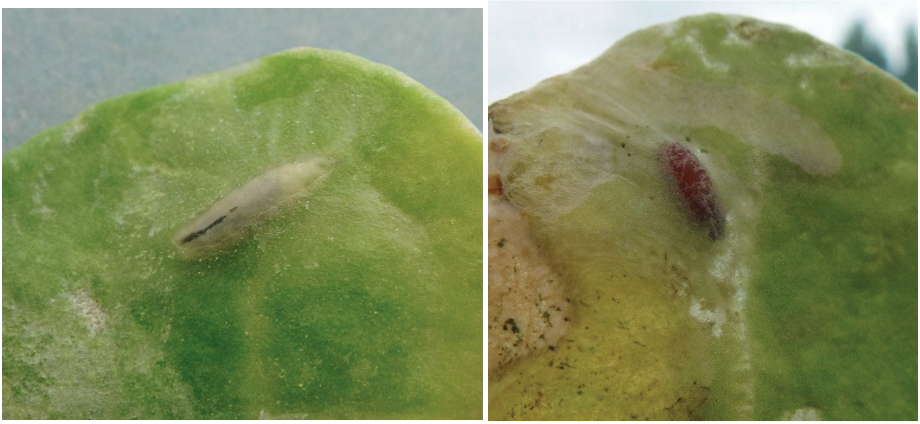
Several larvae could inhabit a mine and they may change leaves to continue feeding, which would explain why I initially failed to find eggs on the mined leaves.

Figs 1-2. *Pegomya cunicularia*: 1, egg cluster; 2, white blotch mine.

Figs 3-4. *Pegomya cunicularia*: 3, mine becoming greenish; 4, mine discolouring with age.

The larvae are white, cylindrical in shape, tapering towards the head end, having a partial black strip on their dorsal surface (Fig. 5), although this is not characteristic to just this species.

Pupariation was found to be either external to the leaf or inside it (Fig. 6). I have also found this behaviour with other reared leaf-mining Anthomyiidae (e.g. *P. bicolor* (Wiedemann) and *P. solennis* (Meigen)). Pupariation inside a leaf may be a facultative response to captive rearing, but it is not mentioned in the literature examined so far.



Figs 5-6. ***Pegomya cunicularia*****: 5, larva within mine; 6, pupariation within a mine.**

The puparia were a reddish brown colour and approximately 6mm x 2mm with low spiracular bases (Fig. 7). They bore resemblance to those of *P. betae* but not *P. hyoscyami*, the latter having even more reduced spiracular bases (Fig. 8).

Fig. 7. ***Pegomya cunicularia*****: puparium viewed from above.**

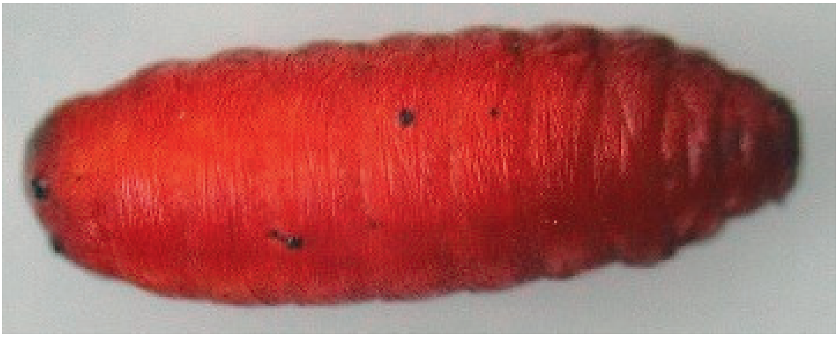


Fig. 8. ***Pegomya hyoscyami*****: puparium viewed from above.**

I dissected an adult male and was very surprised to find that the 5th sternite had the distinctive two tufts of dark setae at the bases of the posterior processes, which identifies the species on this host as *P. cunicularia*. A further male was dissected to confirm this identification and a photograph shown to Michael Ackland.

The British records of *P. cunicularia* are almost all on the coast (Anthomyiidae Recording Scheme data on the NBN Atlas). My house is situated besides the tidal River Great Ouse and is approximately 10 miles from The Wash so the adults may have originated from the North Norfolk coast.

The phenology of this uncommon leaf miner is interesting as adult records are from May to August with a peak in June (Anthomyiidae Recording Scheme data on the NBN Atlas). It appears to be univoltine.

Pegomya cunicularia is now confirmed as mining perpetual spinach (*Beta vulgaris)* inland in Britain.

Acknowledgments

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Dipterists Digest 2022 **29,** 39-43

Covering sapping beech stumps to attract *Brachyopa panzeri* Goffe (Diptera, Syrphidae)

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Summary

Various methods of covering sapping beech stumps attracted *Brachyopa panzeri* Goffe, 1945. Some stumps provided breeding sites for one year.

Introduction

Brachyopa panzeri Goffe, 1945 is mostly found in humid *Fagus* forests but also in alluvial *Populus* forest, mixed *Carpinus-Quercus-Pinus* forests and even in coniferous forests (van Steenis *et al*. 2020). The Danish Red List (Bygebjerg 2019) lists *B. panzeri* as endangered, but it seems to be increasing. The species is dependent on a continuous supply of old trees.

Prior to the finds mentioned in this article, the larva of *B. panzeri* had been found in a sap run on *Fagus sylvatic*a (Stuke and Schulz 2001). Krivosheina (2015) described the larva based on six larvae from a fir stump. As no adults were reared, however, van Steenis *et al*. (2020) stated that the larva was undescribed, but included it in the identification key. Shparyk and Zamoroka (2021) described the puparium and redescribed the third-instar larva based on larvae from a crack in a pedunculate oak (*Quercus robur*) stump filled with rotten wood.

Four *Brachyopa* species are known from the region where the forests mentioned in this article are located: *B. panzeri*, *B. insensilis* Collin, 1939, *B. pilosa* Collin, 1939 and *B. testacea* (Fallén, 1817).

First observation

In the early spring of 2015, I observed a sapping beech stump with a diameter of approximately 110 cm in Vindum Skov (56.394487, 9.548441), a Danish national forest in the central part of the peninsula of Jutland.

To protect the sap from sun and rain, the stump was covered with a block and pieces of wood. The purpose was to see whether the sap would attract *Brachyopa pilosa*, a species common in the forest. In July, there were more than 30 larvae underneath the block. A few larvae collected hatched in 2016. They were all *Brachyopa panzeri* and the first record for this location.

Later that summer, the cover had been removed. As the heavy block lay 2-3 metres away from the stump and the pieces of wood were spread metres away around the stump, an animal could be ruled out as a culprit. There were no larvae or puparia. Finding mature larvae under the block spurred the idea to see if it was possible to provide temporary breeding sites by covering sapping beech stumps.

Methods

Method 1: Sapping stumps were covered with blocks and pieces of wood found at the site.

Method 2: As it is often difficult to find suitable pieces of wood at a site, ordinary MDF (medium density fibreboard) sheets were used in combination with pieces of wood. MDF was chosen as it is lightweight and easy to break into pieces. Although there is no health risk to people from the amount of formaldehyde gas given off by MDF, the sheets were left to gas off for several weeks in a carport. The purpose was also to reduce any toxicity to larvae.

Each piece of sheet was secured to the stump with a screw in the middle or with pieces of wood.

Method 3: To try and protect MDF sheets against the weather, raw linseed oil, which is non-toxic for humans and animals, was applied onto the rough side of ordinary MDF sheets - the side facing the stump. The use of exterior-grade MDF sheets was considered but rejected because of the costs and possible toxicity.

The pieces were secured with nails - a rather bad idea as this makes it difficult to remove pieces when checking for larvae without harming them.

Fig. 1. Block of wood and beech stump with larvae of *Brachyopa panzeri*.

Identifying larvae and reared specimens

Larvae collected and preserved were identified using the key of Krivosheina (2015) and rechecked in 2021 using the key of van Steenis *et al*. (2020). Reared adults were identified using the key of Speight and Sarthou (2017) and the key in Nationalnyckeln (2009).

Results

Method 1 – blocks and pieces of wood:

Covering the first sapping beech stump in 2015 resulted in more than 30 larvae of *B. panzer*i. A few larvae were collected, and five males emerged around 7 May 2016.

In June 2016, biologist Jan Grundtvig Højland of the Danish Nature Agency and I covered a few stumps with pieces of wood a few hundred metres from the first stump. It resulted in a few *B. panzeri* and *B. pilosa*. The stumps were probably too small and did not have enough sap.

Method 2 – ordinary MDF sheets and pieces of wood:

In the middle of May 2018, sapping stumps of recently felled beech in another part of Vindum Skov (56.389333, 9.545437) were covered; several small stumps with a diameter of 20 to 40 cm and two with a diameter of approx. 80 cm (Fig. 2).

While the first stump was being covered, a few *Brachyopa panzeri*, *B. pilosa*, *Xylota segnis* (Linnaeus, 1758) and *X. sylvarum* (Linnaeus, 1758) were already attracted to the sap.

Fig. 2. Beech stump covered in 2018.

In late June, only one of the small stumps still had sap and approximately 15 larvae of *B. panzeri*. The best of the two large stumps hosted approximately 100 larvae, with an estimated 95% *B. panzeri* and 5% *B. pilosa*.

The other large stump hosted fewer larvae. On that stump, 3-5mm thin twigs had been placed between the stump and cover to create space. This seems to be counterproductive, as it creates access for beetles and centipedes. The number of larvae had decreased every time the stump was checked.

The summer of 2018 was unusually hot and dry. The sheets got dry and sucked the stumps dry, leaving no sap for larvae or causing mature larvae to die from desiccation. As a consequence, most larvae died, especially on the best stump, which was exposed to the sun during midday.

Two *B. panzeri* larvae were collected on 28 October 2018. Males emerged on 16 April 2019 and 26 April 2019, respectively. Six larvae of *B. panzeri* and one of *B. pilosa* collected and preserved were identified using the key of Krivosheina (2015) and rechecked in 2021 using the key of van Steenis *et al*. (2020).

Method 3 – MDF sheets treated with raw linseed oil and pieces of wood:
For one last attempt in 2019, another national forest in the region was chosen in order not to affect the number of the endangered species on the first location even more negatively. The location chosen was Fussingø Skov (56.467476, 9.831063). Three stumps with a diameter of 100 to 150 cm in partially shaded situations were covered (Fig. 3).

Periods with heavy rain followed dry periods. The MDF sheets got dry or soaked, but not to an extent that killed larvae. Only one stump had sufficient sap to attract females. When the stump was checked in July 2019 and blocks of wood and a few pieces of MDF sheet were removed, there were approximately 30 larvae of *B. panzeri* and a few of *B. pilosa* and *Sphegina*, presumably *S. clunipes* (Fallén, 1816). The low number of larvae is probably the result of selection felling in most parts of the forest in 2019, and consequently a high number of suitable stumps.

Blocks of wood were removed only twice to check for larvae, as it is extremely difficult to put a block back on the stump without crushing larvae. A few larvae were collected on 2 February 2020, and a male of *B. panzeri* emerged on 28 April 2020. In late April, several puparia were found in moss at the edge of the stump.

Fig. 3. Beech stump covered in 2019.

Sheets and blocks were left on the stumps to benefit other larvae. In the autumn of 2020, no larvae of *B. panzeri* were found, only a few of *Sphegina* sp. and *Xylota segnis*. Larvae found in a hole filled with water and sap under a piece of sheet in 2019 turned out to be *Eristalis pertinax* (Scopoli, 1763).

Discussion

Covering sapping stumps does enable larvae to reach pupation; such sites, however, are only suitable for one or maybe two years. It is time-consuming or sometimes impossible to find sapping stumps, and they may quickly dry out. It is also problematic that MDF sheets may suck up sap and cause larvae to die, especially during hot periods.

The method can, however, be used to see whether *B. panzeri* is at a location. It may also work for other species depending on sap.

Recommendations

The projects were too small to reach conclusions about the optimum approach; only recommendations can be made.

Sapping stumps in a partially shaded situation are the most suitable. The two best stumps had a diameter of 80 and 150 cm, respectively. Blocks and flat pieces of wood placed directly on the stump offer the best protection for larvae, but care must be taken when removing a block to check for larvae and putting it back on again. A solution may be to screw washers with a thickness of 1-2 mm into the block.

Untreated MDF sheets are problematic as they may absorb sap, resulting in death of larvae. Sheets applied with raw linseed oil are better. Secure sheets by placing branches or pieces of wood on the sheets, or with screws, if permitted by the forest owner or local authorities.

Acknowledgements

I would like to thank the following persons: Biologist Jan Grundtvig Højland of the Danish Nature Agency for providing me with felling plans and giving me permission to carry out various small projects in national forests; Lars Mørk of the Danish Nature Agency for providing me with maps showing where and which kind of tree was to be felled; Somporn Phanla-or Carstensen for helping me find and cover sapping stumps.

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***Liriomyza pisivora* Hering (Diptera, Agromyzidae) new to Wales –** On 28.vii.2021, numerous mines (Fig. 1) of *Liriomyza pisivora* Hering, 1954 were found on several plants of broad-leaved everlasting-pea (*Lathyrus latifolius*) on the edge of a footpath through a wooded area of Grangemoor Park (V.C. 41), a former moorland that was repurposed as a domestic landfill from the early 1970s until the mid-1990s and subsequently redeveloped into a public park by Cardiff City Council, opened in 2000. The parkland is now designated as a Site of Importance for Nature Conservation (SINC). Although *Lathyrus latifolius* is quite widespread within the park, mines have so far only been located in one relatively small area (ST173738). Although widespread, it is a seldom recorded species, with just 28 records (from twelve vice-counties) within the National Agromyzidae Recording Scheme database (Barry Warrington *pers. comm.*)

Fig. 1. Characteristic mines of *Liriomyza pisivora* Hering, 1954 on *Lathyrus latifolius*.

I am grateful to Barry Warrington for his advice on the identifying characteristics for this species and for confirmation that this species is new to Wales – **ANNIE IRVING**, Penarth, Wales

Dipterists Digest 2022 **29,** 45-48

New records of *Calliphora* Robineau-Desvoidy (Diptera, Calliphoridae) from the Isle of Skye and Raasay, Scotland

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Summary

Four species of *Calliphora* Robineau-Desvoidy, 1830 were collected during a two-week-long visit to the Isle of Skye and Raasay, Scotland, including the pNationally Scarce species *C. loewi* Enderlein, 1903 and *C. uralensis* Villeneuve, 1922. Collection data and ecological information are provided.

Introduction

The author decided to focus attention towards locating two uncommon blowfly species *Calliphora loewi* Enderlein and *C. uralensis* Villeneuve during a two-week visit to the Isle of Skye and Raasay in August 2020. *Calliphora loewi* has been recorded across northern Scotland but is by no means abundant (van Emden 1954; Smith 1986). It has yet to be recorded from Skye, although there is a singular observation made by Stephen Bungard from the adjacent island of Raasay (Macdonald 2016). *Calliphora uralensis*, which has been the focus of many distributional studies by Macdonald (2014; 2016; 2017; 2018) (using records collected post-2000), has been shown to have a confirmed distribution encompassing the Shetland Islands, Orkney, the Outer Hebrides, the western coast of the Scottish mainland, in addition to newer disjunct observations from East Lothian and Bass Rock, which are likely associated with the Forth seabird colonies. There is a clear deficit of records for this species from the Inner Hebrides, but this is wholly a consequence of the lack of active recorders within the region.

During the visit both species were successfully recorded, including two new locations for *C. uralensis* and the first record of *C. loewi* for Skye. The two ubiquitous species *C. vicina* Robineau-Desvoidy and *C. vomitoria* (Linnaeus) were also recorded from Skye and Raasay. The new records for the four species are provided below in addition to notes on their habitat and behaviour. All specimens noted in the records section were mounted, identified using the draft key to British Blowflies (Calliphoridae) and woodlouse flies (Rhinophoridae) by Falk (2016), and stored in the author's collection.

Species Accounts

Calliphora loewi Enderlein, 1903 (**Fig. 1**)

Records. 2♀, Sligachan, Skye, Scotland. 27.viii.2020. NG 37328 30967. leg. Thomas D. Hughes, det. Olga Sivell. ex. mackerel bait trap.

Remarks. Despite several attempts to locate *C. loewi*, only 2 females were encountered after placing a single mackerel-baited trap for two days in an isolated, thinly planted pine woodland surrounded by expansive bogs and moorlands at 72masl. Sampling of similar habitats in the area only turned up *C. vomitoria* in large numbers.

Fig. 1. ♀ ***Calliphora loewi*** **Enderlein, 1903. Sligachan, Skye, Scotland. 27.viii.2020. NG 37328 30967: Lateral view.**

Fig. 2. ♂ ***Calliphora uralensis*** **Villeneuve, 1922. Fiskavaig Bay, Skye, Scotland. 18. viii.2020. NG 33614 34652: Lateral view.**

Calliphora uralensis Villeneuve, 1922 (**Fig. 2**)

Records. 1♂**,** Fiskavaig Bay, Skye, Scotland. 18. viii.2020. NG 33614 34652. leg./det. Thomas D. Hughes. ex. *Columba livia* (rock dove) carcass; 1♂, Coral Beach, Skye, Scotland. 19.viii.2020. NG. 22351 55223. leg./det. Thomas D. Hughes.

Remarks. At both locations *C. uralensis* was never abundant and was easily outnumbered by *C. vicina* and *C. vomitoria*. The *C. uralensis* from Coral beach was caught basking on an east-facing rocky outcrop 100m (14masl) from the shoreline and the other from Fiskavaig Bay was caught visiting the carcass of a *Columba livia* (rock dove) resting just above the high tide mark (2masl). By the presence of several other older skeletons and numerous feathers it was apparent this was a common and regular roost for *C. livia*.

Calliphora vicina Robineau-Desvoidy, 1830

Records. 1♂, 1♀, Carbost, Skye, Scotland. NG 38378 31390. 16.viii.2020. leg./det. Thomas D. Hughes; 1♀**,** Fiskavaig Bay, Skye, Scotland. 18. viii.2020. NG 33614 34652. leg./det. Thomas D. Hughes. ex. *Columba livia* (rock dove) carcass; 1♂, Carbost, Skye, Scotland. NG 38378 31390. 21.viii.2020. leg./det. Thomas D. Hughes; 1♂, Inverarish, Raasay, Scotland. 25.viii.2020. NG. 54918 36452. leg./det. Thomas D. Hughes.

Remarks. Easily the most encountered of the *Calliphora* species; *C. vicina* was very abundant in synanthropic and coastal sites, becoming less abundant in coniferous woodland, where it was replaced by *C. vomitoria*. It was most often caught basking on walls, fences and cliff faces.

Calliphora vomitoria (Linnaeus, 1758)

Records. 1♀, Fiskavaig Bay, Skye, Scotland. 18.viii.2020. NG 33614 34652. leg./det. Thomas D. Hughes. ex. *Columba livia* (rock dove) carcass.

Remarks. A very commonly encountered species; *C. vomitoria* was present at lower abundance than *C. vicina* but became extremely abundant in woodland settings; typically along sunlit woodland rides dominated by Apiaceae (umbellifer) flowers. A single female specimen from Fiskavaig bay was caught whilst visiting the carcass of a *Columba livia* (rock dove) (2masl).

Discussion

Despite successfully locating the two target species, the time taken to sample appropriate habitats over a short period means the number of records still remains relatively low for Skye and Raasay (with this study providing three additional data points for the two species combined). The records of *C. uralensis* were entirely coastal (<100m from the shore) and associated with relatively sheltered locations. It is highly likely that *C. uralensis* is present around the entire coastline of Skye and Raasay, but focused sampling would be required to separate them out from the more abundant *C. vicina* and *C. vomitoria*. The singular record of *C. loewi* from a mackerel-baited trap may suggest that the species demonstrates a greater habitat specificity, or simply occurs at lower frequencies than other *Calliphora* on both islands. Interestingly, Macleod and Donnelly (1956) noticed that baited traps produce mutable results, showing that some adult calliphorids are irregularly distributed across habitat types and at variable densities. Therefore, the low occurrence rate of *C. loewi* may be a product of our failing to sample appropriate habitats thoroughly enough to compensate for these variable densities. Despite this, the Highland

Biological Recording Group (HBRG) database shows *C. loewi* is relatively scarce throughout the Highlands, with a total of 54 records in 27 hectads, compared to *C. vicina* (432 records in 149 hectads) and *C. vomitoria* (226 records in 106 hectads) with the records for *C. loewi* representing all encounters, but those for the other two species representing significant undercounts (M. Macdonald *pers. comm.*). The same could be said for the scarce species *C. subalpina* (Ringdahl), which despite having several records from Raasay (Macdonald 2016), was not encountered during this visit and is only represented by 57 records in 16 hectads on the HBRG database (M. Macdonald *pers. comm.*). Furthermore, the two ubiquitous species, although abundant across the two islands, showed some degree of habitat preference, with *C. vicina* favouring synanthropic sites and *C. vomitoria* in woodland areas. Unfortunately, no flies were sampled above 140masl, which inhibited the possibility of searching for the remaining British species *C. stelviana* (Brauer & Bergenstamm). Although this species is incredibly rare and has not been recorded from either island previously, its desired altitudinal range between 500-1070masl (Horsfield 2002) suggests it could occur in upland areas of Skye such as the Cuillin Hills, awaiting discovery.

Acknowledgements

I am very grateful to Olga Sivell for reviewing this article and providing help with the identification of *Calliphora loewi*.

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Dipterists Digest 2022 **29,** 49-52

Sylvicola fuscatus (Fabricius) (Diptera, Anisopodidae) new to Britain

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Summary

Sylvicola fuscatus (Fabricius, 1775) is added to the British list, based on a specimen taken in April 2021 from Buckinghamshire and its identification and distribution are discussed.

Introduction

A single male *Sylvicola* was swept from the ground layer in an area of secondary woodland in the Chilterns in the late afternoon of 22 April 2021. It was noticeably large for the genus and was retained for further examination. Running the specimen (Fig. 1) through the key provided by Søli and Rindal (2014) showed it to be *Sylvicola fuscatus* (Fabricius, 1775), which was confirmed by Libor Dvořák based on photographs uploaded to the *Diptera.info* website. The specimen was subsequently dissected, and the male genitalia examined (Fig. 2). Reference to the most recent update to the checklist of the Diptera of the British Isles (Chandler 2021) confirmed this to be a species new for the British fauna. A further specimen was subsequently collected by Matthew Harrow from Ivinghoe Common on 11 July 2021.

Fig. 1. ***Sylvicola fuscatus*** **male, woodland above Incombe Hole, Steps Hill, Ivinghoe.**

Identification

Sylvicola fuscatus is a member of the *S. punctatus* (Fabricius) group (formerly the subgenus *Anisopus* Meigen). The most obvious characteristic of the *S. punctatus* group is that the veins M_1 and M_2 arise from the discal cell at or very near the same point unlike the rest of the genus, within the Palaearctic fauna, where they clearly arise separately. Four species of the *S. punctatus* group are known in the Western Palearctic, of which only *S. punctatus* had previously been recorded in the British Isles. *Sylvicola fuscatus* differs from *S. punctatus* in lacking any shading below the stigma in cells r_{2+3} and r_{4+5} (Fig. 3), as well as in characters of the male and female genitalia described and illustrated by Søli and Rindal (2014). Geoff Hancock (2021 *pers. comm.*) has also pointed out that the wings of *S. fuscatus* (Fig. 3a) are longer and narrower than those of *S. punctatus* (Fig. 3b).

Within the Palaearctic fauna *S. fuscatus* is most similar to *S. stackelbergi* Krivosheina & Menzel from which it differs in details of the male and female genitalia as described and illustrated by Søli and Rindal (2014). Given that *S. stackelbergi* has been recorded from the Netherlands (Beuk 2002), any future British material purporting to be *S. fuscatus* should be checked against this species.

Fig. 2. *Sylvicola fuscatus* male genitalia, ventral view, woodland above Incombe Hole, Steps Hill, Ivinghoe.

Distribution

Sylvicola fuscatus is widely distributed in mainland Europe, including in France, Belgium and the Netherlands (Dvořák *et al*. 2019) and is known also from North America (Pratt and Pratt 1980). The first record of the species from Norway was made in 2009 and by 2014 it occurred commonly around Oslo (Søli and Rindal 2014). Michelsen (1999) stated that *S. fuscatus* became fairly common in the environs of Copenhagen, Denmark between 1991 and 1999. In both Norway and Denmark previous studies of the Anisopodidae had not detected *S. fuscatus*, suggesting that it could have been a recent colonist or have increased in abundance.

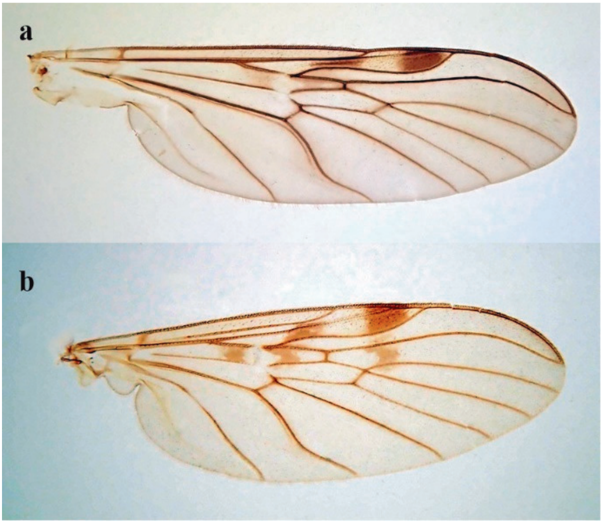

Fig. 3. Wings of *Sylvicola fuscatus* (a) and *S. punctatus* (b) (Photos courtesy of Geoff Hancock).

The presence of *S. fuscatus* at two sites within 1.5 miles of each other suggests that the species is established, at least in a small area of eastern Buckinghamshire. However, as it is a relatively large and conspicuous species, it is considered unlikely to have been present undetected in Britain for any significant amount of time. If *S. fuscatus* is a recent colonist then it will be interesting to observe if it rapidly increases in abundance, as it apparently did in Norway and Denmark.

Material examined

ENGLAND: Buckinghamshire, V.C. 24, woodland above Incombe Hole, Steps Hill, Ivinghoe, SP961156, 1♂ swept 22 April 2021 (leg. and det. S.J. Thomas and confirmed from photograph by L. Dvořák) in coll. SJT.

ENGLAND: Buckinghamshire, V.C. 24, Ivinghoe Common, Ashridge, SP980143, 1♂ swept from crevice in beech (*Fagus sylvatica*) trunk 11 July 2021 (leg. and det. Matthew Harrow) in coll. Matthew Harrow.

Acknowledgments

I would like to thank Libor Dvořák (Tři Sekery, Czech Republic) for confirming the identity of the specimen, providing me with background information and reviewing a draft of this paper, Geoff Hancock (The Hunterian Museum, University of Glasgow, UK) for pointing out the difference in wing shape and providing the images for Fig. 3 and Matthew Harrow (Leighton Buzzard, UK) for arranging collecting permission and allowing me to include details of his *S. fuscatus* record.

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Scottish records of *Polietes meridionalis* Peris & Llorente (Diptera, Muscidae) – *Polietes meridionalis* Peris & Llorente, 1963 was added to the British list by A.C. Pont and S. Falk (2013. *Polietes meridionalis* Peris & Llorente (Diptera, Muscidae) new to Britain. *Dipterists Digest* (*Second Series*) **20,** 45-51). The only Scottish records known at that time were a male and female from Wigtownshire (1.vi.1899) collected by J.G. Gordon and in the National Museums of Scotland collection, where they were identified for Pont and Falk by DH. Currently all records on the NBN are from south of the Lake District. We report here that DH found a single female specimen of *P. meridionalis* among tall herbs at Carlingwark Loch, Castle Douglas, Kirkcudbrightshire (NX7661/7660) on 21.viii.2008 (NMS-10001931), while DS found a male in woodland at Clerkington (NT505724), East Lothian on 20.ix.2021 and a female at Bilsdean (NT763725), East Lothian on 2.xi.2021, sunning on ivy.

Our separation of *P. meridionalis* from the similar *P. lardarius* (Fabricius, 1781) used the characters described by Pont and Falk (*op. cit.*) and by E. Zielke (2016. Observations on the distinctions between *Polietes lardarius* (Fabricius) and *Polietes meridionalis* Peris & Llorente (Diptera: Muscidae). *Journal of Entomology and Zoology Studies* **4(6),** 780-783). We are grateful to Ian Andrews for alerting DS to the Zielke paper, and to Ashleigh Whiffin of the National Museums of Scotland, Edinburgh for retrieving specimen data and checking the collection for additional specimens **– DONALD SMITH,** Garden Cottage, Clerkington, Haddington EH41 4NJ and **DAVID HORSFIELD,** National Museums Collection Centre, 242 West Granton Road, Edinburgh EH5 1JA

Dipterists Digest 2022 **29,** 53-60

The agromyzid leaf miners of plantain (*Plantago* spp): *Phytomyza griffithsi* Spencer and *Phytomyza plantaginis* Robineau-Desvoidy (Diptera, Agromyzidae)

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Summary

The leaf miner *Phytomyza plantaginis* Robineau-Desvoidy, 1851 has been reared from larval mines apparently identical to those of *Phytomyza griffithsi* Spencer, 1963. The occurrence and life histories of these two leaf miners are discussed along with recommendations for future recording.

Introduction

On 30.viii.2019, I found leaf mines on young leaves of greater plantain (*Plantago major*) in the garden (Fig. 1), which seemed to exactly match the description of those created by *Phytomyza griffithsi* Spencer, 1963. Mines started in the petiole, with broad galleries radiating from here into the leaf lamina. Additional leaf mines were found in the next few days on other plants with pupariation occurring either in the petiole or the leaf itself.

Two puparia were extracted for rearing and sent to Barry Warrington to confirm the identity of these leaf miners but unfortunately, both were parasitised by hymenopterous parasitoids, *Dacnusa* species (Braconidae).

Fig. 1. Mine on greater plantain, agreeing with *Phytomyza griffithsi.*

Phytomyza miners of plantain

Phytomyza griffithsi mines were first described by Spencer (1963) as 'initially lower surface but largely upper surface, irregularly linear, finally almost filling the petiole, where pupation takes place.' His illustrations of the mine (Spencer 1963, 1972) match the mines I found in 2019, including pupariation occurring in the petiole. Papp and Černý (2020) stated that the 'puparium is white, pupariation within the mine, often in the petiole'.

The host plant for this species is given as hoary plantain (*Plantago media*) by both Spencer and Buhr (1964), but I was finding identical mines on *P. major.* Buhr (1964) described the mines arising from the petiole in the lower half of the leaf and occurring even in heavily trampled areas and blackening with age. Other known European species on *Plantago* are *Chromatomyia horticola* (Goureau, 1851), *Liriomyza bryoniae* (Kaltenbach, 1858) and *Liriomyza strigata* (Meigen, 1830). *Liriomyza andina* (Malloch, 1934), *L. blechi* Spencer in Spencer & Stegmaier, 1973, *L. sativae* Blanchard, 1938 and *L. trifolii* (Burgess, 1880) are reported for other regions.

Phytomyza plantaginis Robineau-Desvoidy, 1851 was stated by Spencer (1963, 1972, and 1976) to occur as a leaf and stem miner on plantains, particularly ribwort plantain (*P. lanceolata*) and as a leaf miner on *P. major.* Coquilleau *et al*. (2021) reared this species from buck's-horn plantain (*P. coronopus*) in Australia and von Tschirnhaus (1981: 114) reared it as well from *P. coronopus* and from *P. lanceolata*, *P. major* and *P. maritima* in Denmark and Germany and reported ecological details from salt marshes of the North Sea. Eiseman *et al*. (2019) described it as also being found in Wright's plantain (*P. wrightiana*) and Rugel's plantain (*P. rugelii*) in North America.

Spencer (1976) described the mine as being a 'narrow, white linear mine, normally in the leaf but more rarely also in the stem, with the puparium being whitish, with anterior spiracles projecting through the epidermis', pupariation occurring at the end of a mine. Fig. 2 shows a typical *P. plantaginis* mine on *P. lanceolata* with narrow white linear galleries in the leaf lamina.

Fig. 2. *Phytomyza plantaginis* mines in *Plantago lanceolata*.

Rearing plantain miners

From early July (4.vii.2021) through to early August 2021 (4.viii.2021) leaf mines were again found in the garden in *P. major,* identical to those found in 2019 (Figs 3 and 4). Puparia were extracted and adults reared, emerging 14.vii.2021-20.vii.2021.

Fig. 3. Mine originating in the petiole, viewed from above.

Fig. 4. Mine originating in the petiole, viewed from below.

The adults all proved to be *P. plantaginis* with BW confirming by way of genitalia examination (Fig. 5).

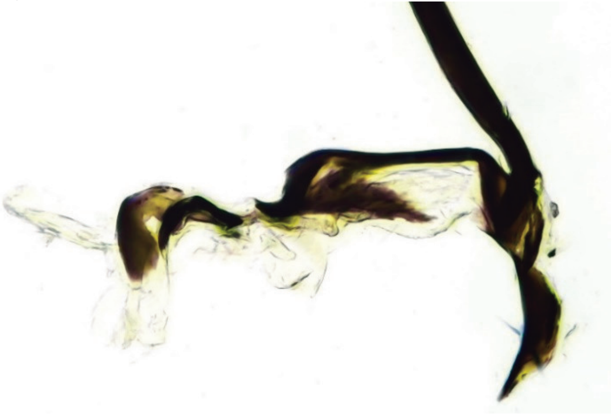

Fig. 5. Phallus of *P. plantaginis* in left lateral view.

This was a surprising result as *P. plantaginis* has rarely been described as forming mines similar to this, but Hering (1957) described mines radiating from the petiole in *P. plantaginis* and pupariation occurring in the petiole or in the centre of the leaf. My own mines largely match his description and illustration, apart from the pupariation site not necessarily being central and also being upper or lower leaf surface. The galleries are initially green but as the remnants of the upper palisade and mesophyll desiccate in the leaf they then turn white. The galleries are mostly upper surface in the leaf. Galleries running from the petiole are broad but may ultimately become narrower and may cross. Mines fitting this description have also been observed by BW (Fig. 6). The frass grains are separated.

Fig. 6. *Phytomyza plantaginis* mines.

Pupariation occurs at the end of a mine and the puparium may be found with anterior spiracles projecting through either the upper or lower epidermis. Pupariation may also occur in the upper surface of the petiole; Fig. 7 shows this with a male and female puparium being formed there.

Fig. 7. *P. plantaginis* mines with two puparia formed in the petiole.

The puparium is described as whitish (Spencer 1976; Papp and Černý 2020, Guglya 2021). I found that they are white when first formed, but rapidly change to a very pale lemon colour (Fig. 8).

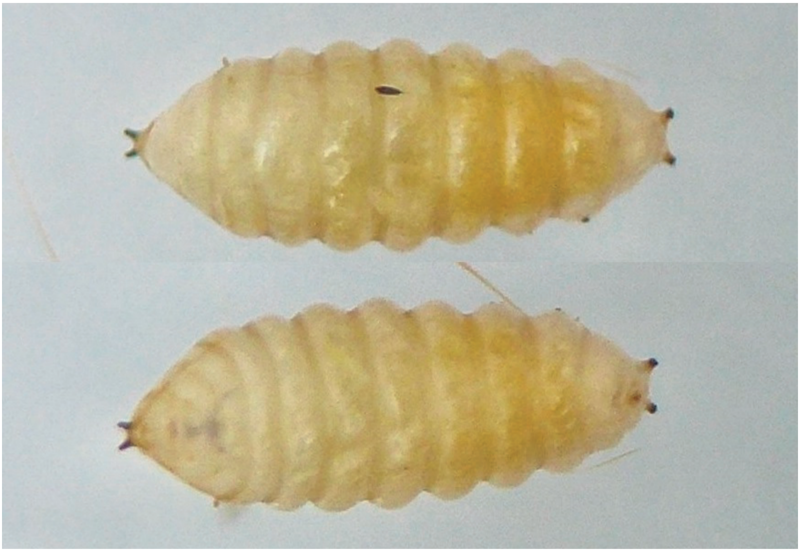

Fig. 8. *Phytomyza plantaginis* puparium; upper, viewed from above; lower, viewed from below.

Occasionally they become a slightly darker yellow (Fig. 9).

Fig. 9. ***P. plantaginis*** **puparium; upper, viewed from above; lower, viewed from below.**

They may also become dark; although this is usually an indication that the larva is parasitised, BW has successfully reared adults from dark puparia (Fig. 10).

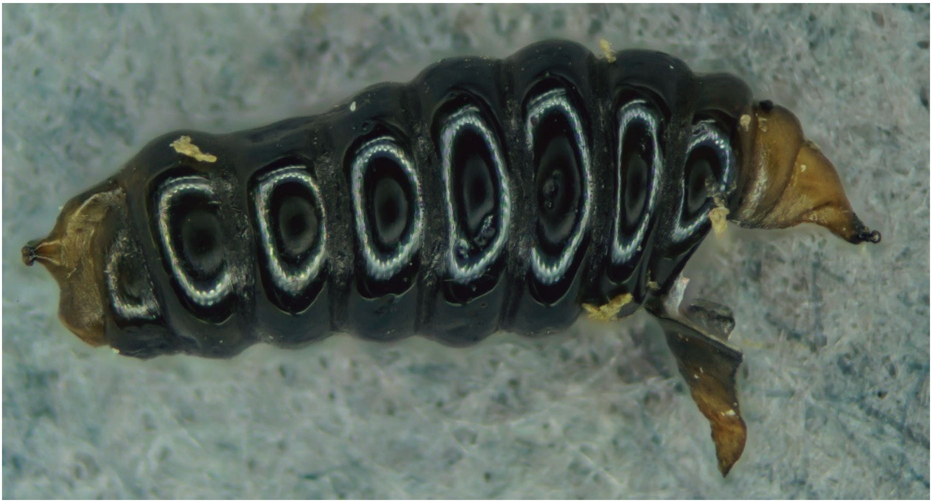

Fig. 10. ***Phytomyza plantaginis*** **dark puparium.**

Morphologically, the adults of *P. griffithsi* closely resemble *P. plantaginis*. Differences are the bright, entirely yellow second antennal segment and the paler upper orbits, with the *vti* always on yellow ground (Spencer 1963*). Phytomyza plantaginis* has a yellowish grey second antennal segment with darkened upper orbits and *vti* on dark ground (Spencer 1972). Fig. 11 shows a female *P. plantaginis* with the darkened second antennal segment. Černý and Heřman (2015) published a photograph of a living *P. griffithsi*.

Fig. 11. Female *Phytomyza plantaginis*.

Spencer (1963) stated that the distiphallus of *plantaginis* is variable. In 2019, BW collected 29 males from *Plantago maritima* on 14.ix and dissected all of them; the size of the distiphallus varied, but all were within the range of the species with nothing to suggest a species-complex is present (Barry Warrington *pers. comm.*). Spencer (1963) stated that in *P. griffithsi* 'the sidepieces of the mesophallus straighter and the two sides of the distiphallus far closer together; the greatly enlarged triangular, right-hand side piece of the basiphallus is distinctive'.

Conclusion

The mines of *P. plantaginis* on *P. major* are identical to those described for the rare *P. griffithsi* and adults must be reared in order to correctly identify them, both on *P. major* and *P. media*. The narrow mines on *P. lanceolata* are distinctive enough to allow confident identification of *P. plantaginis*. Further work needs to be undertaken as to the host plant choice of *P. griffithsi* and the life history of this species needs further elucidation.

Acknowledgements

Thanks to Barry Warrington for many helpful discussions, particularly with this paper, help with the literature and for the photos (Figs 5, 6 and 10) and genitalia dissection. Thanks also to Carina van Steenwinkel for permission to use her photograph of *P. plantaginis* on *P. lanceolata* (Fig. 2). I am grateful also to Michael von Tschirnhaus and Yuliia Guglya for helpful comments when reviewing this paper.

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Dipterists Digest 2022 **29,** 61-67

Larvae and pupae of *Limonia trivittata* (Schummel) (Diptera, Limoniidae) with notes on feeding within decaying Apiaceae plant roots

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Summary

Two previous sources of information on the rearing of *Limonia trivittata* (Schummel, 1829) give the foodplant and some biological data, but the immature stages have not been described. Preserved material from recently reared specimens is figured and compared with related species. A discussion on the apparent life cycle strategy of *L. trivittata* and some other species that share the same habitat is added.

Introduction

Adult records of *Limonia trivittata* (Schummel, 1829) indicate a frequent association, in Britain at least, with usually base-rich damp woodland, often along riverbanks. The few known larval rearing records (Röseler 1963; Brinkmann 1991; Hancock 1987) are from large to medium-sized Apiaceae plants, often referred to as umbellifers, which can be abundant in such areas. Some Scottish records of adult *L. trivittata*, from preserved specimen labels in the Hunterian Museum, in addition to the localities of the reared specimens described below, are from Hamilton (NS584675), South Lanarkshire, 12 May 2012, R. Weddle; Paisley Moss, Renfrewshire, 10 August 1985, E.G. Hancock; Ardmore, Dunbartonshire, 1 July 1961, G. Hosie; Caerlaverock, Dumfries, 19 July 1967, G. Hosie; Strathblane, Stirling, 16 July 1899, R. Henderson and Dunollie Castle grounds, near Oban, Argyll, 7 July 1926, R. Henderson.

Methods

Roots of common hogweed (*Heracleum sphondylium*) and wild angelica (*Angelica sylvestris*) were sampled on 23 April 2021 from the bank of the River Avon near Stonehouse, South Lanarkshire (NGR: NS763477). Dead flowering stems were pulled up and those with associated decaying root remains were retained. Larvae were selectively removed from the rootstock into separate containers. Some of the larvae, and pupae that formed subsequently, were preserved in order to describe the juvenile stages of any adults that might emerge. One larval head capsule was cleared and mounted on a microscope slide. Photographs were taken either with an Olympus Tough T4 digital camera using the built-in stacking image facility or a Zeiss Axioscope 7 (Automatic Stage Digital Photomicroscope). This latter can create a single photographic file from stacked images stitched together, if necessary, from a sequence taken on an x-y grid to accommodate objects that exceed the diameter of a field of view at the required magnification.

Results

Adult *Limonia trivittata* began to emerge on 17 May 2012. Other Diptera present in these roots were *Beris geniculata* Haliday in Curtis, 1830 (Stratiomyidae), identified from both larvae and a female adult that emerged on 26 June 2021 and adult anisopodids *Sylvicola cinctus* (Fabricius, 1787) and *S. zetterstedti* (Edwards, 1923) that emerged over the same period. *Limonia trivittata* has been reared once before in the west of Scotland on 26 June 1986, from old stem bases and decaying roots of the previous year's plants of giant hogweed (*Heracleum mantegazzianum*) collected along the banks of the River Clyde near Carmyle, Glasgow, NGR: NS643612 (Hancock 1987). Adult *Limonia nubeculosa* (Meigen, 1804) and *Rhipidia maculata* (Meigen, 1818) also emerged from these giant hogweed roots but no larvae were preserved at that time prior to the emergences. *Sylvicola cinctus* was reared, and also on several other occasions from giant hogweed growing in the Clyde area.

Fig. 1. Live larvae of *Limonia trivittata*, each 11.0mm long, South Lanarkshire, Scotland, 2021.

Figs 2-3: 2 (left), spiracular field of *Limonia trivittata* from a fresh specimen, South Lanarkshire, Scotland, 2021; 3 (right), spiracular field of *Limonia macrostigma* from Germany (from Lindner 1959, fig 21.).

Description of larvae

The overall appearance is typical of those of other known *Limonia* species (Fig. 1). Particularly noticeable are the two pairs of dark spots within the spiracular field. The dorsal pair enclose the spiracular openings. Creeping welts are on segments 4-10, ventral only on segment 4 but both ventral and dorsal on segments 5-10. The spiracular field of *L. trivittata* has the lower pair of pigmented spots angled medially (Fig. 2) and narrower than those of *L. macrostigma* (Schummel, 1829) which has larger squarish ventral spots (Fig. 3). This latter species was first illustrated in Lindner (1959; fig. 21) whose figure is reproduced in Krivosheina and Krivosheina (2011). Other species of *Limonia* whose spiracular field has been figured are *L. nubeculosa* Meigen, 1804 by Brindle (1967; fig. 15) and Reusch (1988) who also illustrated those of *L. flavipes* (Fabricius, 1787) and *L. phragmitidis* (Shrank, 1781), all on his Plate 25 (figs a, c and d). These figures were also utilised by Krivosheina and Krivosheina (2011).

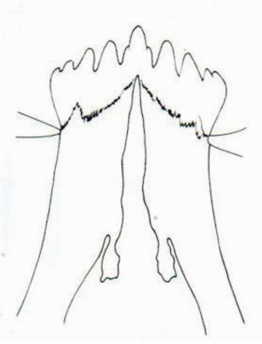
Fig. 4. Head capsule of a larva of *Limonia trivittata* from a fresh specimen, South Lanarkshire, Scotland, 2021; the smaller arrow points to the hypostome, the larger arrow to the distal extremity of the notal plate.

Alexander (1920; fig. 83) described larvae of *Limonia cinctipes* (Say, 1823) and Malloch (1917; Plate XXXIII, fig. 17) that of *Limonia triocellata* (Osten Sacken, 1860) from North America. Both these species are now assigned to *Metalimnobia*, in which genus the spiracular field lacks the ventral pair of pigmented spots. Other characters of value for distinguishing *Limonia* from *Metalimnobia* reside in the head capsule. The hypostoma of *Limonia* species have 9-11 teeth in a low profile (Figs 4 and 5) whereas *Metalimnobia* have 11-13 teeth with the medial one elongated to form a more acute triangular shape (Fig. 6). The status of *Metalimnobia* at generic level is thus supported by robust features in the immature stages.

Limonia macrostigma and *L. trivittata* larvae can be separated easily by examining the head capsule and the length and shape of the notal plates, the term used by Lindner (1959; fig. 15a) to describe this part of the dorsal head capsule, as seen in Figs 4 and 7. There are other differences in details of features in the head capsule although the hypostome is not particularly useful according to Reusch (1988; plate 37, figs c-f), whereas the medial distal area of the notum, which he referred to as the Zuwachszone, does have potential.

Description of pupae

Pupae of *Limonia* spp have been illustrated by Brindle (1967: p. 185, figs 82-84) for *L. nubeculosa*, *L. macrostigma* and *L. phragmitidis* (as *tripunctata*). That of *L. trivittata* is most similar to *L. macrostigma* in the profile of the prothoracic horn and the posterior segments of males and females (Figs 8, 9, 10). After adult emergence the pupal exuvium is left protruding from the decay showing clearly the prothoracic horns identifying it as a species of *Limonia* (Fig. 11).



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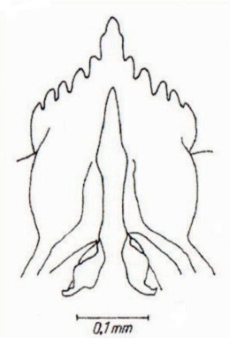

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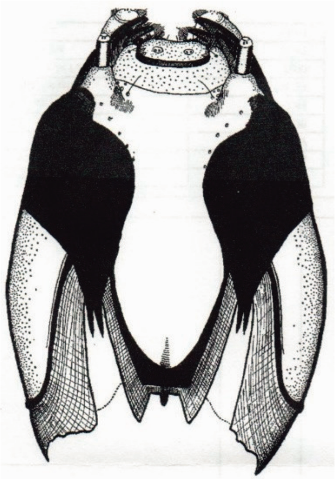

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Figs 5-7: 5, hypostome of *Limonia macrostigma* from Oosterbroek and Theowald (1991, fig. 146); 6, hypostome of *Metalimnobia bifasciata* (Schrank, 1781) from Cramer (1968, fig. 17e); 7, head capsule of *Limonia macrostigma* from Lindner (1959, fig. 23).

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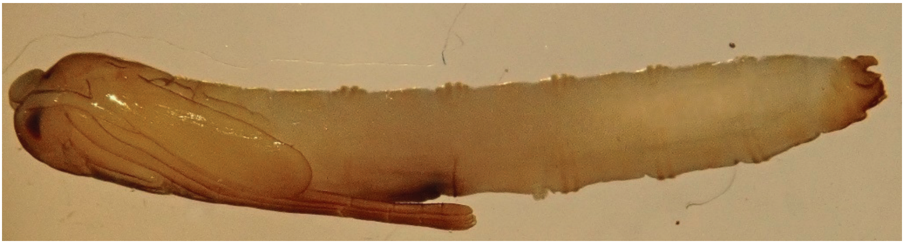

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Figs 8-9: 8, pupa of a female *Limonia trivittata*, 8.7mm long, South Lanarkshire, Scotland, 2021; 9, pupa of a male *Limonia trivittata*, 8.5mm long, South Lanarkshire, Scotland, 2021.

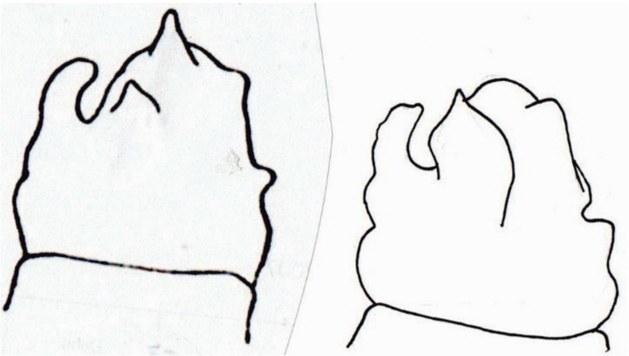

Fig. 10. Terminal segments of male pupa of *Limonia* species: *L. macrostigma* (left diagram) after Brindle (1959, fig 83) and *L. trivittata* from South Lanarkshire, Scotland, 2021 (right diagram).

Fig. 11. Pupal exuvium of a female *Limonia trivittata,* South Lanarkshire, Scotland, 2021.

Discussion

Edwards (1938) stated that *L. trivittata* was found "among butterbur". Adult *Dicranomyia ornata* (Meigen, 1818) are also commonly found amongst butterbur (*Petasites hybridus*) and its larvae were found and reared by Stubbs (1980a). Immature stages of *L. trivittata* have not been found in butterbur and the adult flies probably use it simply for shelter as do many other insects. The first reliable reference to a food source for *L. trivittata* was by Röseler (1963) who reared three males in May 1961 from the rotting roots of *Angelica sylvestris* in the Black Forest area of Germany. Brinkmann (1991) also reared the species and recorded a single annual life cycle with a development time of 358 – 364 days. In laboratory-based studies he recorded that eggs laid on 10 June 1989 were in diapause for 117 days and first stage larvae were not seen until early October and were present for an average of 22 days. Second stages were observed during the following 27 days; third and fourth stage larvae from mid-November and mid-April respectively. On 9 May 1990, pupae were first seen and adult flies began to appear from 18 May through to 24 May that year. Observations on *L. trivittata* in Scotland in 2021 parallel these data for the later stages of development. Roots were collected on 23 April and fourth stage larvae placed in separate tubes within which pupae quickly formed. Adults began to emerge on 5 May and continued to appear over the next 27 days.

Plants of the larger species of Apiaceae provide a larval habitat for a range of species of Diptera. In addition to those named above some *Cheilosia* species (Syrphidae) develop in the decaying roots of this family. *Cheilosia chrysocoma* (Meigen, 1822) has been seen ovipositing on *Angelica sylvestris* (Ball and Morris 2013); *C. illustrata* (Harris, 1780) exploits *Heracleum sphondylium* (Rotheray 1999). When the stems of these plants are pulled up there are two possible outcomes. There may be no wet decay and little remains of the rootstock. This is more often the case with smaller, thinner stems. When wet decay is present, this can vary from substantially complete rootstock remains which have a yellow-brownish coating of decay to those that are more rotted and fragmented so that the end of the stem and the roots are split open and the decay can be seen internally also. When the former are sliced open vertically this internal decay can be exposed to view but can be in a lesser volume than the latter. Whereas stratiomyid and anisopodid larvae can be seen moving around in the external coating of decay in addition to within internal mass, limoniids and Syrphidae appear to feed only internally.

Cheilosia pagana (Meigen, 1822) has been reared from larvae in decaying roots of cow parsley, *Anthriscus sylvestris* (Stubbs 1980b). It is worth noting that although variable in size it is amongst the smallest species of *Cheilosia* and able to exploit this small and fairly delicate plant species. However, larvae of *C. pagana* have been found also in the larger umbellifers (Graham Rotheray *pers. comm*., August 2021) but there may be a link between the volume of root decay that is possible within the largest of the plants in this family and the total number of species of Diptera which can be found as larvae. During plant growth in the summer months there is little or no decaying tissue for the suite of insects which derive nutrition as filter-feeders of micro-organisms. The saprophagous resource they require appears after die-back of the leaves and flowerheads, following which the root stocks below the ground begin to decay.

Bridging the gap between oviposition and growth in autumnal root feeders

This period has to be survived before any substantial growth can begin. Adults emerge in late spring or early summer, mate and oviposition takes place and of those that have been studied slightly different strategies can be recognised. These species are all univoltine. As described above for *L. trivittata*, Brinkmann (1991) established that egg diapause of some 16 weeks between June and October accounts for the summer period before autumnal and winter feeding can begin. Rotheray (1999) observed that larvae of several *Cheilosia* species remain small during the summer months, during which period they are probably feeding by shredding living plant tissue but begin to grow more rapidly in the roots of the various plants when they start to decay. *Cheilosia illustrata* utilises *Heracleum sphondylium* and larvae that were found in October, tunnelling in the larger bulbous roots, continued to feed until pupariation in December (Rotheray 1999). The rest of the winter is spent in the soil until adults emerge. The peak of adult activity is June-July during which mating and egg-laying will take place.

The anisopodid *Sylvicola zetterstedti* is known to lay eggs in jelly-like masses in the leaf bracts that wrap around the stem of *Angelica sylvestris*. The bracts can subtend small quantities of water where egg masses, and first and second stage larvae have been seen from early July through to early September (Hancock, *pers. obs*.). The young larvae are assumed to make their way into the base of the plant, although precisely when or the exact route is unknown. During winter and the following spring, when decaying roots are sampled, second and third stage larvae can be seen. They complete their growth within yellow/brownish decaying matter in the roots and pupate in May and June. About six days later, immediately prior to adult emergence, the pupae move to the surface and the empty pupal exuvium is left protruding as is seen in *L. trivittata* (Fig. 11) and many other nematocerans.

These examples show a range of strategies that have evolved to enable autumnal saprophagous root feeders to bridge the time between adult mating times, oviposition and larval growth.

Acknowledgements

Pjotr Oosterbroek and Herman de Jong kindly supplied copies of some literature and confirmed that preserved specimens in Naturalis (Leiden) that were listed in Oosterbroek and Theowald (1991) are examples from those collected by P.-F. Röseler. Hunterian Museum colleagues have provided research access and Dr John Faithfull instruction on using various instruments.

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Investigating the behaviour of cyclorrhaphan larvae (Diptera, Cyclorrhapha)

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Summary

Behaviour is integral to cyclorrhaphan larvae and a valuable source of information. Larval behaviour is rich in potential for making discoveries. In this paper, suggestions are made for investigating behaviour from the means to study it to introducing a selection of feeding, movement and respiratory behaviours to raise awareness and encourage others to find subjects to investigate.

Introduction

Chapter 7 of the Dipterist's Handbook is about fly behaviour or the ways in which flies respond to other organisms and their surroundings (Chandler 2010). Chapter 7 deals with adult behaviour, but not that of the larva and pupa. This paper attempts to fill the gap for cyclorrhaphan larvae.

Pupal behaviour is limited to wriggling to escape adversity, find air for breathing or reach a place for the adult to emerge. In taxa with a puparium, such as the Cyclorrhapha, pupal wriggling is obviously curtailed. In the Cyclorrhapha, pupal movement is confined to shunting when projecting pupal spiracles through the puparium wall (Keister 1953, Roddy 1953). In contrast, and except possibly for macrolarviparous larvae that develop inside the mother, behaviour is integral to the larva, from breaking out of the egg to feeding, moving, respiring, responding, defending and selecting a place to pupate.

Despite its significance, larval behaviour is poorly known and the potential for making discoveries is high (Roberts 1971, Rotheray 2019a). Larvae are more or less translucent, especially at the head end which facilitates observation and particularly of a major component of many behaviours, the head skeleton (Rotheray and Lyszkowski 2015). Compared to adults handling and observing larvae is straightforward, for instance flight is not a consideration and reproductive imperatives that can complicate interpretation of adult behaviour, do not concern larvae.

For so-called simple organisms that are soft, and without legs or eyes, surprisingly elaborate larval behaviours have been discovered. Sokolowski (1980) observed that larvae of the saprophage *Drosophila melanogaster* Meigen (Diptera, Drosophilidae) are distinguished behaviourally. They possess one or other of two genetically determined foraging traits, characterised as roving and sitting. In decaying fruit, roving larvae forage over greater distances and locate decay not reached by sitters. Sitters develop more slowly and match development to ongoing decay. These differences possibly reduce competition and are effective for exploiting decay that develops patchily in space and time.

Vijendravarma *et al*. (2013) reported other unexpected behaviours in *D. melanogaster*. Healthy larvae consumed wounded or dead individuals which, apart from being a source of nutrients, probably helps to prevent contamination. Moreover, crowding and starvation induced a last-ditch attempt at survival in young larvae: cannibalism of older individuals. How far these behaviours characterise other cyclorrhaphan larvae is unclear and for most larvae, baseline information about feeding and locomotion is incomplete or missing (Rotheray 2019a).

In this paper background information about larval perception is provided, and suggestions for how to observe behaviour and investigate certain general behaviours are made. Following this a selection of specific feeding, movement and respiratory behaviours are introduced. The aim here is to raise awareness of the diversity of larval behaviour and identify subjects for investigation. This is the last in a short series of papers whose aim is encouraging others to study cyclorrhaphan larvae. Previous papers include an assessment of techniques for finding larvae in the field, evaluation of a promising method of analysing larval morphology and an account of the extraordinary yet misunderstood larval head (Rotheray 2016, 2020, 2021b).

Perception

Larvae process sensory data from physiological and environmental cues into signals that elicit and guide behaviour. Hence, perception is fundamental (Sawin *et al*. 1994). For example, in most cyclorrhaphan larvae the antennae and maxillary sense organs project together at the front of the head. Hungry larvae move towards food in response to olfactory signals picked up by their antennae and, on touching it, gustatory signals from their maxillary palpi elicit feeding (Cobb 1999, Oppliger *et al*. 2000).

Larval ability to perceive extends beyond these conspicuous structures. Sensory pits and pores are present on the head and other body segments (Nye 1959, Hartley 1961, Ferrar 1987, Rotheray and Gilbert 1999). They work alongside a far more extensive system of neurons embedded in the body wall that enable larvae to respond to stimuli down to parts of individual segments. They cue behaviour from a wide range of environmental factors from temperature to noxious chemicals (Liu *et al*. 2003, Hwang *et al*. 2007, Xiang *et al*. 2010). For instance, Bolwig's organs, a group of photoreceptor cells in the larval head, cue movement from light to dark, but Xiang *et al*. (2010) discovered that light perception in *D. melanogaster* larvae is not confined to Bolwig's organs. Photoreceptor neurons are present all over the body and cue precise adjustments to light enabling, for instance, a larva to move the entire body out of the light rather than leaving part of it exposed after the head enters the dark. Behaviour appropriate to the intensity of the stimulus is also a feature. For instance, squashing the body cues responses appropriate to the degree of distortion. Hence, slight squashing results in larvae shuffling forward, whereas pinching leads to vigorous wriggling or rolling and moving rapidly away. These studies demonstrate that cyclorrhaphan larvae are far more capable of perception than might be thought.

Behavioural responses to environmental factors and stimulus intensity are expected and are probably an attribute of a more inclusive taxon than the Cyclorrhapha. Even so, much remains to be discovered about these factors and responses. Much less predictable are behaviours such as roving and sitting that are more likely to be situation or taxon specific. Given the morphological diversity of cyclorrhaphan larvae, the enormous range of circumstances under which they develop and the high proportion of species whose larvae are unknown, the incidence of specific behaviours must be far higher than currently recognised.

Observing and investigating

Investigating behaviour requires watching larvae move. Although they can be observed with the naked eye or hand lens, more is revealed with a binocular microscope and even more by videography. The latter is an especially valuable observational and analytical tool (Rotheray 2020). Videoing can be done directly using a camera's video option or by attaching a camera to a binocular microscope (Rotheray and Lyszkowski 2015, Wilkinson and Rotheray 2017). When working out what occurs, replaying videos in either direction and freezing action is particularly helpful, for instance, in working out how head skeletons operate or assessing small or fast-moving components. Videography also provides a means of checking and confirming details in a permanent record and quantification is also possible. During replay, events can be counted, timed and distances and angles measured and so on (Rotheray and Lyszkowski 2015).

Subdued light is best for observing larvae as bright light tends to elicit escape behaviour.

Larvae may need prompting. Prod them with a brush or increase activity by making them hungry. To do this, isolate individual larvae in containers for periods of up to 36 hours, and add moist tissue to prevent desiccation. Except for endoparasitoids that live inside a host, most larvae are straightforward to observe. Concealed larvae are usually tolerant of being gently uncovered, at least partially. Even inside plants phytophages can be observed with appropriate preparation. Leaf-miners can be seen by shining a light at the mine and looking from the other side. Stem and root borers can be monitored in split sections tied together and opened to reveal them and so on.

Usually, each larval stage of a species behaves in a similar way albeit with changes due to size and physical ability, but stage-specific behaviours are also known. For example, certain first stage, leaf-mining, larvae of *Pegomya* Robineau-Desvoidy (Diptera, Anthomyiidae) excavate linear mines whereas third stages make blotch mines with the switchover apparently taking place in the late first or second stage (Hering 1951, Rotheray 2019b). Furthermore, recognising where a final stage larva, usually the third, has reached in its development may be necessary for resolving what to expect. At some point, final stages end feeding and disperse, aestivate or hibernate before pupariation. These individuals are usually recognised by their large size, body swollen with fat and slow movement. At development sites they tend to move away from food, although factors such as crowding and starvation can also elicit this, itself a subject to investigate.

Most time as a larva is spent in the final stage, and larvae develop to it in a few days (Ferrar 1987, Rotheray and Gilbert 2011). Identifying larval stages can be difficult, especially towards ecdysis when the stages either side of it are alike in size. Stage indicators usually exist in the head skeleton or respiratory structures, but it is not possible to generalise and to find differences, the larval stages of each species must be examined individually.

Field-collected larvae may be parasitised which can lead to unusual or aberrant behaviour, which in itself is a subject for investigation. Parasitised larvae need to be recognised. Rearing through to the adult is one method. Searching larvae for parasites is another. Parasite larvae that live in the host haemocoel can be found by placing the host larva under a cover slip in a drop or two of water on a glass slide. Using a binocular microscope, all parts of the haemocoel are searched by rolling and manipulating the larva using the cover slip. The larva is squashed by this treatment but with care, no harm is done. Alternatively, larvae can be dissected (Fig. 1).

A valuable preparation before investigating behaviour is the simple act of watching larvae as they go about their lives. Observations of this kind are about the process of familiarisation. They may take time, but are nearly always worthwhile. Seeing larvae feed, move and interact shows what is involved and informs what to investigate. General topics for investigation include directional movements or taxes and non-directional movements or kineses that are responses to variables such as light, gravity, temperature, touch and food. The basic technique is to expose larvae to a range of values of a variable and see how they respond. This type of investigation can be used to determine preferences and suitabilities. It can also be used to assess performance. For example, testing how substrate quality effects locomotion under the expectation that not all substrates are equally preferred or testing food viscosity under the expectation that not all viscosities can be imbibed equally well.

For investigating behavioural roles and functions, an important principle is that form follows function, i.e. the characteristics of a morphological structure will match its function (Arnold 1983, Kingsolver and Huey 2003). For instance, the mandibles of larvae that feed on soft and hard food appear to follow this principle in that the hooks of soft food feeders are typically elongate and flattened on their rear margins. In contrast, those of hard food feeders are shorter, wider and often have smaller hooks alongside the main one (Ferrar 1987, Rotheray and Lyszkowski 2015). Observing these mandibles gathering food reveals their significance. An elongate, flattened hook is an effective shape for pulling portions of soft food towards the mouth whereas a shorter, wider hook withstands the greater mechanical demands of fragmenting hard food. Observation also reveals other characteristics. For instance, in soft food feeders the paired mandibles diverge on gathering food which opens the oral cavity to receive it. In contrast, the mandibles of hard food feeders are not only closer together, they concentrate fragmentation power by remaining close during food gathering (Rotheray 2020).

Long, thin versus short, wide mandible hooks is a conspicuous contrast. Inconspicuous, fine-grained, morphological differences are widespread between related taxa and cannot be dismissed as trivial without investigation. For instance, slight differences in head skeleton size and mandible shape occurs among species of saproxylic *Lonchaea* Fallén (Diptera, Lonchaeidae) (MacGowan and Rotheray 2008). Mandible shape correlates to other fine-grained differences that include the nature of the locomotor organs and the size, shape and flexibility of the thorax. Observations reveal how these differences integrate with behaviour for specialised ways of life under bark, such as living and moving among fibrous networks and sucking up oily food or living in narrow gaps and scraping relatively dry food (Rotheray 2020).

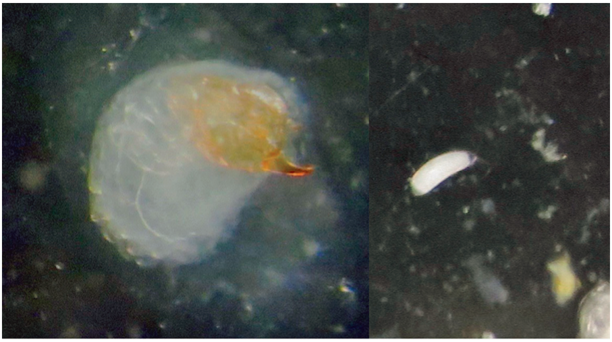

Fig. 1. Left hand image, an unidentified parasitoid larva (Hymenoptera), head capsule with exposed mandible uppermost, about 3mm long, and egg, 1mm long, not to scale, dissected from the haemocoel of leaf mining, third stage larvae of *Pegomya solennis* (Meigen) (Diptera, Anthomyiidae), Dumfriesshire, Scotland, 2016.

Life functioning

A range of behaviours comprise each life function. They offer diverse springboards for furthering knowledge. To raise awareness of this diversity and help identify subjects for investigation, a selection of readily observed behaviours involved in feeding, locomotion and respiration are introduced below.

Feeding

Despite their importance feeding mechanisms, i.e. the behaviours and morphologies involved in transferring food from an external source into the gut, are not well known (Rotheray 2019a). The wide array of foods and circumstances over which feeding occurs suggests that feeding mechanisms will be diverse. Supporting this possibility, among twelve saprophagous larvae, Rotheray and Lyszkowski (2015) recorded seven distinct feeding mechanisms: cut and scoop, brush, sweep, scrape, shovel, spot-suck and suck. Most are specialisations that match particular ways of life and undoubtedly many more exist.

Whatever the feeding mechanism, ubiquitous behaviours are also present. For instance, area-restricted behaviour is a response following contact with resources, such as food, in which a forager slows down and obtains what it needs. It results in foragers remaining in areas where resource density is high (Kareiva and Odell 1987). Area-restricted behaviour is best known in predators and parasitoids that search for discrete items of prey or hosts. It is unclear if larvae that live immersed or surrounded by food, such as many saprophagous and phytophagous larvae, behave in this way.

Feeding should cycle between hunger and satiation, but cycling may not be straightforward. Periodicity can influence it. For instance, certain aphidophagous syrphine larvae (Diptera, Syrphidae) are crepuscular, a feature consistent with crypsis (Rotheray 1986). During winter, tree-hole syrphid larvae (Diptera, Syrphidae) are often unable to feed due to lack of microbial food. During winter they survive on accumulated fat and resume feeding when levels of food recover in the spring. This feature explains in part, their asynchronous life cycles (Hartley 1961, Rotheray *et al*. 2013). Hunger level is another factor. Starved larvae may be less selective and accept suboptimal food, such as young *D. melanogaster* larvae (Vijendravarma *et al*. 2013). Starved larvae may also feed for longer periods and/or more rapidly, but such dynamics are little understood. When they switch leaves, leaf-mining larvae of *P. solennis* are deprived of food. In new mines greater quantities of leaf tissue were consumed by such larvae compared to similar-sized larvae that have not switched leaves (Rotheray and Rotheray 2019).

If food is within reach high levels of hunger may not be experienced and feeding may be a ‘topping-up’ process with feeding adjusting to minimise movement and hence, the amounts of energy used. Rotheray and Wilkinson (2015) found that predatory larvae of *Phaonia subventa* (Harris) (Diptera, Muscidae) fed first on prey fluids and then on tissues and organs. Feeding on tissues and organs appears to be more costly in time and energy; for instance, it requires more vigorous head skeleton movements. Topping up in this larva and perhaps other predatory larvae, might consist of removing body fluids in preference to tissues and organs.

Some larvae face unpredictability in food supply. For example, sap runs on trees are prone to dry out. If the sap stops flowing larvae of the genus *Brachyopa* Meigen (Diptera, Syrphidae) face desiccation and starvation. In drying conditions *Brachyopa* larvae curl up and enter a state of aestivation. How long they can persist in this state is unknown, but it is certainly months and when the sap starts flowing, they uncurl and resume activity (Rotheray and Gilbert 2011). Similar behaviour is indicated in sap run larvae of the Periscelididae (Diptera) (Rotheray and Robertson 1998).

Satiated larvae usually remain close to the place where they last fed, but not always. Aphidophagous syrphine larvae often leave their prey after feeding and hide in concealed positions, such as inside leaf curls. This is another feature consistent with crypsis and governed by a mix of geo- and photo-negative and thigmokinetic responses. The latter involves inhibition of movement relative to how much the body is in contact with a substrate. These responses are reversed in hungry larvae (Rotheray 1986). Movement away also occurs in the bird brood ectoparasitic larvae of *Neottiophilum praeustum* (Meigen) (Diptera, Piophilidae) and *Protocalliphora azurea* (Fallén) (Diptera, Calliphoridae). After feeding these larvae move off their hosts to hide among nest material, presumably to avoid being pecked off (Keilin 1924, Owen 1957).

Groups of larvae often feed together at the same development site and although individuals may be tolerant of one another or possess features that reduce or avoid competition, such as roving and sitting in *D. melanogaster* larvae, they may compete. For instance, scramble competition in which successful competitors are those that consume resources at the fastest rate is most likely at relatively small, ephemeral development sites where food and living space is limited, such as certain types of carrion, fruits, fungi, dung, etc.

Contest competition may also occur in which certain individuals take over and monopolise resources. An example appears to be the rose-hip tephritid, *Rhagoletis alternata* Fallén (Diptera, Tephritidae). Bauer (1986) found that despite infestation levels of up to 14 larvae per hip only one or two survive and hypothesised that larvae compete. Dissection of rose hips in Scotland showed that dead larvae are often present (author, unpublished results). In Petri dishes larvae attacked one another with the second stage larva being particularly aggressive. Larval fighting may be the mechanism behind the competition suggested by Bauer (1986) (Fig. 2).

Another possibility is the opposite of competition. Larvae may gain proportionally more food relative to group size, the so-called Allee effect (Stephens *et al*. 1999). Bulb-feeding *Eumerus* Meigen larvae (Diptera, Syrphidae) fragment tissue but do not imbibe all the fragments. The excess is digested by microbes. The size of the resulting bloom, which appears as a dark oily liquid, is governed by larval abundance in the direction of proportionally more oily decay with increasing group size. This is significant because larvae rely on bloom material to complete development (Creager and Spruijt 1935). Another example is carrion-developing calliphorid larvae (Diptera, Calliphoridae). Their joint activity causes temperature increases and proportionally enhanced rates of feeding and development (Gennard 2007). Nonetheless, group-feeding risks food becoming contaminated by metabolic wastes or dead larvae (Joshi and Mueller 1988). A mechanism mentioned above that eliminates contamination is consumption of dead and wounded individuals by healthy larvae (Vijendravarma *et al*. 2013). Also, interactions between larvae may reduce feeding rates by, for example, larvae spending time interacting rather than feeding (Hassell 1976). Much more work is needed before consensus is reached on these or any other aspect of larval feeding behaviour (Rotheray 2019a).

Fig. 2. Aggression between larvae of *Rhagoletis alternata* Fallén (Diptera, Tephritidae), second (smaller) and third stage larvae removed from rose hips and placed in a Petri dish, Dumfriesshire, Scotland, 2018; a, following contact by the second stage larva both larvae wrapped round and lunged at each other with their head skeletons; b, third stage larva lunging unsuccessfully against the body wall of the second stage larva.

Movement

Movement typically consists of repeated actions, such as sets of peristaltic waves or feeding lunges. Monitoring repeated actions reveals patterns in behaviour and outcomes, and analysing what occurs during a single action serves as a standard for making comparisons. Underpinning movement is a body organised into modules (Green *et al*. 1983, Rotheray 2019a). The rear module, from the anal segment to the posterior end of the metathorax, grips the substrate. The middle one, from the front of the metathorax to just behind the anterior spiracles at the back of the prothorax, lifts. This enables the front module, from the anterior spiracles to the mandibles, to grip the substrate or lunge for food. Modules may combine to form functional complexes (Yang 2001). For example, the middle and front modules of leaf mining Agromyzidae integrate to minimise movement and optimise time spent feeding (Rotheray 2019b).

Crawling in cyclorrhaphan larvae might seem unsophisticated, but lack of limbs and peristalsis are effective for organisms that live in submerged or confined conditions (Schneeberg and Beutel 2014). Videography shows that crawling in cyclorrhaphan larvae is a specialised form of peristalsis (Berrigan and Leighton 1993, Heckscher *et al*. 2012, Rotheray 2019a). Key to effective crawling is attachment to the substrate (Tanaka *et al*. 2012). Larval attachment structures vary from tubercles and friction mats to prolegs and suckers, but the most widespread structure is an anchor pad (Rotheray 2019a). Anchor pads are paired, fleshy, spiculate protuberances straddling segment borders from the rear of the metathorax to the anterior margin of the 7th abdominal segment (Fig. 3). An anchor pad is also on the anal segment near the anus, the anal lobe. Segment-straddling anchor pads are also present in empidoid larvae but not, apparently, in other brachycerans. The form of the anal segment separates cyclorrhaphan from empidoid larvae. The anal segment is bulb-shaped in most brachycerans including empidoids, but in cyclorrhaphans it is not like this and although varied in form, it is never bulb-shaped (Fig. 4).

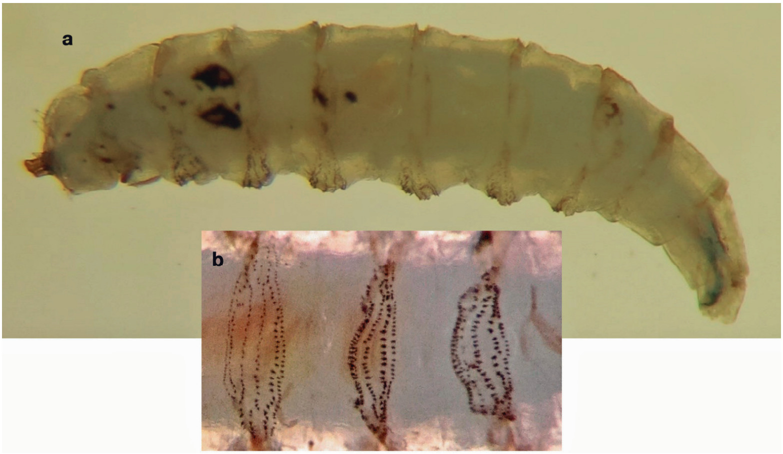

Fig. 3. *Chymomyza costata* (Zetterstedt) (Diptera, Drosophilidae), third stage larva from under bark of fallen *Pinus* tree, Inverness-shire, Scotland; a, whole larva, lateral view, head to the right, about 8mm long, segment borders, telescoped or infolded and spiculate anchor pads straddling them, irregular black marks on the body wall are scars; b, anchor pads from right to left, straddling abdominal segments 4/5, 5/6 and 6/7.

A typical forward crawl begins with muscular infolding of the anal segment, which lifts and releases it from the substrate. The anal segment moves forward, unfolds and reattaches and a peristaltic wave begins. It comprises abdominal segments infolding at their borders along the ventral margin, which lifts and detaches the attachment structure from the substrate. They move forward, lower and reattach and a matching bulge of body fluids moves slightly ahead along the body. These movements end at the anchor pad straddling abdominal segment one and the metathorax. Ahead of this point, the wave continues to the head and the thorax cantilevers forward to complete the crawl. The head may or may not anchor the front end using mandible hooks, saliva or suction from the head pump. In empidoids a peristaltic wave starts with the anal segment compressing and deflating rather than infolding (Rotheray 2019a) (Fig. 4). Infolding appears to distinguish cyclorrhaphan larvae crawling and in this respect, they are similar to caterpillars (Lepidoptera) (Trimmer and Issberner 2007, Griethuijsen and Trimmer 2014).

The gut complicates locomotion. It is attached to the anus and the head skeleton and during crawling, does not stretch to accommodate distance changes between these attachment points, i.e. when the anal segment moves forward, the distance shortens and when the head moves forward, it lengthens. Observations show that the gut shunts forwards and backwards during crawling, and the foregut folds to accommodate these movements. Unlike the midgut and hindgut, the foregut is usually empty since food passes through it during feeding, a feature that facilitates folding (Rotheray 2019a). Gut shunting may be important in locomotion. Being full of food and digested remains, the midgut and hindgut carry much of the body weight and shunting relative to the body wall shifts the centre of gravity of the larva. Since gut-shunts are in time with a peristaltic wave, they probably optimise the energy costs of crawling (Simon *et al*. 2010, Heckscher *et al*. 2012).

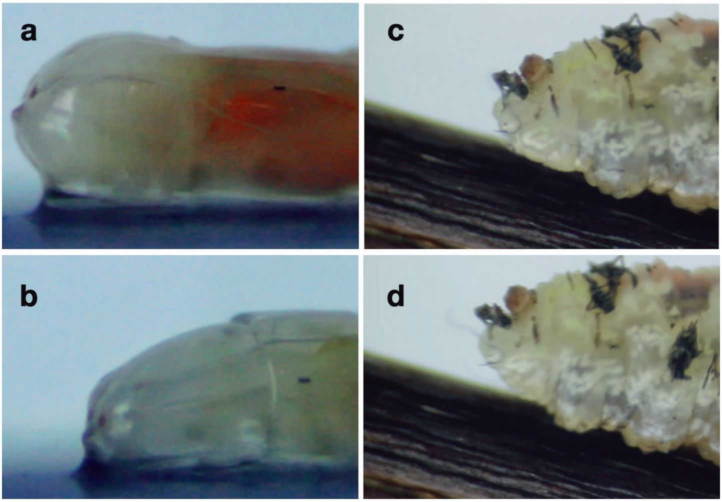

Fig. 4. Larval anal segments, lateral view, anterior end to the right, stills from videos by Geoff Wilkinson; a-b, unidentified empid larva (Diptera, Empidoidea) from leaf litter; a, position immediately before a crawl, anal segment inflated with body fluids, red hind gut visible; b, crawl initiated, anal segment compresses, deflates and inclines and the red gut in a, has shunted forward and is no longer visible; c-d *Syrphus ribesii* (Linnaeus) (Diptera, Syrphidae), third stage larva, black material on the body is prey remains; c, position before a crawl, attached to the substrate, d, at the start of a crawl, anal segment infolds and lifts.

Larvae move through material by squeezing their front modules into it and pushing it aside. In harder material they excavate tunnels. Armature in the form of plates, hooks and spicules protects larvae from abrasion, helps in turning material aside and in a few cases, is used for excavation (Rotheray 2019a). To excavate, larvae usually grip the tunnel sides with an inflated middle module. This helps counter the tendency to slide backwards when the mandibles rasp the tunnel face (Rotheray 2019a, 2021a). Some larvae use tension energy to enhance crawling. The mandibles anchor the front of the body and when a peristaltic wave reaches the head, the mandibles retain their grip which holds up the wave. When the mandibles finally let go tension is released and the head springs further forward than if the mandibles had not held on (Fig. 5).

Cyclorrhaphan larvae vary in capacity for locomotion and those in extreme confinement, such as certain gall-forming, parasitic and macrolarviparous larvae, are the least mobile. In contrast, syrphine and chamaemyiid larvae (Diptera, Chamaemyiidae) are adept at locomotion. Many are prehensile in that both the anal and head ends are able to bend and grasp substrates (Rotheray 2020). They can also move by caterpillar-like 'inching' (Fig. 6). Crawling is modified in other ways and undoubtedly, many mechanisms exist that have yet to be discovered. Leaf-mining larvae move on their lateral margins (Hering 1951). Larvae of the Lonchopteridae and Microdontinae are able to move sideways and dome-shaped larvae of the latter can turn on their diameters, which is effective for reversing direction in the confined tunnels and spaces of ant nests in which they develop (Rotheray and Lyszkowski 2015).

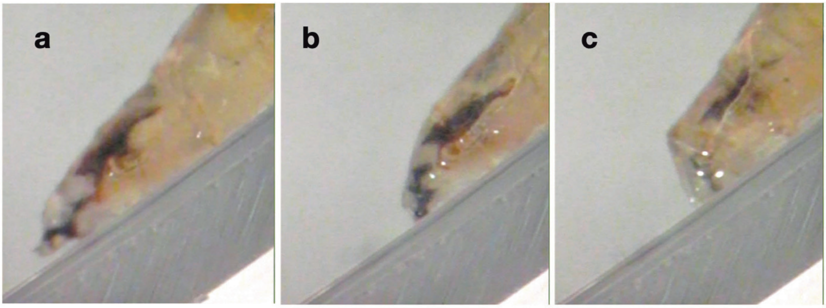

Fig. 5. ***Silba fumosa*** **(Egger) (Diptera, Lonchaeidae), third stage larva, from a decaying stem of** ***Heracleum mantegazzianum*** **(Sommier & Levier) (Apiaceae), Stirlingshire, Scotland, lateral view, head end, stills from a video by Richard Lyszkowski; a, stretching out at the end of a crawl, mandibles lowering to the substrate; b, mandibles holding on as the next peristaltic wave reaches the head; c, mandibles retain their grip and thoracic segments concertina and bulge with body fluids before the mandibles lift and the head and thorax move forward as in a.**

Larvae usually complete development within one development site, but not always. If they run out of food, certain leaf mining larvae (Hering 1951, Rotheray and Rotheray 2019) and heleomyzid larvae (Diptera, Heleomyzidae) (Rotheray and Ayre 2013) will shift between development sites. Little is known about the speeds and distances larvae are capable of travelling (Berrigan and Leighton 1993). Chandler (1969) recorded first stage *Episyrphus balteatus* (De Geer) larvae (Diptera, Syrphidae) crawling a metre or more and Greenberg (1990) found that certain calliphorid and muscid larvae (Diptera, Calliphoridae and Muscidae), were capable of moving 10+ metres. Few systematic, quantitative assessments have been made of crawling capacity relative to taxon, substrate or inherent variables, such as suppleness, attachment structure, body shape and development stage (Berrigan and Pepin 1995, Rotheray 2019a). The scope for investigation is considerable.

Apart from crawling, certain larvae jump, swim or dive (Ferrar 1987, Rotheray 2019a). Jumping depends on a sudden release of tension energy acquired by the larva grasping the anal segment with the mandibles and tensing body wall muscles. Against the leverage of a firm substrate, when the mandibles let go the larva springs upward (Maitland 1992). As for swimming, the larva of *Episyrphus balteatus* (De Geer) (Diptera, Syrphidae) copes with falling into water by swallowing air which improves buoyancy (Laska 1999). It is unable to swim, i.e. move through water in a systematic way, although by wriggling it makes haphazard progress until it reaches a substrate on to which it can attach and move out of the water. Certain aquatic Sciomyzidae (Diptera) have incorporated air-swallowing into swimming. Berg (1953) and Barraclough (1983) reported that they swallow air for buoyancy and swim upside down by beating movements of the anal segment. They brake by rolling right side up and curling down the anal segment. Certain aquatic, long-tailed, eristaline larvae (Syrphidae, Eristalinae), dive. With the tip of the breathing tube at the water surface, they are able to sink at speed and return just as fast by moving air rapidly in or out of their breathing tubes (Rotheray 2019a).

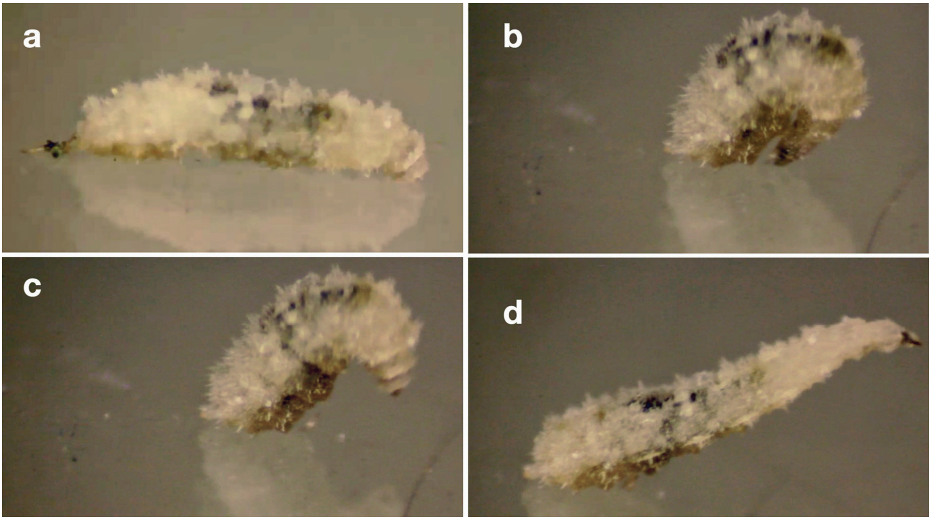

Fig. 6. Unidentified chamaemyiid larva (Diptera, Chamaemyiidae), stills from a video by Geoff Wilkinson, lateral view, head to the right, 'inching' locomotion; a, position between movements; b, anal end draws up behind the head which grips the substrate with sticky saliva and suction; c, with the anal end gripping the substrate using frictional forces and/or sticky faeces, the head lifts; d, head end stretches forward to resume position as in a.

Respiration

Few cyclorrhaphan larvae live in the open or with ready access to the air as do surface roaming chamaemyiid and syrphine larvae and many ectoparasites. Some phytophagous larvae also have ready access to the air. Others live submerged or concealed lives where access is restricted or absent. To respire these larvae must project their spiracles into the open or into air pockets and the mechanisms by which they do this are diverse but poorly recorded. An alternative route exists of absorbing dissolved oxygen through the body wall, but measurements show that this is insufficient for larval needs, especially in the final stage (Fraenkel and Herford 1938).

Typically, cyclorrhaphan larvae possess two pairs of projecting spiracles. The anterior pair at the back of the prothorax and a posterior pair on the anal segment, either above or at the apex. Investigators in the 19th and early 20th centuries determined their roles by monitoring the effects of blocking them. They discovered that the posterior spiracles were important in larval respiration and the anterior spiracles in pupal respiration, and acting as back-up should the posterior spiracles become blocked or damaged (Weise 1938, Keilin 1944).

To access air, a common mechanism is to project the posterior spiracles into it via elongate and tapered terminal segments (Fig. 7b). Elongation varies from a slight upturn in semi-aquatic sciomyzid larvae (Sciomyzidae) to rear segments up to body length or more in long-tailed eristaline larvae. Between these extremes lie an array of intermediates. Larvae with little or no elongation that live submerged appear to hang down with the posterior spiracles anchored at the surface (Green *et al*. 1983). Wetting is prevented by hydrophobic oils secreted by interspiracular glands and anchoring is due to surface tension enhanced by ‘float’ hairs on the margins of the spiracular plates (Keilin 1944).

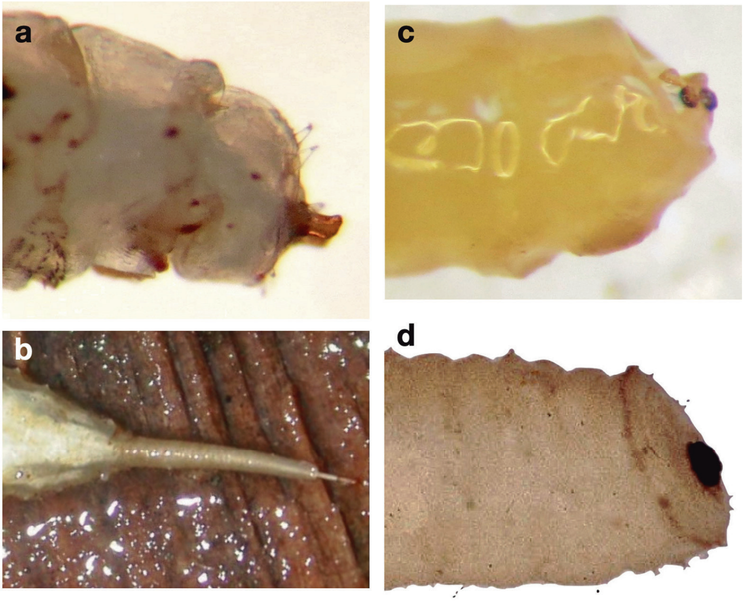

Fig. 7. Variation in the rear body segments of third stage cyclorrhaphan larvae, not to scale; a, *Chymomyza costata*, saprophage, under bark, apex of anal segment forming a disc with projections round the rim; b, *Blera fallax* (Linnaeus), saprophage, in rot holes, anal segment tapered and elongate; c, *Palloptera usta* (Meigen) (Diptera, Pallopteridae), saprophage, under bark, disc without vestiture, but possesses a pair of projections above the spiracles; d, *Portevinia maculata* (Fallén) (Diptera, Syrphidae), phytophage, tunneller of roots, disc well defined and margin coated in vestiture.

Diversity exists in the behaviour of projecting the posterior spiracles. Upturning the anal end enables sciomyzid larvae to project the posterior spiracles and maintain a horizontal position just beneath the water surface, an optimal position for encountering prey (Barraclough 1983). The tube-like apex of the anal segment in the sap run species *Aulacigaster leucopeza* (Meigen) (Aulacigastridae) trails at the surface as do the tracheae extruded from the anal segment by first stage *Brachyopa* larvae (unpublished observations). In contrast, third stage *Brachyopa* larvae do not extrude their tracheae and instead, turn up their elongate, tapering terminal ends.

Other mechanisms include the extraordinary lance-shaped, posterior spiracles in certain aquatic larvae of the Chrysogasterini (Diptera, Syrphidae) and Notiphilini (Diptera, Ephydridae). These larvae respire by piercing the stems of water plants to reach the air spaces within (Keilin 1944, Houlihan 1969). Remarkable mechanisms characterise endoparasitic larvae (Keilin 1944). These larvae frequently make a hole in the host body wall or its trachea from which to project the posterior spiracles. Some Tachinidae co-opt the host immune response. Making a hole in the host body wall or trachea can initiate an immune response from the host that results in a tube-like connection between the hole and the posterior spiracles of the parasitic larva, the so-called respiratory funnel, illustrations in Ferrar (1987).

Cyclorrhaphan larvae are not known to groom their spiracles and they lack internal closing mechanisms. Hence submerged larvae risk them being inundated, blocked or biofouled. A variety of passive mechanisms protect them, such as secretion of hydrophobic oils mentioned above, spiracle forms that make it difficult for materials to attach or penetrate, felt chamber walls (space under the spiracles) coated with setae for filtering out air-borne material and, spines, ridges and inclined spiracular plates that deflect material away (Keilin 1944, Rotheray 2019a).

Active mechanisms include those of endoparasitic Cuterebridae and Gasterophilidae that protect their spiracles by enclosing them in folds of the body wall (Ferrar 1987). Larvae of the Aulacigastridae, Canacidae and certain Drosophilidae, Ephydridae and Eristalinae protect their anterior spiracles by withdrawing them into specialised pockets in the body wall (Hartley 1961, Ferrar 1987). Burrowing and tunnelling larvae use a mix of passive and active mechanisms. The anal segment is often contracted into a disc-like form at the end of the body (Fig. 7a, c & d). Disc margins are usually raised into a rim and are characterised by arrangements of fleshy projections and vestiture that, during locomotion, deflect material away (Rotheray 2019a). As always, much remains to be investigated about the operation and effectiveness of these mechanisms.

Also requiring investigation are the dynamics of respiration. For instance, observations show that in artificial rot holes, short-tailed larvae of *Callicera rufa* Schummel (Diptera, Syrphidae) interrupt other activities and come to the surface to breathe 3-7 times/hour (Rotheray 2013). In general, how larvae organise respiration alongside other activities remains little-known. Some larvae bypass the issue of interrupting activity to respire with elongate breathing tubes. In tree holes long-tailed larvae of *Blera fallax* and *Myathropa florea* (Linnaeus) (Diptera, Syrphidae) anchor their breathing tubes at the surface for most of the time, less during winter, and will withdraw them rapidly if disturbed (Rotheray 2013).

Discussion

This paper is about investigating cyclorrhaphan larval behaviour. Larval behaviour is a neglected subject and behavioural repertoires must be many times more diverse than currently known. Hence, the potential is high for making discoveries.

Observing living material is key and facilitating investigation, most cyclorrhaphan larvae are amenable to being observed and manipulated. Observation is the way to find new behaviours. It enables behaviours that characterise particular taxa or ecological situations to be recognised. It also reveals how morphological structures relate to one another during movement which enables functions to be assessed. For example, how head skeleton components work together to gather food or how the body moves in locomotion. Although behavioural diversity is high, some behaviours are ubiquitous. These include certain taxes and kineses and possibly, area-restricted behaviour. Recognising and accounting for these behaviours is far from complete.

Investigation across many subjects is possible. For example, enumerating ways of life, many outlined by Ferrar (1987); analysing individual behaviours (Berrigan and Leighton 1993, Roberts 1971); determining performance (Rotheray 2019b) and comparing behaviour within and between ecological or taxonomic groups (Berrigan and Pepin 1995, Rotheray and Lyszkowski 2015).

Expensive apparatus and elaborate procedures are not required. Observation with a binocular microscope supplemented by videography acquires information sufficient for many objectives. Nonetheless, elaborate and sophisticated recording and analysing techniques have been deployed. Drosophilid workers have pioneered a number of them, such as the work on crawling by Heckscher *et al*. (2012) and Günther *et al*. (2016).

The so-called father of modern studies in behaviour, Niko Tinbergen (1907-1988), advocated observing animals in their natural habitats before attempting to investigate or experiment with them. Just observing cyclorrhaphan larvae going about their lives is indeed invaluable for ‘getting to know’ what to expect. Preliminary observation invariably leads to a more informed ability to frame appropriate questions and design investigations. Preliminary observation gains even greater significance when it includes comparisons with related species, either taxonomic or ecological.

More and better investigations of cyclorrhaphan larval behaviour would be a major step towards resolving the ‘black box’ of unknowns that this neglected life stage represents. It will improve knowledge of flies and their ways of life. A further result is the spur behavioural investigation would give to a wider acceptance of the information value of the larva, and to the importance of including this stage in studies of not only the Cyclorrhapha, but of other groups of flies.

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Dipterists Digest 2022 **29,** 84-86

Chalcosyrphus piger (Fabricius) (Diptera, Syrphidae) new to Britain

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Summary

Chalcosyrphus piger (Fabricius, 1794) is reported from a British location for the first time. Details of the record are provided and characters enabling recognition of this species are discussed.

Introduction

On 3 July 2021, on a visit to West Stow Country Park (V.C. 26 – West Suffolk), TL799715, AT photographed a striking black hoverfly with a red abdomen on a fence post along the edge of a narrow fringe of Scots pine *Pinus sylvestris*. After researching its possible identity, AT suspected it was *Chalcosyrphus piger* (Fabricius, 1794) but was uncertain because it was not listed as a British species. The photographs were later posted on the UK Hoverflies Facebook group (Facebook 2021) where they were recognised by GP as *C. piger*, a very distinctive western European species. The specimen was not retained and no further visits have been made to establish the wider presence of *C. piger*.

Recognition

At a casual glance, *C. piger* might be mistaken for *Brachypalpoides lentus* (Meigen, 1822), but with tergites from 2 onwards almost completely red (with the exception of a black V-shaped marking on the anterior margin of tergite 2). When the wings are folded over the abdomen, the extent of red coloration on the tergites may be obscured; hence the potential for confusion in Great Britain where its presence is unexpected. In this example, the wings are folded but the red pigmentation as far as tergite 4 can be discerned and for this reason, *B. lentus* can be discounted. In addition, the hind femora are strongly swollen in both sexes (much more so than *B. lentus*) and the frons is broader and more silvery in *C. piger* when viewed from above. Closer examination (not obvious in photographs) will also show that *C. piger* lacks the golden-yellow pile on tergites 2 and 3 that is present in *B. lentus*. As there is no other species in western Europe with which this species might be confused, it was identified as *C. piger*.

Distribution and biology

Chalcosyrphus piger occurs widely through northern Europe according to records presented on GBIF (the Global Biodiversity Information Facility). Speight (2020) reported it to be increasingly montane southwards to the Pyrenees. Its occurrence across France and Spain is not discernible from GBIF as there is very low data coverage for these countries. The map provided in Bot and van de Meutter (2019) suggests that it occurs locally in The Netherlands and Belgium. Its range in the Netherlands and Belgium as well in other parts of Europe is still increasing (GWAP *pers. obs.*).

Speight (2020) listed sources of larval biology that point to a close association with a range of conifers and in particular with decaying sap under the bark of larch *Larix* sp. and pines *Pinus* sp. Windthrown, but still living trees may provide particularly suitable habitat, especially where there is damage that causes weeping wounds (e.g. woodpecker workings). Adults are reported to occur on sunlit stumps and foliage in woodland clearings but may also visit a wide variety of flowers (Speight 2020; Pennards *et al*. 2021). The close proximity of West Stow Country Park to a huge area of conifer plantations (The Kings Forest) fits well with potential breeding sites.

Fig. 1. The photographs of *Chalcosyrphus piger* taken by AT on 3 July 2021. Note the thicker hind femora and red tergite 4 when compared with *Brachypalpoides lentus* (Fig. 2)

Fig. 2. *Brachypalpoides lentus* from Denny Wood, New Forest (photo Steven Falk). Note the distinctive black fourth tergite and the smaller extent of the frons.

Bot and van de Meutter (2019) indicated that whilst peak emergence in The Netherlands is May and June (somewhat earlier in Belgium) it may be recorded well into September. The record from West Suffolk is therefore broadly consistent with core flight times in The Netherlands.

Discussion

Recent analysis by Pennards *et al*. (2021) reported that after a period of decline *C. piger* has returned across much of central Europe from around 2000. Given that its distribution in mainland Europe is stable or possibly increasing, the IUCN Red list of Threatened Species (Pennards *et al*. 2021) lists *C. pige*r to be of 'Least Concern'. Its appearance on the British mainland does not come as a complete surprise, given the relatively close proximity of West Suffolk to mainland Europe. It must, however, remain a matter of conjecture how and when this species reached British shores.

There are several extensively coniferised areas in both Suffolk and Norfolk, but almost all are relatively recent (i.e. planted in the 20th Century). Some are reaching the end of the first felling cycle and therefore it is possible that conditions suitable for *C. piger* are currently being created, as seems to be the case elsewhere for *Xylota jakutorum* Bagatshanova, 1980 and *Callicera rufa* Schummel, 1842 (Ball and Morris 2021), i.e. cut stumps with rotting timber and decaying sap. Such plantations also have a tendency for windthrow in high winds and although conjecture it is possible that such events may have contributed to available habitat. West Stow Country Park is partially coniferised and cut trunks are left more or less where they fall and stumps are left to rot naturally. Various stages of decay are present, ranging from recently cut conifer logs with bark still attached, to logs that have lost their bark and to cut stumps in an advanced state of decay. The Park lies within a few hundred metres of The Kings Forest that is in excess of 2,000 ha of coniferous woodland that comprises a mixture of Scots pine, Corsican pine *Pinus nigra* and larch *Larix* sp. It therefore seems likely that there are parts of this forest that suit *C. piger*. Further visits to both West Stow Country Park and to The Kings Forest may help establish the extent to which *C. piger* occurs there. Wider surveillance of coniferous areas in both Suffolk and Norfolk would also be useful, as there is no obvious reason why this record is unique to West Stow Country Park.

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Dipterists Digest 2022 **29,** 87-100

BRIAN ROBIN LAURENCE 1928 – 2018

An obituary by John O'Sullivan (2018) appeared in the *Bedfordshire Naturalist* and a tribute to Brian was included in the 2021 Autumn Bulletin. In view of Brian's contribution to many aspects of dipterology, a fuller account of his life as a dipterist is presented here.

Brian was born at St Albans, Hertfordshire on 31 March 1928, son of John Scott Laurence and Alice Minnie Duperey, who had married there in 1922; his father was a clerk at the travel agents, Thomas Cook. He had an elder brother Donald, born in 1924. Brian's paternal grandparents Robert Laurence and Margaret Scott were Scottish. They had moved to Colchester, where his father was born, by 1887 and to St Albans by 1911; Robert was a foreman in a boot factory. His mother's family had moved to St Albans from Clerkenwell in London; her father John Duperey worked in printing as a compositor. By 1933 the family had moved to Luton, where Brian attended Maidenhall infants' school, going on to Luton Grammar School in 1938. From there he went in 1946 to study zoology at University College, London, leaving with a BSc in zoology in 1949.

OFFICERS AND COUNCIL 1946-52

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R. Palmer, H. A. S. Key, W. E. K. Piercy, His Grace the Duke of Bedford, O. G. Pike, Miss E. Proctor, W. H. Bonnett

[*Photograph by F. Jewell Harrison*

The Officers and Council of the Bedfordshire Natural History Society (from the Society's journal for 1951). Brian is at the right of the middle row. John Dony and Horace Barnes are at each end of the back row.

Brian had been introduced to natural history by his father, who provided him and his brother Donald with a brass microscope, with which they examined the organisms in pond water (O'Sullivan 2018). He evidently joined the Bedfordshire Natural History Society soon after its foundation and contributed an article (1947a. *Notes on Bedfordshire Diptera*) to the first issue of the Society's Journal. Apparently, he was encouraged by John Dony, a botanist who taught history at Brian's school. Brian soon became involved in the running of the Society, appearing in the 1951 photograph of the Society's Council, in which John Dony is also present. Behind Brian in this photograph is Horace Francis Barnes (1902–1960), then working at the Rothamsted Experimental Station, where he specialised in gall-midges (Cecidomyiidae). From 1946 until 1956, Barnes authored the *Gall-midges of economic importance* in seven volumes; in the 1920s he had been interested in craneflies, producing several papers on their ecology and distribution in Wales. Also, then active in the Society were two of Brian's entomological friends of those days, Victor Chambers (1911–1984), whose interest was in Hymenoptera, and Bernard Verdcourt (1925–2011), who covered a range of insect orders. Bernard's later career was in botany, from 1964 to 1987 at the Royal Botanic Gardens, Kew after a spell in East Africa – he was an authority on African plants and molluscs, but retained an interest in entomology after retirement, being often seen at Dinton Pastures during BENHS open days.

While living at Luton, Brian cycled to the local woods and fields to collect Diptera, concentrating on the Fancott area north-west of the town (O'Sullivan 2018). He contributed 18 items on the fauna of Bedfordshire from 1944 to 1956, half of them on Diptera but also including notes on butterflies, shield bugs, grasshoppers, harvestmen and water fleas. The soldierfly *Odontomyia argentata* was a notable early find (1945d). His first publication in 1944 was in the *Entomologist's Record*, and a series of notes followed both there and in the *Entomologists' Monthly Magazine*. Brian acknowledged the role of the county in the early development of his interest in entomology when in 1987 he gave a collection of Diptera to the Bedford Museum. This comprised 737 specimens collected from 1943 to 1956, which are presumed to be a predominantly local collection, though not entirely, as the species list in the museum's database includes the New Forest fly *Hippoboscа equina*. A wide range of Diptera was included, the main groups represented being hoverflies (232), soldierflies and allies (97), Empidoidea (86), craneflies (79) and calyptrates (101).

Predation was an early interest, and a series of notes and articles appeared on this subject from 1947 onwards. The wide range of dipterous predators and their prey were discussed in an article in the *Bedfordshire Naturalist* (1950a. *Predators and prey*): asilids, empids, scathophagids and muscids featured among the predators, and the contribution that identification of prey insects could make to local records was stressed – for example a cerambycid beetle he had found as prey of the robber fly *Neoitamus cyanurus* was a new county record. A detailed study of the prey of "tree trunk frequenting" Empidoidea (*Tachypeza nubila* and *Medetera* species) soon followed (1951d). Another new biological observation in this group (1949c) was of females of *Microphor crassipes* feeding on prey in spider's webs.

After graduation, Brian began a PhD at Rothamsted. His subject was the larvae developing in cow dung. This resulted in a series of notes (1952b, 1953c, 1954, 1955b, 1955c) on the associated Diptera. The first of these (1952b) describes a species of Sphaeroceridae new to science, *Philocoprella quadrispina* (originally described as *Limosina*), and adds a sepsid *Sepsis nigripes* to the British list. The latter was concluded by Adrian Pont, in the handbook to this family, to be a dwarf form of *S. fulgens*. A psychodid he reared from a rot-hole in lime at Rothamsted was described by Paul Freeman (1953) as *Telmatoscopus laurencei*. Brian was awarded his PhD in 1953.

On completion of his PhD, Brian became an assistant lecturer at Birkbeck College in London, where he was based from 1951 to 1956, interrupted by National Service. In 1952, he married a zoologist Edna Beryl Carr in Lewisham, where she had been born on 5 June 1927. She also worked at the College, where she spent her entire career while they were living in London – her main interest there was in cell division in cancer research.

The two years of National Service, from 1953 to 1955, were with the Royal Army Medical Corps, where his previous experience and knowledge of Diptera led to him teaching medical entomology to officers of this regiment at their college in Millbank. While he was undergoing training with the army, he was based at Catterick, where he took the opportunity, in May-June 1954, for some local entomology; he investigated predation by empids along the Colburn Beck, a stream entering the River Swale three miles below Richmond – this resulted in his paper (1955d) on the empids of a Yorkshire stream, in which he thanked J.E. Collin for the identification of the specimens. Prey records were presented for 6 species of Empididae and 5 species of Hybotidae, the prey often including other members of these families; the complexity of predator-prey relationships at the site was discussed. His tubes of specimens in spirit were carefully hidden to ensure they weren't found during kit inspections (Roy Crossley *pers. comm.*).

National Service was shared with John Stevenson, later an agricultural biologist at Rothamsted, who joined him on some field excursions and became a lifelong friend. He recalls that an insect found at the base was sent by an officer to the Natural History Museum for identification but, unknown to that officer, the Museum sent it to Brian who was responsible for the identification; it was presumably one of the dung feeding flies that he worked on for his PhD.

During that period, Brian also took an interest in winter gnats (Trichoceridae), resulting in publications both on their biology (1956a) and identification (1957).

In 1956, Brian left Birkbeck College to join the staff of the London School of Hygiene and Tropical Medicine, starting as a junior lecturer in the Entomology Department and rising through the ranks, to Senior Lecturer in 1962 and Reader in 1968. Brian wrote an eight-page memoir (2003) about his 30 years at the London School, in which he reports that he applied in the autumn of 1955 for the post in the Entomology Department, which was then headed by Professor Patrick Alfred Buxton (1892–1955), who wrote to congratulate him on his appointment, but who had died on 13 December 1955, before Brian took up the post in January 1956. Buxton is well known to dipterists for his work on rearing from fungi and he had written an article (Barnes and Buxton 1953) on the cecidomyiids he reared, co-authored with the above-mentioned Horace Barnes – the main paper on rearings of other families of Diptera was posthumous (Buxton 1960).

Brian mentions in the memoir that the initial appointment for three years was expected to involve training for a post in the colonial service or medical service overseas, a prospect in which he declined any interest during the interview as he had a working wife, so he was surprised to be appointed. Buxton was replaced by Douglas Bertram, who had become a prisoner of war when captured while working in an RAMC anti-malaria unit in Crete. Bertram was said by Brian to be good at encouraging diversity of interest in the Entomology Department, continuing the attitude of Buxton in permitting staff to indulge in any research that took their fancy, which Brian appreciated. This freedom was later affected by the problem of obtaining research grants to fund the employment of technical assistants. The teaching programme was structured to enable "several months of freedom for research, both in the laboratory and overseas". There is no mention in the memoir of any overseas travel, though he did travel widely in the tropics, particularly to Africa, India, Sri Lanka and the Seychelles; he advised the World Health Organisation on how to control insects ahead of tourist developments in Seychelles and Tanzania (Ray Laurence *pers. comm.*).

Much of the memoir concerns working with a succession of colleagues, describing how tensions, personality clashes and continual reorganisation adversely affected the operation of the School. There are few references to the students, though they were said to be a major reason for staying – they were from a wide range of backgrounds, and he says "it was a pleasure to have these students from different countries at home at Christmas adding to the education of my two young boys". He was pleased for the opportunity to take early retirement in 1983, though remaining as an Emeritus Reader until 1986.

At the end of his memoir, he quotes the poet Ernest Dowson:
“They are not long, the days of wine and roses: Out of a misty dream our path emerges for a while, then closes within a dream”.

The research he carried out while at the London School centred on the biology of mosquitoes, especially those in the genera *Mansonia*, *Anopheles* and *Aedes* that were vectors of elephantiasis, a tropical disease for which the causative organism was the filarial nematode worm *Brugia malayi*. In his memoir, he describes his involvement in setting up the first laboratory colonies of *Mansonia* mosquitoes outside the tropics, and in culturing in the laboratory the filarial worms *Brugia pahangi* and *B. papei*, which cause filariasis in cats and dogs.

He authored 55 publications from 1958 to 1991 on the biology of the mosquito vectors and the filarial worms. The mosquito *Mansonia* lays its eggs on the floating leaves of water plants, and its larvae and pupae obtain oxygen by penetrating the submerged parts of these plants. A regular development site was in stagnant rainwater in coconut plantations. He also wrote about the history of elephantiasis; in one case (1970a) he investigated the concentration of the disease in the Malabar area of India, leading to it being known as St Thomas’ curse because of it was endemic in the indigenous Christian population, alleged to have been converted by St Thomas.

There were also several articles on an oviposition attractant pheromone in the mosquito *Culex quinquefasciatus* (Laurence and Pickett 1982 and 1985, Laurence *et al*. 1985, Otieno *et al.* 1988, Dawson *et al*. 1989). This was employed in traps to control these mosquitoes by breaking the oviposition cycle, and was the subject of a presentation by his co-author John Pickett (of Cardiff University) at a conference (Insect Olfaction and Taste in 24 Hours Around the Globe) in August 2021 (*pers. comm*. by Mary Cameron, who was a co-author – as M.M. Pile – of the last two of the above listed publications on this subject).

Also during this period, Brian was a co-author of five publications describing new species of Acari, with J.B. Walker, a tick from the reticulated giraffe (1973), and with Alex Fain four species of mites parasitic on birds (1974, 1979, 1986) and one (1975) causing mange in the Tasmanian devil, also an article (1981, with J. Gaud, in French) on polymorphism in feather mites of the kiwi.

While working in London, Brian and Edna lived initially at Forest Hill, and then at Woking. Their two sons, Duncan and Raymond, were born in 1959 and 1963 respectively. By 1979 they had moved to Islington, where he found it interesting “to identify the flies that have survived in an area that has been built over for more than 100 years” (1982). He noted that most were common and ubiquitous species but there had been some surprises, the most unexpected being the cave-dwelling fungus gnat *Speolepta leptogaster* – an adult male was first noticed in May 1979 in an old coal cellar beneath the pavement, accessible from the basement of his house (built in the 1830s) in Colebrooke Row. During 1980, larvae were found on the walls of this cellar – their gut contents were found to be fungal spores and algae; their pupae were suspended from the ceiling. Observations of emergent adults indicated that there were three generations a year. Almost as surprising was the presence of the keroplatid *Macrocera fasciata*, whose larvae preyed on the *Speolepta* larvae. He speculated on the origins of this population of *Speolepta*, noting that the cellar was near the tunnel for the Regent’s Canal, which might support the gnat. He later (1989a) gave a more detailed account of its biology, based on observations of 21 generations over a 6-year period, estimating the peak numbers of the summer generation as 650 to 700 adults, but with wide fluctuations during the period studied. Observations ceased in the spring of 1986, when he moved to Norwich.

While Brian was resident in Norwich, an extensive survey of East Anglian wetlands was carried out, using water traps, by Andrew Foster and Deborah Procter of the Nature Conservancy Council. Diptera from this survey were sorted into taxonomic groups and circulated to specialists for identification. Brian evidently volunteered to deal with the Sciaridae and Dolichopodidae.

His article (1995a) reporting the results for Dolichopodidae included the addition to the British list of *Achalcus thalhammeri*.

For the Sciaridae, he found that the then recent Royal Entomological Society handbook by Paul Freeman (1983) was insufficient to identify all the diversity of species obtained in this survey (the handbook included only 101 species – the full extent of the British fauna, now 267 species, was not then appreciated). The consequence was that Brian's contribution to taxonomy of Diptera was on Sciaridae. Brian added ten species of Sciaridae to the British list (1994a, and 1996 with R. James). Five species were described as new but only *Bradysia dolosa* remains a valid name, three others falling to synonymy, having been described shortly before in Germany, one by Hans-Georg Rudzinski and two by Frank Menzel and Werner Mohrig, while *Corynoptera echinocordyla* is now considered not to be a distinct species from *C. forcipata*. Brian's slide-mounted sciarid collection was loaned to me in 2003 and all were examined by Frank Menzel, enabling the records to be included in the update of the British fauna of Sciaridae (Menzel *et al.* 2006). Among the many additions to the British list in that paper to which Brian's records contributed, six species were added solely on his specimens. At Brian's request the entire collection of slides has been deposited at the Oxford University Museum; Brian had earlier given some type material of Sciaridae to the Norwich Museum (Tony Irwin *pers. comm.*).

Also, while he was at Norwich, Brian assisted the Department of Biological Sciences of the University of East Anglia with fieldwork. This included a survey of the Diptera of Bradfield Woods in Suffolk, using water traps and pitfall traps, with the intention of comparing areas at different stages of the coppice rotation. The site was by then a reserve managed by the Suffolk Wildlife Trust; it was a mixed broad-leaved woodland, which was known to have been coppiced at least since the 13th century. This survey took place in July and October 1990 and May and August 1991. The results were reported in *Dipterists Digest* (1997b. *Flies from ancient coppiced woodland in Suffolk*), including a list of 304 species identified. In a previous article in *Dipterists Digest* (1996. *Beyond the Red Data Book*), Bradfield Woods was one of five areas for which the results of surveys were compared; these five areas differed widely in location and habitats. The species in common between the sites were listed: of 1105 species identified, 994 were found at only one or two, 68 at three, 29 at four and only 14 at all five – the reasons for these differences were discussed.

Brian wrote a letter to *Antenna* (1989d) entitled *Where do dipterists go – and why?* about the then recent loss of taxonomists from the Natural History Museum Diptera section. There were responses in a later 1989 issue (**13,** 158-160) from Chris Thompson, Dick Vane-Wright and Jason Londt, and a related letter from Henry Disney about the crisis in funding of taxonomy. A reply from Brian (1990b. *Disappearing dipterists and other things*) summed up the position, and he expressed doubts about whether he should deposit types of new species of Sciaridae at the museum. Then Ken Smith (1990. *Antenna* **14,** 116-117), who had recently retired from the Diptera section, wrote in support of Brian, leading to a rebuttal by Ian Gauld (1990. *Antenna* **14,** 166-168). In his second contribution (1990b), referring to an article by the Royal Entomological Society librarian Brenda Leonard, which had recently appeared (Dipterists of Yesteryear: the Wainwright correspondence. *Antenna* 1989 **13,** 89-102), Brian concluded with "As one of your Dipterists of Yesteryear…, I have still an interest in the future of my subject."

From 1991 onwards, there were 10 contributions on the fauna of the Northern Isles, three (1991a, 2000, 2003) among his six articles published in *Dipterists Digest*. Holiday visits with his wife Edna to Orkney and Shetland had begun in 1981, and continued after they moved to Berwick-upon-Tweed in 1994. The islands had become a favourite area of study. A full list of his finds (1997c) included 365 species, the results of collecting there in most of the previous 15 years. He continued to add to this list in later years. Brian attended the International Congress of Dipterology at Oxford in 1998, and I enjoyed visiting him at Berwick on several occasions when I was regularly travelling to Edinburgh in the years following.

Brian's long publication record ceased in 2003, about the time that his wife Edna became unwell. Brian cared for her at home until it was necessary for her to go into a care home, where he visited her daily. Edna died aged 84 on 24 February 2011. In June 2013, Brian made a return visit to Bedfordshire and, with his old friends Charles Baker and John Stevenson, visited one of his favourite meadow sites at Fancott, now containing a large electricity sub-station and part of the M1 Motorway, but still retaining some of the original habitat (John Stevenson *pers. comm.*). They lunched at the Fancott pub, which was distinguished by having in the garden a model railway, one of Brian's longstanding interests. He had set up an impressive model railway at home while living at Woking and this was then transferred to each subsequent residence. He also supported heritage railways, including that in the Aln Valley in Northumberland.

During that 2013 visit to Bedfordshire, John O'Sullivan and Alan Outen (from the Bedfordshire Natural History Society) visited Brian at John Stevenson's house and interviewed him about his life, the basis for the obituary that appeared in the *Bedfordshire Naturalist* (O'Sullivan 2018), recalling that he was full of self-deprecating fun and was excellent company. They followed this up with visits to Fancott and kept in touch with Brian. In 2014, Brian gave many of his entomological books to Dipterists Forum; some were distributed to members, while others were placed in the library at Dinton Pastures.

Brian in 2002 (photo supplied by his son Ray Laurence)

Brian served on the Council of the Royal Entomological Society from 1960 to 1962, and was Vice President in 1962. He was on the Council of the British Society for Parasitology from 1971 to 1973. He was Vice President of the International Society for Invertebrate Reproduction from 1975 to 1979, and was Treasurer of the Royal Society for Tropical Medicine & Hygiene from 1981 to 1984.

Some archival material concerning Brian is now held by the Natural History Society of Northumbria, which is based at the Great North Museum: Hancock (June Holmes *pers. comm.*). This includes correspondence from 1996-2004 (including a batch from the Shetland Entomological Group and the Orkney Field Club, and some from Paul Freeman and Douglas Kettle); of especial importance are 28 letters from 1948-1958 from James E. Collin. Unfortunately, there is nothing from the intervening years. Also included is original artwork by Brian of ten insects and mites of medical importance. Most of these were published in the book *Medical and Veterinary Entomology* by Douglas Kettle (1995). These items were received by June Holmes in 2018 from Brian's son Duncan. Brian died on 21 February 2018.

Apart from the specimens mentioned above, that are now at the Bedford, Norwich and Oxford University Museums, Brian occasionally donated specimens to the Natural History Museum, London (Nigel Wyatt *pers. comm.*). It has not been established, from enquiries with museum curators in the Insect Collection Managers Group, where the bulk of Brian's collection is now located.

I am grateful to John O'Sullivan for providing copies of items from the *Bedfordshire Naturalist* and for obtaining the list of specimens donated by Brian to the Higgins Bedford Museum. I also thank him and John Stevenson for other information, and June Holmes for details of the archival material. Ray Laurence kindly provided a comprehensive list of Brian's publications, from which the bibliography has been compiled, and he also supplied a copy of Brian's memoir written in 2003 and many other relevant details. Duncan Laurence also provided information that refined some details.

Peter J. Chandler

New species of Diptera described by Brian Laurence

Limosina quadrispina Laurence, 1952 (now *Philocoprella quadrispina*) (Sphaeroceridae)
Bradysia dolosa Laurence, 1994 (Sciaridae)
Bradysia semantica Laurence, 1994 (= *Scatopsciara fritzi* Menzel & Mohrig, 1992 (Sciaridae)
Corynoptera echinocordyla Laurence, 1994 (= *C. forcipata* (Winnertz, 1867)) (Sciaridae)
Plastosciara taractica Laurence, 1994 (= *Cratyna spiculosa* (Rudzinski, 1993)) (Sciaridae)
Scatopsciara subvivida Laurence, 1994 (= *S. subcalamophila* Menzel & Mohrig, 1991) (Sciaridae)

New species of mites and ticks (Acari) described by Brian Laurence

Margaropus wileyi Walker & Laurence, 1973 (Ixodoidea: Ixodidae)
Ibisidectes debilis Fain & Laurence, 1974 (also a new genus) (Astigmata: Hypoderatidae)
Sarcoptes armatus Fain & Laurence, 1975 (also a new genus) (Astigmata: Sarcoptidae)
Neottialges (*Pelecanectes*) *platalea* Fain & Laurence, 1979 (Astigmata, Hypoderatidae)
Neottialges (Caloenectes) distinctus Fain & Laurence, 1986 (Astigmata: Hypoderatidae)
Neottialges (Pelecanectes) tauraco Fain & Laurence, 1986 (Astigmata: Hypoderatidae)

Species named after Brian Laurence

Telmatoscopus laurencei Freeman, 1953 (Psychodidae)

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Dipterists Digest 2022 **29,** 101-106

The deer nostril fly *Cephenemyia auribarbis* (Meigen) (Diptera, Oestridae) in Highland Region, north Scotland

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Summary

The deer nostril fly *Cephenemyia auribarbis* is confined in Britain to the north of Scotland where it is widely distributed. 27 records of adults and data on larvae from 150 post-mortem examinations on red deer on Rum are analysed. Up to 74 late instar larvae were detected in over half the deer between January and April. Adults were recorded from April to July with a peak in June. While the fly does not appear to be under any immediate threat, its future is probably dependent on policies governing commercial deer management on sporting estates.

Introduction

The deer nostril fly *Cephenemyia auribarbis* (Meigen, 1824) is, as a larva, parasitic in the nasal passages and pharynx of deer (Cervidae). It is found in Scotland and widely in mainland Europe: The Netherlands[1]; Austria and Hungary (Leitner *et al*. 2016); the Czech Republic and Slovakia[2]; and Spain (Bueno-de la Fuente 1998). It is, however, absent from Finland, Sweden and Norway (Nilssen *et al*. 2008). In Britain it is confined to the northern half of Scotland[3], where the principal host is the red deer *Cervus elaphus* Linnaeus, 1758 although the fallow deer *Dama dama* (Linnaeus, 1758) may also be attacked (Smith 1989).

Cephenemyia trompe (Modeer, 1786) was introduced to Scotland with its host the reindeer *Rangifer tarandus* (Linnaeus, 1758) (Falk and Pont 2017), but is now considered extinct there.

The Highland Biological Recording Group (HBRG) was first alerted to *C. auribarbis* by O'Driscoll (2009). We now hold 27 records of the adult fly, and these are analysed here. Another 10 records from other datasets (excluding duplicates) are currently held on the National Biodiversity Network (NBN) Atlas.

Methods

Records of adults provided to HBRG are mostly casual and opportunistic with no systematic survey or monitoring. This has implications for interpretation of the data. All determinations were from competent entomologists or were confirmed from photographs. All but six of the records date since 2009 and all lie in the Highland Council local authority area which covers vice-counties 96, 97, 104-109 and parts of 95 and 98 (see Fig. 1).

Data on larvae on Rum were obtained from the University of Edinburgh Red Deer Project. Age, sex, and details of larval load in 150 deer which were subject to post-mortem examination from 2014 to 2021 were used in the analysis. Larval instars were not separated, and 10 records were of minimum larval numbers only. 129 (86%) deer subject to post-mortem had died of natural winter mortality, with the rest from accidents and calving complications or had been shot. The deer that died of winter mortality were dominated by young animals less than two years old

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[1] https://www.gbif.org/species/1587331, accessed 12 July 2021.

[2] https://www.gbif.org/species/1587331, accessed 12 July 2021.

[3] https://records.nbnatlas.org/occurrences/search?q=lsid:NBNSYS0000030015, accessed 12 July 2021.

in poor condition (86, 67%) and those over 10 years old (36, 28%). Adult and late instar larvae are shown in Plate 1.

Plate 1. Adult *Cephenemyia auribarbis* (left) and late instar larvae found at post-mortem of red deer on Rum (right). © Sean Morris.

Distribution

The distribution of HBRG records of *C. auribarbis* in Highland is shown in Fig. 1. Records range across the area from Lochaber north to Sutherland, almost entirely to the north and west of the Great Glen. Our records range from close to sea-level to mountain-tops at 786m elevation. While some gaps may be a result of under-recording in remote areas, the presence of only two records of this summer-flying insect in the entomologically well-studied areas of the Cairngorms and Strathspey is striking and might represent a real difference in either distribution or abundance, possibly related to deer ecology or management practices. It is also strange that there are no records from Skye given the strong presence on nearby Rum. A report of what might have been several on the summit of the Sgùrr of Eigg in July 2021 is intriguing but can never be confirmed. Though Eigg has no resident red deer, it is less than 10km from Rum and surely within dispersal distance, at least with wind assistance.

Elsewhere, it is recorded from vice-counties 88 (Mid Perthshire), 92 (South Aberdeenshire), 98 (Argyllshire) and possibly 87 (West Perthshire)[4]. It is relatively common in the eastern Cairngorms including vice-county 90 (Angus) (Iain MacGowan *pers. comm.*).

As the host is recorded from almost every hectad in our recording area some other factors must be limiting its distribution.

Behaviour

SM has frequently observed the behaviour of red deer when they are being attacked by larvae-positing *C. auribarbis*. *Cephenemyia* species deposit tiny live larvae into the nostrils of deer while hovering in front of the nostrils (Zeegers 2001). When adult flies become active their presence is easily detected in the behaviour of the deer. When attacked by *C. auribarbis* red deer react by pushing their muzzles down close to the ground or into tufts of grass, presumably to prevent easy access to the flies. Sometimes, when stationary, the deer will wave their heads about in all directions and on occasion with good views it is possible to see the adult *C. auribarbis* flying in front of the muzzle. It is also possible to hear much snorting and snuffling from the deer

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[4] https://records.nbnatlas.org/occurrences/search?q=lsid:NBNSYS0000030015, accessed 12 July 2021.

as they presumably try to expel deposited larvae and they will frequently be seen scratching at their nostrils with a hind hoof perhaps due to irritation caused by the deposited larvae. They will also frequently run a considerable distance to escape the attentions of the adult flies.

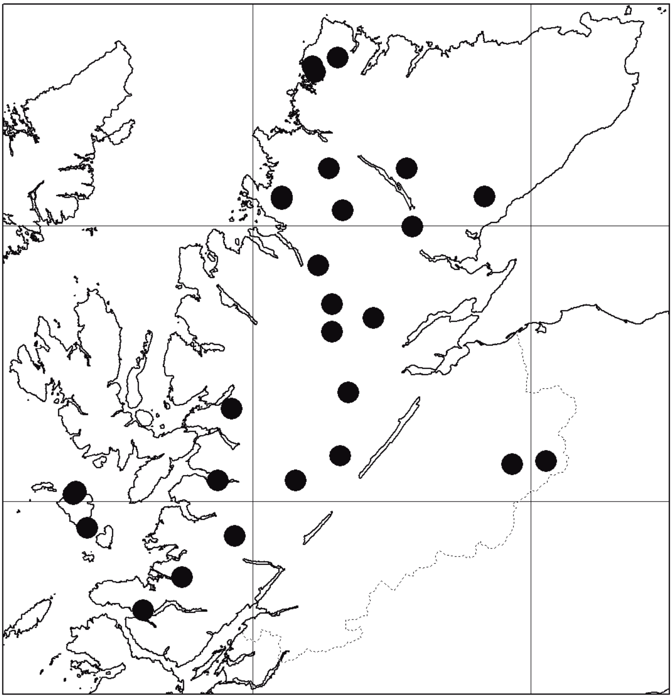

Fig 1. Distribution of records of *Cephenemyia auribarbis* in the Highland Biological Recording Group database, plotted at monad precision and 8km diameter, and restricted to the Highland Council local authority area (within the dotted boundary).

One of us (MM) has twice been the object of special attention from *C. auribarbis*. One flew persistently within a metre of his face in a swinging pendular motion. On another occasion a female sitting on a rock at ground-level persistently rotated on the spot to track his movements. It seems likely that both behaviours are applied in selection of host animals.

Summiting or hill-topping behaviour[5, 6] (Catts 1964; Downes *et al.* 1985; Skevington 2008; Zeegers 2001) has frequently been mentioned as a feature of Oestridae generally and *Cephenemyia* specifically. At least two of our records were of insects on summits at over 700m. Lowe (2014) mentioned this behaviour as characteristic of males on Rum which he describes as ‘restricted to hill tops or outcrops of rock’ in contrast to females which were found wherever there were deer.

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[5] https://diptera.info/forum/viewthread.php?thread_id=40025, accessed 12 July 2021.

[6] https://bugguide.net/node/view/260338, accessed 12 July 2021.

Phenology of adults

Fig. 2. shows the flight season of *C. auribarbis* in Highland. Our extreme dates are 3 April and 24 July.

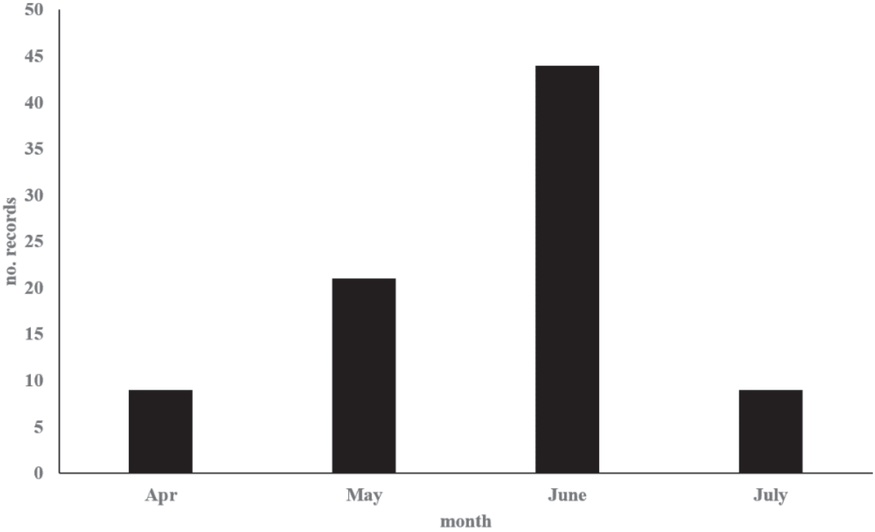

Fig. 2. Phenology of adult *Cephenemyia auribarbis* in Highland from the Highland Biological Recording Group database.

Larvae

On 3 March 2009, O'Driscoll (2009) found about a dozen larvae around 25mm long in the pharynx of an aging red deer stag, probably over 12 years old. Post-mortem data from Rum recorded larvae between January and April in just over half the animals examined. Smaller early instar larvae must have been present from July to December, but these will perhaps have been present in the nasal passages rather than the pharynx, and less likely to be detected. There was no apparent relationship between number of larvae recorded and the age or sex of the host animal, those in their first year having a 0 to 74 larvae, and others up to 19 years old with no larvae at all (Table 1, Figs 3, 4).

		number of maggots						
Host sex		**0**	**1-10**	**11-20**	**21-30**	**31-40**	**>40**	**max / mean infected / mean all**
Female n=86	**number**	40	27	5	7	4	3	67 / 13.9 / 7.4
	%	46.5	31.4	5.8	8.1	4.7	3.5	
Male n= 54	**number**	27	11	3	6	4	3	74 / 22.3 / 11.2
	%	50.0	20.4	5.6	11.1	7.4	5.6	
All n=140	**number**	67	38	8	13	8	6	74 / 17.0 / 8.9
	%	47.9	27.1	5.7	9.3	5.7	4.3	

Table 1. Numbers of larvae of *Cephenemyia auribarbis* at post-mortem of red deer on Rum, 2014-2021.

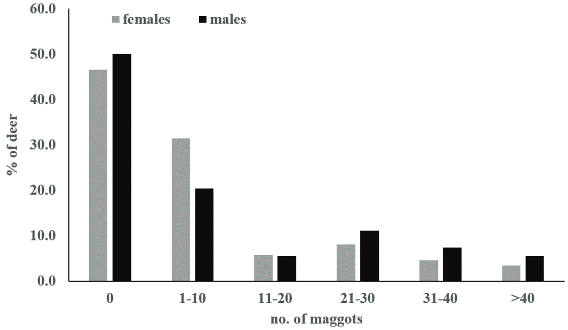

Fig. 3. Number of maggots of *Cephenemyia auribarbis* at post-mortem of red deer on Rum, 2014-2021, separated by sex of host.

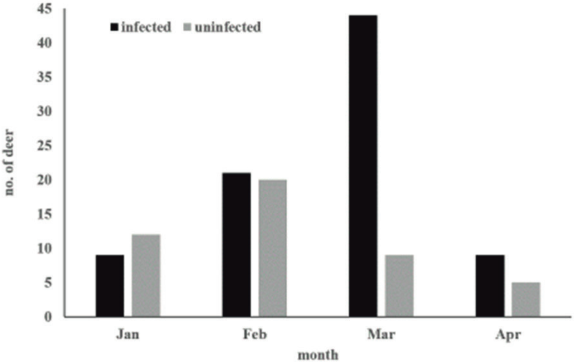

Fig. 4. Number of red deer infected with *Cephenemyia auribarbis* at post-mortem on Rum, 2014-2021.

The phenology of larval infections and adults suggest that larvae are pupating outside the host from March, emerging as adults from April. Full-grown larvae are sneezed out by the host after which pupation takes place in the ground (Zeegers 2001).

Discussion

Cephenemyia auribarbis is widespread in Highland and probably numerous in many areas where red deer populations are high. The very restricted British range is puzzling given the much greater range occupied by the host. Also of possible interest is the apparent concentration to the north and west of the Great Glen and relative absence in the areas farther east.

Cephenemyia auribarbis is of some conservation concern. Falk and Pont (2017) rated it as pNationally scarce, while the current UK Species Inventory (v. 50) lists it as Notable. Our data have it in 24 hectads in Highland, and the other sources add another 8 hectads. Although the range in Britain is very restricted, the fly is likely to be seriously under-recorded within that range, which comprises much remote and difficult country, and is almost certainly present in many more hectads there.

In the absence of any apparent specific habitat requirements other than the presence of red deer, any threat would appear to stem from reduction of the red deer population. In Scotland that is an important sporting resource on private estates, though apart from some supplementary feeding the animals are fully wild. Red deer numbers in the north of Scotland increased steadily from 1961 to 2000, though have declined somewhat since 2000 (Albon *et al.* 2019). The Scottish Government have a policy of managing the population to minimise the impacts of deer that damage wider public and environmental interests and a target density of not more than 10 deer per square kilometre (Pepper *et al.* 2020). This will involve culling, which may be significant in reducing deer populations locally, as numerous areas have densities well above that target (Albon *et al.* 2019). Whether this will constitute a threat to *C. auribarbis* will depend on the population dynamics and behaviour of the flies, but, if so, as the Scottish red deer population increased significantly during the second half of the 20th century, the fly may in fact have benefited from that increase (Falk and Pont 2017).

Acknowledgements

We are grateful to all the naturalists who provided the records to HBRG. The map was prepared with DMAP. SM is the Field Assistant on the University of Edinburgh Rum Red Deer Project, which is funded by the Natural Environment Research Council, and permission to use the data on larvae was kindly provided by Prof. Josephine Pemberton.

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Dipterists Digest 2022 **29,** 107-109

Tephritis matricariae (Loew) (Diptera, Tephritidae) new to Ireland from Co. Dublin

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Summary

Tephritis matricariae (Loew, 1844) (Tephritidae) is recorded as new to Ireland.

On 15 March 2021, I caught a single male specimen of *Tephritis matricariae* (Loew, 1844) by sweeping an area of rough grassland along a roadside verge at Kilcrea, Donabate, Co. Dublin (Irish Grid Reference: O213481). Sweeping was concentrated mainly around alexanders *Smyrnium olusatrum* and ivy *Hedera hibernica* along a 10-metre section of the roadside verge. The specimen was collected and was photographed (Fig. 1) on returning home and then pinned. A query accompanied by a photograph of the live specimen was posted on the "UK Diptera" Facebook page as to the identity of this *Tephritis* species. David Clements gave an initial identification of the photographed live specimen as one of the *Tephritis conura/matricariae* pair and provided a copy of the Picture-wing Flies test key. The specimen was keyed by CB using the test key and additional confirmatory characters were photographed (Figs 2 and 3) and added to the Facebook query. Laurence Clemons (UK Tephritid Flies Recording Scheme Organiser) later verified the determination by email and confirmed that the species was new to Ireland. The specimen has been lodged in the NMI National Museum of Ireland, Dublin (accession number: NMINH: 2021.8.1).

Fig. 1. *Tephritis matricariae* male live specimen from Kilcrea, Donabate, Co. Dublin, 15 March 2021. Photo: C. Byrne.

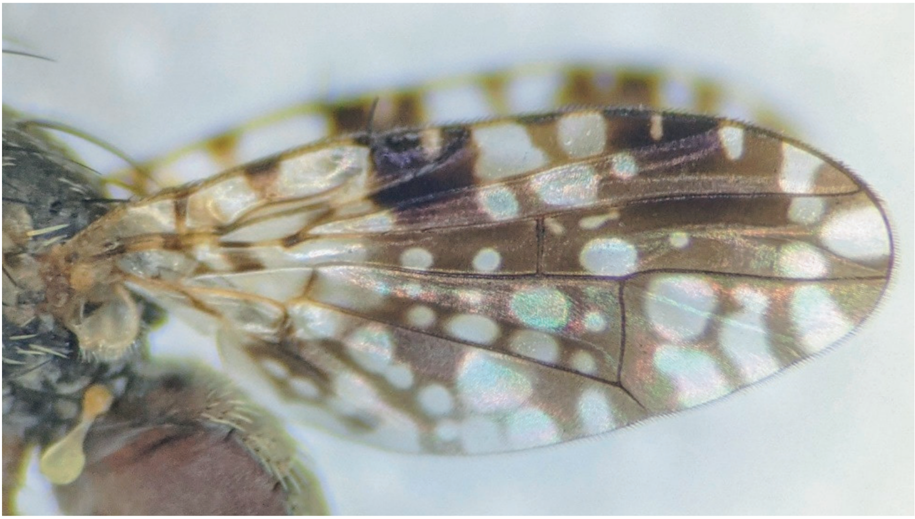

Fig. 2. ***Tephritis matricariae*** **male pinned specimen wing detail (wing length = 4.5mm). Photo: C. Byrne.**

Fig. 3. ***Tephritis matricariae*** **male pinned specimen showing pale posterior notopleural bristle. Photo: C. Byrne.**

The Irish checklist (Chandler *et al.* 2008) listed 27 tephritid species as occurring in Ireland, while the most recent listing of Irish tephritids in Chandler (2021) includes 29 species. Since the 2008 Irish checklist, two more species have been added to the Irish list: *Terellia tussilaginis* (Fabricius, 1775) by Alexander (2009) and *Campiglossa producta* (Loew, 1844) by Chandler and O'Connor (2010). One other species, *Acanthiophilus helianthi* (Rossi, 1794), has also been found in Ireland by Aideen O'Doherty at Belfast Airport Road West (J381783) on 11 July 2019; an image of the fly was added to iRecord and accepted by Laurence Clemons (*pers. comm.*) as correct.

In common with many species of Tephritidae, *T. matricariae* develops in flower-heads of composite flowers (Asteraceae). *Tephritis matricariae* was added to the British list from east Kent by Clemons (2000), who described rearing the species from *Crepis capillaris* (smooth hawk's-beard) and *Crepis vesicaria* (beaked hawk's-beard). It has since become widespread in England and Wales, with records as far north as Cumbria (Laurence Clemons *pers. comm.*).

Acknowledgements

I am very grateful to David Clements who gave an initial identification of the photographed live specimen as one of the *Tephritis conura/matricariae* pair and provided access to the Picture-wing Flies test key and information on the discovery of *Tephritis matricariae* in Britain. I would also like to thank Laurence Clemons (UK Tephritid Flies Recording Scheme Organiser) for verifying the determination and confirming that the species was new to Ireland.

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Corrections and changes to the Diptera Checklist (47) – Editor

It is intended to publish here any corrections to the text of the latest Diptera checklist (publication date was 13 November 1998; the final 'cut-off' date for included information was 17 June 1998) and to draw attention to any subsequent changes. All readers are asked to inform me of errors or changes and I thank all those who have already brought these to my attention.

Changes are listed under families; names new to the British Isles list are in bold type. The notes below refer to the addition of 5 species, resulting in a total of **7229** species (of which 41 are recorded only from Ireland) and 1 introduced species that is considered not to be established.

An updated version of the checklist, incorporating all corrections and changes that have been reported in *Dipterists Digest*, is available for download from the Dipterists Forum website. It is intended to update this regularly following the appearance of each issue of *Dipterists Digest*.

Limoniidae. The following introduced species was added by A.E. STUBBS (2021. *British Craneflies*. 434 + xvi pp, 63 plates. British Entomological and Natural History Society, Reading):
Atypophthalmus ***umbratus*** (de Meijere, 1911 – *Dicranomyia*)
It is a widespread tropical species that was recorded in a tropical house at Kew Gardens in 1987, but has not been seen since 2002. It has been found in similar situations elsewhere in Europe.

Mycetophilidae. The following change was made by J.P. LINDEMANN, G. SØLI and J. KJÆRANDSEN (2021. Revision of the *Exechia parva* group (Diptera: Mycetophilidae). *Biodiversity Data Journal* **9,** 1-122. e67134. https://doi.org/10.3897/BDJ.9.e67134):
Exechia ***neorepanda*** Lindemann in Lindemann, Søli & Kjærandsen, 2021 (= *E. repanda*: Edwards, 1941, misident., not Johannsen, 1912)

Cecidomyiidae. A change in assignment of the following species, from the 2004 placement in *Dasineura*, was adopted in later editions of the world catalogue, e.g. by R.J. GAGNÉ and M. JASCHHOF (2017. A Catalog of the Cecidomyiidae (Diptera) of the World. Fourth Edition):
Rabdophaga marginemtorquens (Bremi, 1847 – *Cecidomyia*)

Anisopodidae. The following species is added in the present issue:
Sylvicola ***fuscatus*** (Fabricius, 1775 – *Tipula*)

Syrphidae. The following species is added in the present issue:
Chalcosyrphus ***piger*** (Fabricius, 1794 – *Syrphus*)

Psilidae. The following species is added in the present issue:
Chamaepsila ***pectoralis*** (Meigen, 1826 – *Psila*)

Agromyzidae. The following changes result from V.V. ZLOBIN (2002. Review of mining flies of the genus *Liriomyza* Mik (Diptera: Agromyzidae). I. The Palaearctic *flaveola*-group species. *International Journal of Dipterological Research* **13**(3)**,** 145-178):
Liriomyza ***europaea*** Zlobin, 2002 (English paratypes)
Liriomyza ***pedestris*** Hendel, 1931 (stat. rev., raised from synonymy with *L. richteri*)

Calliphoridae. The families Rhiniidae and Rhinophoridae have been returned to Calliphoridae as subfamilies RHINIINAE and RHINOPHORINAE by L. YAN, T. PAPE, K. MEUSEMANN, S.N. KUTTY, R. MEIER, K.M. BAYLESS and D. ZHANG (2021. Monophyletic blowflies revealed by phylogenomics. *BMC Biol* **19,** 230. https://doi.org/10.1186/s12915-021-01156-4). Other changes in this article are synonymy of Helicoboscinae with AMENIINAE and of Melanomyinae with Calliphorinae.

Changes to the Irish Diptera List (32) – Editor

This section appears as necessary to keep up to date the initial update of the Irish list in Vol. **10,** 135-146 and the latest checklist of Irish Diptera (Chandler *et al*. 2008). Species are listed under families. The gain of two species cited in the present issue brings the total Irish list to 3463.

Tephritidae
Acanthiophilus helianthi (Rossi, 1794) (added by Byrne in the present issue)
Tephritis matricariae (Loew, 1844) (added by Byrne in the present issue)

Dipterists Digest 2022 **29,** 111-118

Variation in puparium coloration in some species of Agromyzidae (Diptera)

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Summary

Variation in puparium coloration is reported for four species of Agromyzidae. The puparia of *Ophiomyia heringi* Starý, 1930, *Chromatomyia asteris* (Hendel, 1934), *Phytomyza crassiseta* Zetterstedt, 1860 and *Phytomyza plantaginis* (Robineau-Desvoidy, 1851) are discussed, highlighting colour variants which are not cited in recent literature. Illustrations are given for each species.

Introduction

The puparium of the Agromyzidae can take various forms, in terms of coloration [from pale yellow in many *Melanagromyza* to shiny metallic black in some *Cerodontha*] and shape [flattened in some *Cerodontha* to barrel-shaped in many *Phytomyza*].

Puparium coloration is, on the whole, relatively stable within each species but variation is frequently observed and reported; the puparium of *Liriomyza eupatorii* (Kaltenbach, 1873) can range from bright yellow to orangey-brown (Eiseman and Lonsdale 2018), the puparium of *Chromatomyia syngenesiae* Hardy, 1849 is usually white but may also be darker, brownish (Spencer 1976), whilst seasonal dimorphism, the condition of having two distinct varieties which appear at different seasons, accounts for the variation in puparium coloration of *Phytomyza tetrasticha* Hendel, 1927 [yellowish-brown in summer generation, deep black in over-wintering generation (Spencer 1972)]. During my rearing of the Agromyzidae, seemingly unpublished colour variations have been observed for the following species: *Ophiomyia heringi* Starý, 1930, *Chromatomyia asteris* (Hendel, 1934), *Phytomyza crassiseta* Zetterstedt, 1860 and *Phytomyza plantaginis* (Robineau-Desvoidy, 1851). The most frequently used identification literature (Spencer 1972 and 1976, Papp and Černý 2015, 2016, 2017 and 2020) and excellent recent papers (Guglya 2021, Eiseman and Lonsdale 2018, Eiseman *et al.* 2019) which cite puparium coloration for the aforementioned species, do not discuss the variations highlighted within this article. Although early to mid-twentieth century workers such as Buhr, Hering and de Meijere may have previously noted these variations, they are not apparent in recent works; therefore, it is considered appropriate to draw attention to the puparium colour variability for the species considered here.

Discussion

Ophiomyia heringi Starý, 1930

This species is stated to have an all-black puparium (Spencer 1976), which is typical of the genus. However, rarely, *O. heringi* can form a puparium which is pale yellow with black transverse bands on the upper surface, with the lower surface completely pale yellow (Fig. 2). This variation has also been observed by Julia Guglya (*pers. comm.*), with a single male having been reared from a similarly striped puparium in Ukraine. Sometimes, puparia become striped if they contain a fully developed, alive or dead, Chalcidoidea parasitoid; however, as adults were successfully reared from the illustrated puparia, that does not always apply. Although striped puparium is seemingly very rare within the Agromyzidae, the specific epithet of the Nearctic species *Phytomyza tigris* Eiseman & Lonsdale, 2018 refers to ‘the puparium’s striped pattern which is reminiscent of that of a tiger’ (Eiseman and Lonsdale 2018); the transverse bands are present only on the lower surface, with no banding apparent on the upper surface [one puparium has no bands at all, Owen Lonsdale *pers. comm.*]. Both *O. heringi* and *P. tigris* pupariate just under the epidermis, with the transverse bands being present only on the surface facing outwards [not the surface adherent to the stem].

Fig. 1. *Ophiomyia heringi* puparium [*in situ* on *Sonchus* stem with epidermis removed].

Fig. 2. *Ophiomyia heringi* puparium; upper, viewed from above; lower, viewed from below.

***Chromatomyia asteris* (Hendel, 1934)**
In the works of Spencer (1972 and 1976) and Griffiths' study (1976) on boreal Agromyzidae miners on Astereae, the puparium is stated to be 'whitish' and 'white' respectively. Griffiths examined reared material from Magdeburg and Dagebűll/Nordsee [Germany], Kent and Sussex [England], Llanrhidian (Gower Peninsula) [Wales] and Poulnaclogh Bay, Co. Clare [Ireland] and did not highlight different puparium coloration. In Scotland, puparia (Fig. 3) collected by Keith Bland are either 'almost white, pale or light brown' (Charles Godfray *pers. comm.*).

In the Agromyzidae collection at the Natural History Museum, London (Scott and Smith 2014), there are 31 specimens of *C. asteris*, with only three possessing their puparium: '1♀, Amager, Copenhagen [Denmark], 10.viii.1927, Gudmann', '1♀, La Baule, Loire i. [France], 10.v.1943, Dr. H. Buhr' and '1♀, La Baule, Loire i. [France], 04.v.1943, Dr. H. Buhr', with all three puparia being pale

Fig. 3. *Chromatomyia asteris* puparium viewed from above agreeing with the published descriptions.

It is intriguing that my personal observations are yet to discover the pale puparium of this species; I have reared dozens of adults and observed over 700 *C. asteris* larval mines, all of which produced completely dark puparia (Fig, 4). The puparium is dark brown, almost black, with a distinct shine, regardless of the season [seemingly ruling out the possibility of seasonal dimorphism as seen in some species]; larval mines with dark puparia have been recorded from April to November [with adults emerging in the year of collection] and have been observed in England [*pers. obs.*], Germany [Michael von Tschirnhaus *pers. comm.*], Scotland [Skye, empty dark puparia observed in September, Stephen Bungard *pers. comm.*; Higginsneuk, Keith Bland *pers. comm.*] and Wales [Merionethshire, Mike Lush *pers. comm.*].

Three pale *C. asteris* puparia [coll. 9.viii.1989, Scotland, Keith Bland] were kindly loaned to me for comparison; dark puparia are on average 11.6% longer and 12% broader than pale puparia and posterior conical projections which bear posterior spiracles are short in pale puparia [as mentioned by Griffiths] but larger, more elongate in dark puparia (Fig. 5). The number of bulbs on posterior spiracles is variable in both pale and dark puparia and is not considered to be of any significance.

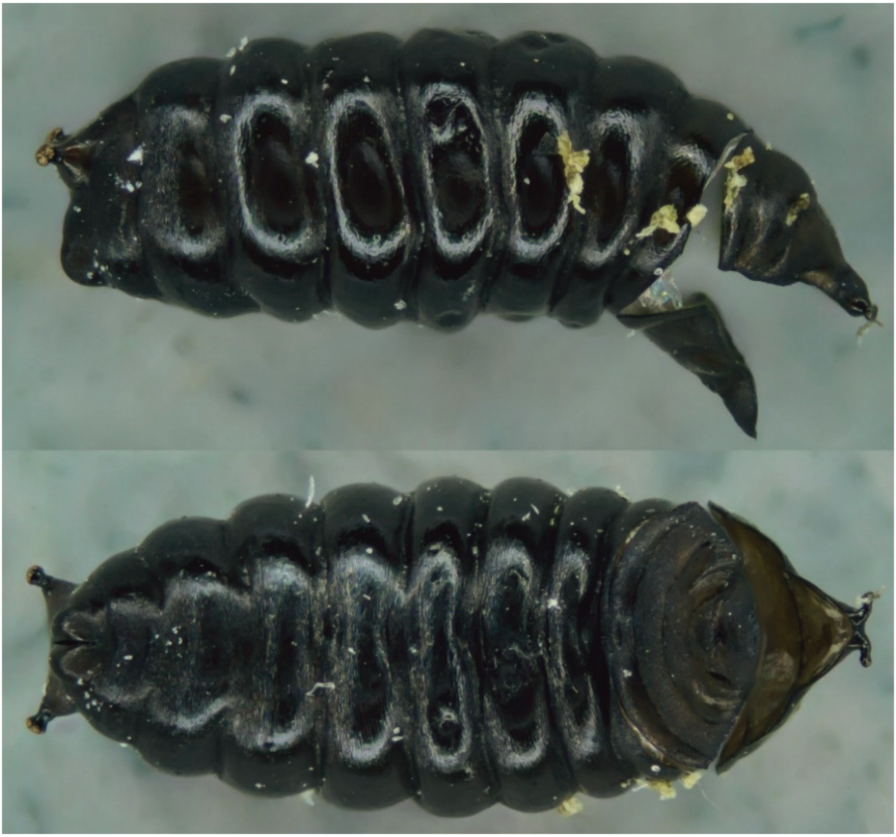

Fig. 4. ***Chromatomyia asteris*** **puparium [coll. 30.v.2019, em. 2.viii.2019]; upper, in lateral view; lower, viewed from below.**

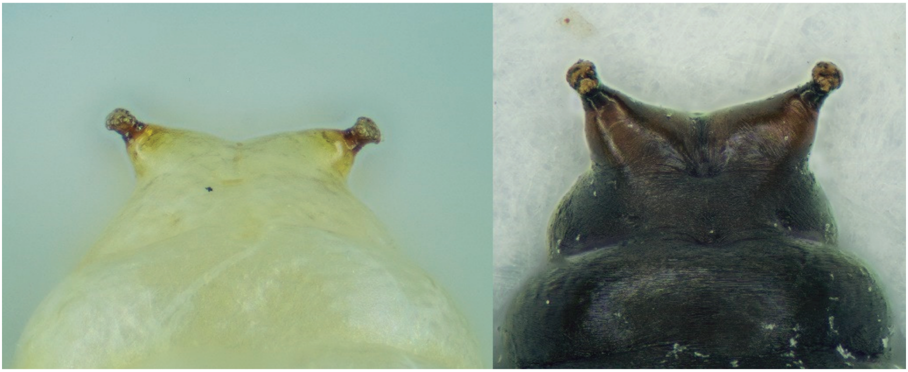

Fig. 5. Comparison of posterior conical projections in *C. asteris* pale and dark puparia.

Phytomyza crassiseta Zetterstedt, 1860

The puparium of *P. crassiseta* is described as ‘white or yellowish, with a conspicuous dark band running centrally along the ventral surface’ (Eiseman and Lonsdale 2018, Spencer 1972 and 1976), ‘white or yellowish’ (Papp and Černý 2020) or ‘greenish-white with a dark length line’ (Ellis 2017); Fig. 6 (upper) illustrates this typical description.

On several occasions [May, June and July (*pers. obs.*)], this species has been observed to form a completely dark [dark brown, black] puparium (Fig. 6, lower). Nowakowski (see Conclusion) mentions dark puparia for this species but attributes it to over-wintering puparia; that may not be always applicable as the dark puparia collected in May, June and July produced adults in May, July and August the same year.

Fig. 6. _Phytomyza crassiseta_ puparium: upper, typical puparium with dark central band viewed from below; lower, all dark variation of non-overwintering generation viewed from below.

Phytomyza plantaginis (Robineau-Desvoidy, 1851)

This species is cited to have puparium ‘whitish’' (Eiseman *et al.* 2019, Papp and Černý 2020, Spencer 1976) or ‘colourless, translucent’ (Guglya 2021). Light coloured puparia are also frequently observed [yellowish to light brown (Charles Godfray *pers. comm.*, Edmunds 2022)].

Contrary to these observations, I have reared this species (Edmunds 2022) from very dark brown, almost black puparia (Fig. 7).

In describing the puparium of *P. plantaginis*, Ellis (2017) stated that 'parasitised puparia are black!'. Although this is frequently the case in the Agromyzidae on the whole, as this manuscript highlights, it isn't always so; Charley Eiseman (*pers. comm.*) and I have reared adults [of various species] from puparia which, due to their coloration, suggested they were parasitised yet still produced adult flies.

Fig. 7. *Phytomyza plantaginis* puparium; upper, in lateral view; lower, viewed from below.

Conclusion

The significance of puparium coloration is poorly understood and, as no detailed study has ever been undertaken, any theories relating to variation are, at present, hypothetical.

In Britain there are several species which show [published] variation in puparium coloration: *Cerodontha* (*Dizygomyza*) *luctuosa* (Meigen, 1830) [pale yellowish to reddish-brown], *Chromatomyia primulae* (Robineau-Desvoidy, 1851) [white to reddish-brown] and *Phytomyza fallaciosa* Brischke, 1880 [white to dark brown], along with the species mentioned within this manuscript; it is interesting that the majority of species which show variation pupariate within the mine. Nowakowski (1962) discussed cyclomorphism [= a seasonal dimorphism] and noted this in four species: *Ophiomyia maura* (Meigen, 1838), *P. crassiseta*, *P. fallaciosa* and *P.*

tetrasticha; however, none of the dark puparia of the species [*O. heringi*, *C. asteris*, *P. crassiseta* and *P. plantaginis*] discussed within this manuscript belong to over-wintering generations as adults emerged within the same year of collection [Charley Eiseman (*pers. comm.*) has reared *O. maura* from dark puparia which were also not of the over-wintering generation].

It could be that diapause for hibernating/over-wintering may begin, uncharacteristically, in early summer, triggered by external environmental factors or as an adaptation to preserve a population, in that imagines emerge partly in the same year, partly the next [or in some cases, two years later] therefore reducing the risk of a whole generation/population being lost.

Species which exhibit known seasonal dimorphism can also have dark puparia in their early generation(s); Rob Edmunds (*pers. comm.*) observed vacated [the operculum opening suggests eclosion of the imago, as opposed to a parasitoid] *Ophiomyia aquilegiana* Lundqvist, 1947 puparia which were black [as opposed to pale] in August, whilst I have collected dark *P. tetrasticha* puparia in July which produced adults two months later.

Nowakowski discussed *Phytomyza autumnalis* Hering, 1957 and *Phytomyza spinaciae* Hendel, 1935 (as *affinis*), citing that 'seasonal dimorphism has already created a taxonomic mistake', in that the larval differences between the two species are simply differences between two larval generations [seasonal dimorphism] and therefore synonymised *autumnalis* with *spinaciae* [= "*affinis*"]; however, currently, these two species are treated as distinct. Griffiths (1959) illustrated the puparium posterior 'horns' [= conical projections] of *autumnalis* and *spinaciae* [as *affinis*], highlighting the small projections in *spinaciae* and the much larger ones of *autumnalis*; I possess reared material of both species and Griffiths' illustrations are true representations.

The male genitalia of *autumnalis* and *spinaciae* are indistinguishable [ejaculator of *autumnalis* may be more strongly sclerotised than the hyaline one of *spinaciae*], with adult morphology also being extremely similar [knees of *spinaciae* possibly narrower yellow than in *autumnalis*; *spinaciae* being a smaller species]; the species are seemingly separated primarily on their larval morphology and phenology.

Both species have recently been subjected to DNA barcoding; the results are consistent with the two species being conspecific. However, to fully resolve the question whether these are genetically distinct species or not, additional specimens from other regions are required and/or the entire genome requires sequencing [though most accepted species show a distinct difference in their barcodes, some very recently diverged species don't, so other genes are needed to try and separate them].

It is interesting that the posterior conical projections of pale and dark *C. asteris* puparia mirror the conical projections of *spinaciae* and *autumnalis* respectively, in that pale puparia possess short conical projections, with dark puparia possessing larger, more elongated conical projections.

The genitalia of *C. asteris* males reared from dark puparia are seemingly identical to the illustrations [of material ex pale puparia] by Griffiths and Spencer. Although dark *C. asteris* puparia can be found throughout the year, could the difference in posterior conical projections and the smaller size of pale puparia indicate a species complex or, conversely, simply suggest natural species variation. Until further molecular analysis is undertaken on the problematic pair *autumnalis* and *spinaciae*, workers will remain unsure on how to interpret variation in puparium coloration and morphology within species.

Acknowledgements

I would like to thank Keith Bland (Edinburgh, UK), Rob Edmunds (Norfolk, UK), Charley Eiseman (Northfield, Massachusetts, USA), Professor Sir Charles Godfray (Oxford Martin School, Oxford, UK), Julia Guglya (Museum of Nature, Kharkiv, Ukraine), Owen Lonsdale

(Agriculture and Agri-Food Canada), Sonja Scheffer (United States Department of Agriculture) and Dr Michael von Tschirnhaus (University of Bielefeld, Germany) for their much-valued correspondence on the subject.

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Dipterists Digest 2022 **29,** 119-126

An inland occurrence of the potential West Nile virus vector *Culex modestus* Ficalbi (Diptera, Culicidae) in Ely, Cambridgeshire, UK

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Summary

Numerous immatures and adults of the mosquito *Culex modestus* Ficalbi, 1890, an important vector of West Nile virus, were found at a ditch in flood meadows adjacent to the small city of Ely in Cambridgeshire, V.C.29 between 23.viii.2021 and 27.ix.2021. This species was the most common mosquito sampled at the ditch during this period. Apart from a 2012 record of two 4th instar larvae from Wicken Fen (V.C. 29), the Ely occurrence is the only inland British record of this mosquito which is concentrated on the coasts of north Kent and Essex. After notifying Public Health England, a programme of sampling was planned for 2022 to understand the phenology and habitat requirements of this species, particularly with regards to an inland population near a town.

Introduction

Culex modestus Ficalbi, 1890 is widespread across the Palaearctic region from England to China, and India to northern Africa (Becker *et al*. 2020). It occurs in several countries bordering the Mediterranean and its range is expanding northwards, with recent records from the Netherlands and Belgium, and an established population in southern England.

This mosquito is a vector of West Nile virus (WNV) in mainland Europe, transmitting it from birds to humans and horses (Becker *et al*. 2020). Symptoms of the virus in humans include fever, headache, muscle pain, sore throat, rash and swollen lymph nodes. It usually affects children more severely than adults. Symptoms usually last about one week until recovery. Occasionally it can cause severe meningoencephalitis, myocarditis, acute pancreatitis and hepatitis; it can be fatal. No cases (human, avian or equine) of the virus have been reported in Britain. Migratory birds are a potential source of the virus, and health risks to humans and horses could arise if a mosquito vector is resident at migration destinations or stopovers.

Cx. modestus was first recorded in Britain (3 adults, 10 larvae) at Portsmouth in 1944 (Marshall 1945). Since that first occurrence, no further British records were obtained until 2010 when a large population was discovered in the marshes of the north coast of Kent (Golding *et al.* 2012). This population has been monitored continuously since then (Vaux *et al*. 2015).

British records of *Cx. modestus* are strongly concentrated on the coasts of north Kent and Essex; there is a single record of an adult female in 2011 from Arne, Poole Harbour, Dorset (Medlock and Vaux 2012). It has not been recorded in Ireland. It has been suggested (Golding *et al*. 2012) that the coastal populations of north Kent and Essex have arisen from specimens imported by international sea traffic. However, there is an emerging consensus that the mosquito may have been present for much longer. For example, Hutchinson *et al.* (2007) reported large numbers of *Cx. torrentium* from the Isle of Sheppey saltmarshes (north Kent) collected in June-September 2003, but it is now considered more likely that these were *Cx. modestus* (J. Medlock *pers. comm*., November 2021).

The only inland record of *Cx. modestus* in Britain is of two 4th instar larvae from a systematic survey conducted by Public Health England (then known as the “Health Protection Agency”) at Wicken Fen NNR, Cambridgeshire, V.C. 29 in 2012 (Vaux and Medlock 2012), since when no further records for this reserve or any inland site were forthcoming until the occurrence at Ely reported here.

Fieldwork

The small city of Ely (population 20,112 in 2020) lies within the Cambridgeshire fenlands and is located on an outlier of Cretaceous greensand surrounded by Jurassic (Kimmeridgean) clay. The landscape within five miles of the city is dominated by arable and vegetable crops, with an extensive networks of deep ditches draining the fields. Immediately to the east of the city is the River Great Ouse, a major watercourse of East Anglia.

Fig. 1. Annotated Google map of the Ely wetlands showing the main ditches (red lines). Springhead Lane meadow lies between the railway line and Springhead Lane. On Ely Wash rows of trees define boundary ditches.

Associated with the river at Ely is a tract of flood meadows adjacent to Roswell Pits SSSI. The setting and arrangement of ditches in the flood meadows and wet grassland are shown in Fig. 1. There are sub-parallel linear ditches 3-5 m wide connected to boundary ditches. The wetlands adjacent to Ely comprise three distinct areas: (a) Springhead Lane meadow – wet grassland, meadow and ditches (2a, 3a, 5a, 6) bordered by the railway line and public amenity paths and parks; (b) river flood meadows and ditches (1, 2b, 3b, 4 and 5b) between the railway line and the riverside path; (c) Ely Wash – wet grassland and ditches between the river and a raised north-south road running from Ely to Queen Adelaide. The boundary ditches on Ely Wash are lined by willows.

Ditches in Springhead Lane meadow are isolated from the River Great Ouse by the mainline Cambridge-King's Lynn railway (the "Fen Line" originally constructed in the 1840s but later reinforced) which forms an impermeable embankment. These ditches are filled by rainwater when the field floods and retain >1.5m of water throughout the year. The river flood meadows and Ely Wash are regularly grazed by cattle, whereas Springhead Lane meadow is not.

Fig. 2. Representative view of the vegetation in ditch 3a, comprising common bulrush, water mint and a partial covering of duckweed.

Ditches 2, 3 and 5 are cut by the railway line. Ditch 6 runs alongside the railway and has formed by the ponding of rainwater against the embankment; this ditch is connected to ditches 2a, 3a and 5a. All three wetland areas are subject to flooding in spring and winter. The railway embankment acts as a dam, allowing retention of water in ditches 2a, 3a, 5a and 6 throughout the year, although significant draw-down can occur in dry summers. Ditches 1−5 on Springhead Lane meadow and the river flood meadow are open and unshaded; ditch 6 is covered by overhanging willow and is completely shaded throughout the spring and summer.

In 2021, a cold, dry April was followed by a very wet and cool May that resulted in extensive flooding of the Ely wetlands, particularly of Springhead Lane meadow of which almost half was flooded for six weeks (May to mid-June). However, by the end of July, floodwater on Springhead Lane meadow remained only in ditches and their immediate margins. Extensive drying of the River Great Ouse flood meadows and Ely Wash occurred in August; only the ditches in Springhead Lane meadow (2a, 3a, 5a, 6) retained a significant depth of water (~1.5m) due to the damming effect of the railway embankment. Ditches elsewhere were either dry and grassed over or covered with matted draw-down vegetation, which was moist underneath.

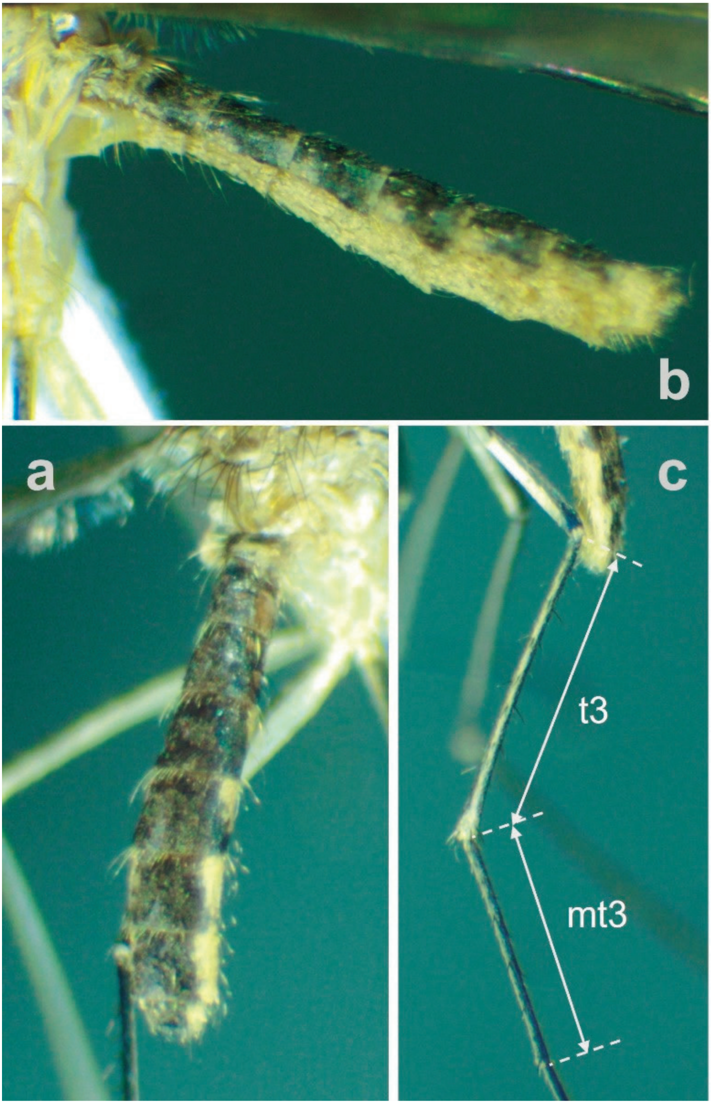

Fig. 3. ***Culex modestus*** **♀ from Ely: (a) dorsal view of the abdomen showing dark brown surface lacking pale markings and edged by golden scales; (b) lateral view showing the extensive golden scaling of the sternites and edges of tergites; (c) hind leg showing the relative lengths of the tibia and metatarsus.**

Opportunistic sampling of ditches 2a and 3a at Springhead Lane meadow (TL55158035 and TL55278042, respectively) was carried out between 23.viii.2021 and 10.ix.2021 using a heavy-duty pond net. Four visits, each of approximately an hour at each ditch, were made. Between 4 and 6 brief (~20 sec), gentle, shallow trawls of the aquatic margins of the ditches were made on each visit. Sampling of adults around the ditch margins used a standard sweep net and direct bottling. No attempt was made to carry out a structured dipper-based survey as only a general idea of numbers of *Cx. modestus* present was sought at this early exploratory stage. After contacting Jolyon Medlock at Public Health England, it was also decided to run a mosquito magnet device at ditch 3a for three weeks (see below). This battery-operated device releases a chemical attractant and sucks mosquitoes into a nylon collection bag. An additional attractant is provided by a supply of propane gas which is warmed and then reacts with oxygen (in air) to produce carbon dioxide.

Numerous larvae and pupae of *Cx. modestus* were obtained from ditch 3a, as is described below. This species was not encountered at ditch 2a, for which *Anopheles claviger* (Meigen) and *Culiseta annulata* Schrank were the commonly encountered mosquitoes along with small numbers of *Cx. pipiens* Linnaeus. *An. maculipennis* (Meigen) s.l., common at ditch 3a, was not recorded from ditch 2a. The water level in the ditches is approximately 1.5–2m deep, depending on the level of draw-down; these ditches do not dry out. The most obvious difference between ditches 2a and 3a was the amount of emergent vegetation, which was well-developed in 3a (water mint *Mentha aquatica*, common bulrush *Typha latifolia* and duckweed; Fig. 2), but very limited and primarily reed *Phragmites* sp. at ditch 2a. The main aquatic predators encountered in both ditches were three-spined stickleback *Gasterosteus aculeatus* Linnaeus, and water boatmen *Corixa* and *Notonecta* spp.

Identification

Identification of larvae and adults used Cranston *et al*. (1987). Eclosed adults were kept alive for at least 24 hours to allow hardening of the cuticle and in the case of males, 180° rotation of the hypopygium and abdominal segment 8. Hypopygia of males were cut off and slide-mounted in Berlese liquid for microscopic examination and photography at magnifications up to ×400 using a GX-SMART compound microscope. Larvae (cleared in 10% KOH) and larval and pupal casts were also mounted in this medium and examined microscopically.

The adult of *Cx. modestus* is one of the smaller mosquitoes, with a body length of ~10 mm. The dorsal surface of the abdomen of the adult is dark brown and lacks any pale scaling or banding (Fig. 3a). Sternites and the downturned edges of tergites are covered with golden scales in both sexes (Fig. 3b), making for a very striking and attractive small mosquito. Fresh adults have yellow/pale-brown thoracic pleura. The metatarsus of the hind leg is much shorter than the hind tibia (Fig. 3c). Male palps are sparsely covered with very short setulae, in contrast to the hairy palps of most other male *Culex*; the hypopygium (Fig. 4) is also distinctive. The 4th instar larva (Fig. 5) has two ventral rows of long hair tufts along the siphon (Fig. 6); these rows of tufts overlap with the pecten rows. Although other British *Culex* species can have ventral hair tufts, the arrangement of tufts and pecten of *Cx. modestus* is diagnostic (Cranston *et al*. 1987).

Results

Immature specimens of mosquitoes (pupae, 2nd, 3rd and 4th instar larvae) were taken home for microscopic examination and rearing to adults. Totals of 35♀ and 6♂ adult *Cx. modestus* were reared. Seven specimens were retained as larvae and a further fourteen adults (all ♀) were trapped using a Mosquito Magnet (see above and below). Five adult *Cx. modestus* (4♀ and 1♂) were swept from marginal vegetation on 1.ix.2021. Six biting females were bottled from the author's arms and legs on 28.viii.2021. Thus, over 60 specimens of *Cx. modestus*, predominantly females, were obtained at ditch 3a from 23.viii – 27.ix.2021.

An. maculipennis s.l. was a common congener of *Cx. modestus* at ditch 3a. Small numbers of *Cs. annulata* and *Cx. pipiens* were also sampled as immatures and reared to adults. On the four occasions when sampling of ditch 3a was carried out, *Cx. modestus* and *An. maculipennis* *s.l.* were by far the most frequently encountered immature mosquitoes. *Cx modestus* was not found at ditch 2a, for which *Cs. annulata* and *An. claviger* were the species most commonly sampled as immatures. The significance of the differential occurrence of *Cx. modestus* (present/absent) at the two ditches requires further study.

Although the initial discovery made on 23.viii.2021 was towards the end of the peak for adult *Cx. modestus* (July-August), further opportunistic sampling of larvae and pupae at ditches 2a and 3a was carried out in September. A Mosquito Magnet (Liberty Plus model, American Biophysics, Rhode Island, USA) provided by Public Health England was also installed within 4m of ditch 3a and operated from 9.ix–27.ix.2021 to sample adult females. The first week of magnet operation 9.ix–15.ix.2021 gave the following: 13 *Cx. modestus,* 2 *Cs. annulata*, 8 *An. claviger*. Continued magnet sampling from 15.ix–27.ix.2021 provided a single *Cx. modestus* and 17 *An. claviger*. Despite being a common congener of *Cx. modestus* at ditch 3a, no specimens of *An. maculipennis* s.l. were caught by the Mosquito Magnet.

Fig. 4. Photomicrograph (11 stacked images) of the hypopygium of *Culex modestus* ♂ from Ely.

Discussion

The predominance of coastal records of *Cx. modestus* in Britain is consistent with this mosquito having been imported from overseas by sea traffic. However, the occurrence of an inland population in Britain, albeit at low abundance, is not so easily explained. Becker *et al*. (2020) state that in continental Europe "Distribution of the species is patchy and usually limited to fresh- or slightly saline waters of marshes, irrigation canals and inundation areas of rivers overgrown by reeds or rice fields". This description would seem to allow for inland wetlands in Britain being suitable habitats for this species.

Fig. 5. Live 4th instar larva of *Culex modestus* from Ely.

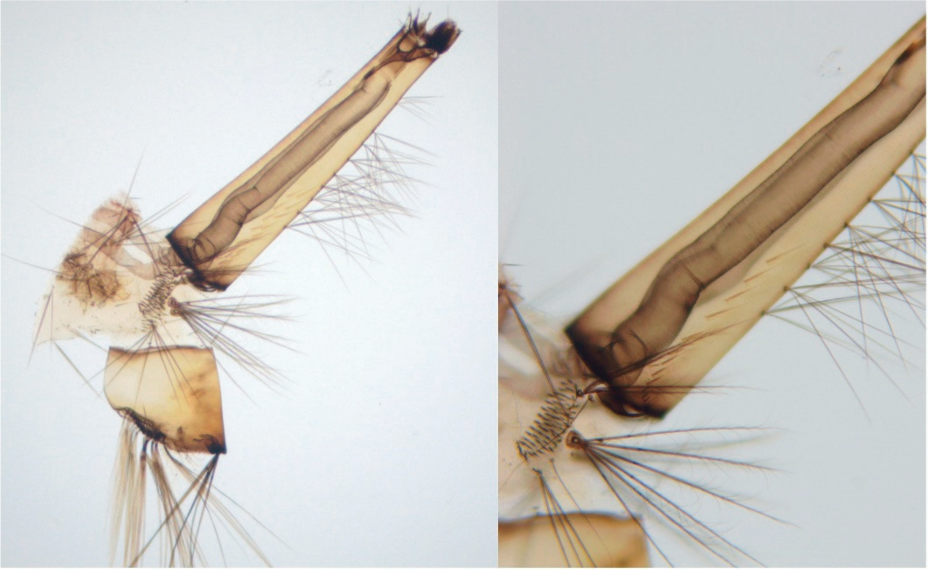

Fig. 6. Photomicrograph of segments VIII-X and siphon of 4th instar larva of *Culex modestus* from Ely, with (right) a close-up of the siphon showing the overlap between the ventral hair tufts and the pecten that is diagnostic of the species among British mosquitoes.

Becker *et al*. (2020) also state that in continental Europe *Cx. modestus* has a very low dispersal range, with females remaining near larval sites. Ely is 100 km from the nearest coastal populations of the species in Essex. If this mosquito has only been in the UK since 2010, then a dispersal rate of at least 10 km/year is suggested, which contrasts with the low dispersal noted above.

Is there an alternative explanation for the origin of inland populations of this mosquito? One possibility is that small, localised inland populations of *Cx. modestus* may have existed in Britain for some considerable time but have been overlooked. If this were the case, then the large coastal populations discovered recently would be extraneous additions to an already established native population in Britain.

The Ely occurrence of *Cx. modestus* provides a timely opportunity to carry out a small-scale "cameo" study of this mosquito's phenology and ecology, e.g. the overwintering strategy (only females?); the development of immature stages. The size of the Ely population of *Cx. modestus* is unknown. Rewetting of the ditches either side of the River Great Ouse may lead to a local expansion of this mosquito, and so monitoring at Ely could provide valuable new information about the dynamics of inland populations. A programme of structured monitoring will be carried out in 2022 and 2023 by the author in collaboration with Public Health England.

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