

is specifically parasitic upon the pupae of the British species of this genus) but the biology and taxonomy of the relations with beetles remain to be recorded. The feeding habits of British Asilidae are outside Europe the scant information, or sometimes of other beetles, is a reason to believe that *Laphria flava* wood boring beetles. Here is a lead for up.

popular as the prey of adult Diptera due of the ceratopogonid *Atrichopogon* and *A. oedemerarum* is found on and Empididae will take Coleoptera

and are taken as prey by fly larvae; bark beetles, strawberry weevil (*bius*); Asilidae may take scarabaeid pupinidae take carpet beetle larvae; pupae and adults of bark beetles; Pallopteridae include several species larvae, but they are assumed to be Plants); several Odiniidae have beetles (see Dead Wood) but the

as control agents of Diptera than Coleoptera are predatory, in most or food resources is flies, especially hence points towards flies being the tles. Such predators as staphylinids and carrion, where fly larvae of litter, the same strong relationship true. significant biological control agent and it seems likely that similar st. Some beetles probably specialise

### Beetles as Parasites of Flies

One of the most interesting relationships between beetles and flies is that some staphylinid larvae are parasites of fly puparia. *Aleochara*, which has 29 British species, is recorded as parasitising chiefly calypterates, especially Anthomyiidae, including species of economic importance. It is probable that the beetles are more habitat specific than dependent on certain fly species - for instance *A. algarum* is a parasite of seaweed flies such as *Coelopa* and *Orygma*. A major study by Welch (1965) includes references to the literature. It is possible that some related genera of Staphylinidae may have parasitic associations with Diptera.

### Acknowledgement

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## ANTS, BEES AND WASPS (ACULEATE HYMENOPTERA)

by Christopher O'Toole

Flies interact with aculeates in a variety of ways. The adults of some species are simply predators and may occasionally feed on ants, wasps and bees. The life-histories of others are closely intertwined with those of aculeates: their larvae are scavengers in aculeate nests or are parasites of aculeate eggs or larvae. The adults of such flies frequent the nest sites of the hosts and are more often encountered by hymenopterists than by dipterists. Thus, the dipterist who would collect these flies must become an honorary hymenopterist and develop an eye for the likely nest sites of ants, wasps and bees.

Mining wasps and bees prefer to make their nests in light, sandy well-drained soils. Sandpits, dunes, sandy heaths and open, dry woodland are suitable places to explore. Many wasps and bees also nest in ready-made cavities such as old beetle borings in dead wood, log piles and old fence posts. One local solitary bee *Hylaeus pectoralis* is known to nest only in the vacated galls of the chloropid *Lipara lucens*; the large, cigar-shaped, galls are made on the reed *Phragmites*.

Many species of ant live in light soils, usually under flat stones; decaying logs are also used. The wood ants (*Formica rufa* group of species) are hosts to a variety of Diptera and these ants make conspicuous nest mounds of pine needles or other litter, while some, such as *F. fusca* and *F. lemni*, nest under stones and logs. The records of interactions between flies and aculeates are widely scattered in the literature and are often inaccessible to entomologists who do not live close to a

good library. The published records for the British Isles are therefore gathered together in Appendix 1 (Predators), Appendix 2 (Nest scavengers), Appendices 3-5 (Parasites) and Appendix 6 (commensals). Good general accounts of the biology of parasitic flies are given in Clausen (1940) and Askew (1971) (see Lepidoptera). Good accounts of the flies associated with social wasps and bumblebees are given by Spradbery (1973) and Alford (1975) respectively.

**Adult Flies as Prey of Aculeates** Flies are the exclusive prey of four genera of solitary sphecid wasps - *Oxybelus*, *Crabro*, *Ectemnius* and *Mellinus*. Three other genera, *Crossocerus*, *Rhopalum* and *Lindenius* prey on flies as well as on other small insects. Detailed prey records are given in Hamm & Richards (1926, 1930). The flies are caught, stung and paralysed by the female wasp and are stored in the nest as food for the wasp larvae. An egg is laid on one of the flies in each cell.

**Predatory Adult Flies - Asilidae - Empididae - Scathophagidae** (Appendix 1) No British predatory flies specialise in hunting aculeates. The published records show that aculeates form only a small proportion of the prey taken by these flies. More records are needed and there is much the amateur can do by following asilids, empids and scathophagids and noting what insects are taken as prey. Asilids are most often seen in sandy areas such as heaths and dunes. Species of *Dioctria* are best sought in hedgerows, woodland clearings and the lush vegetation along the sides of streams. These habitats are also frequented by empids. Scathophagids (dung flies) are voracious predators. The commonest species, *Scathopaga stercoraria* spends much of its time at dung pats, where males find mates and both sexes seek mainly dipterous prey. A solitary fly-hunting sphecid wasp, *Mellinus arvensis* also seeks prey at dung pats and is frequently attacked by *Scathopaga stercoraria*. All too often the flies themselves end up as stung and paralysed prey, to be stored by the wasps as food for their larvae.

**Fly Larvae as Nest scavengers - Ceratopogonidae - Sciaridae - Scatopsidae - Milichiidae - Phoridae - Syrphidae - Sphaeroceridae - Fanniidae - Muscidae** (Appendix 2)

Flies which scavenge in the nests of social Hymenoptera (ants, paper-making wasps and bumblebees) are normally tolerated by the workers and are presumably recognised as harmless. The larvae of these flies feed on vegetable debris, dead nest occupants and possibly the faeces of the host.

Insects which spend part or all of their life-cycles in association with ants are called *myrmecophiles*. Scatopsids such as *Colobostema nigripenne* and *Holoplagia richardsi* spend their entire life-cycle in the host nest and adults, as well as larvae and puparia, are found in the nest galleries. Milichiids of the genera *Phyllomyza* and *Milichia* are also closely associated with ants.

Other species, such as those of the syrphid genus *Microdon*, spend their larval and pupal life in the ant nest and the adults live and mate outside, the females entering the nest only to lay eggs. *Microdon* larvae are strange, slug-like creatures, with a tough, reticulately ridged dorsal surface and were originally described as molluscs! So long as the larvae remain upright, the ants ignore them, but if they accidentally expose their soft undersides, the ants attack and often kill them.

To collect the smaller scavengers in ant nests, it is necessary to dig up several handfuls of nest material and take it home in suitable containers such as plastic sandwich boxes. The nest material can then be sifted for dipterous larvae and puparia. Adult sciarids, scatopsids, phorids and sphaerocerids can be collected in this way, using a pooter. Puparia should be segregated and stored individually in tubes in a cool, dry place, such as a garden shed. Remember to mount each puparium on a card beneath the emerged adult when this is staged. Adult ceratopogonids and phorids can also be collected by sweeping gently over the nest mounds of wood ants (*Formica* spp.). Donisthorpe (1927) gives a good account of the dipterous 'guests' of British ants.

The larvae of the syrphid genus *Volucella* live, according to species, in the nests of social wasps and bumblebees. Eggs are laid on the nest envelope and the larvae usually drop down into the nest cavity, where they scavenge. Some larvae remain in the comb and migrate to cells, where they feed on faecal and salivary matter extruded from mature aculeate larvae and are known to be partly predatory. Adult *Volucella* are well-known mimics of wasps (*inanis*, *zonaria*) and bumblebees, (*bombylans*). They can be found at flowers, especially brambles (*Rubus* spp.) and hogweed (*Heracleum*). Males can often be seen hovering at between five and seven feet above the ground in woodland clearings. Larval *Volucella* can be taken in nest debris in early autumn when the wasp or bumblebee colonies have died out. It is a good idea to mark the nest entrance in some way before the colonies have declined, so that they can easily be found in autumn when there is no activity to betray their presence. Pupation does not occur until the spring.

Many species found in wasp's nests are not specific. For instance the long list of published records summarised by Spradbery (1973) includes many flies with generalised scavenging habits and some which are specific to the surroundings of the nest, e.g. the record of *Ctenophora bimaculata* (larvae eat dead wood) and *Protoclythia modesta* (feed on fungi growing on dead wood). This demonstrates how careful one must be in describing the fauna of a nest. Apart from the syrphids already discussed, there are relatively few Diptera specific to wasp nests - *Fannia vesparia* and *Achanthiptera rohrelliformis* are the best examples, these rarely being seen as adults but the larvae are on occasion abundant. There is a similar need to reassess the significance of ant nest associates.

**Parasites - Bombyliidae - Phoridae - Conopidae - Drosophilidae - Tachinidae - Sarcophagidae - Anthomyiidae** (Appendices 3-5)

The dipterous parasites of aculeate Hymenoptera can be divided into three main groups.

(i) **Larvae as Internal Parasites of Adult Aculeates.** The phorid genera *Pseudacteon* and *Megaselia* and the Conopidae comprise the only British flies in this category. There are two British species of *Pseudacteon*, *brevicauda* and *formicarum*, the latter being the commonest. Female *Pseudacteon* lay their eggs in the abdomens of living worker ants. A female is attracted to an ant nest by smell and hovers over the workers before landing on one and inserting an egg between two of the abdominal tergites with its long, pointed ovipositor. Although this has been observed many times, no-one has yet bred *Pseudacteon* from ants and so the larvae and puparia are undescribed. This gap in our knowledge could be filled if large numbers of recently dead ants were collected from nests and kept under

observation. Adult *Pseudacteon* can be collected by sweeping over and around ant nests, especially those of the common black ant of gardens, *Lasius niger*. The chances of catching adults can be increased by exposing some of the ant nest so that the workers rush out, emitting their characteristic scent. The flies can be best seen if the collector squats down so that the area immediately above the exposed nest appears above the sky line. A *Megasella* species has been reared from larvae parasitising a queen *Bombus terrestris*.

Female conopids also lay their eggs in living, adult hosts, namely solitary wasps and bees, social wasps and bumblebees. Smith (1969) outlines the biology of the British species and gives a summary of prey records. Adult conopids are wasp-like in appearance, with an elongate abdomen. Both sexes frequent flowers, the males in search of mates and the females in search of hosts. At the generic level, conopids are fairly host-specific. A female conopid, having found a suitable host, follows it closely and in some cases mimics the host's flight pattern. Eventually the conopid closes in and, while still in flight, lays an egg in the abdomen of the host; the egg is injected into the membrane between two tergites or sternites with a specially adapted ovipositor. The larva remains in the abdomen, feeding on body fluids. The host is not killed immediately and the infected aculeate may carry on foraging for some time before death ensues. Pupation takes place within the body of the host.

(ii) Fly Larvae as Parasites of Aculeate Eggs (Appendix 4). The eggs of aculeates are relatively large and it is not surprising that other insects exploit this rich food source. Two species of the sarcophagid genus *Ptychoneura* have adopted this life-style and have been bred from stem-nesting solitary wasps.

(iii) Fly Larvae as Parasites of Larval and Pupal Aculeates (Appendix 5). Flies in this category can be further subdivided into those in which the larvae are external parasites and those in which the larvae feed on food stored in the host's cell. This latter habit is often called *cleptoparasitism*.

Females of the sarcophagid *Brachicoma devia* larviposit (i.e. lay living larvae) in the nests of bumblebees. The larvae feed externally on the full-grown bumblebee larvae and pupae. They pupate in the nest material (summer generation) or in the soil (overwintering generation). Puparia can be collected from nest material or from the soil around nests. Adults can be collected by watching at the entrance of bumblebee nests, which occur in such places as hedgerow banks, compost heaps, under rubble on waste ground and often in bird nest boxes.

The larvae of some species of Bombyliidae are external parasites of the larvae of solitary mining bees. The adults of the genus *Bombylius* are aptly called 'bee-flies', for in shape and colour these furry flies resemble the orange-coloured species of bumblebee. They have a characteristic, rapid, darting flight and can be found hovering at flowers. *Bombylius major* is the commonest British species and appears in spring, in open woodland, where it visits primroses, bugle and violets. The females spend much of their time flying over dry, sunny banks where there are host nests. Eggs are laid in mid-flight over the nest site, or the female hovers low, dipping her abdomen until it touches the ground when she releases her eggs. The eggs hatch almost immediately and the worm-like first instar larvae migrate into the nest burrows of the host, usually a species of *Andrena*. There the larva seeks an open cell and remains inactive until the host larva is nearly full-grown.

The *Bombylius* larva then sucks the body fluids of the bee larva and eventually pupates within the host's cell. Neither the larva nor the adult of *Bombylius* is equipped to break out of the sealed cell of the host and it is the remarkably active pupa, with its coronet of three pairs of tough spines, which performs this task and then migrates to the surface of the soil. Here the anterior part of the pupa protrudes out of the soil and the adult fly emerges very soon afterwards.

There is considerable doubt as to the British hosts of *Villa*, though a parasitic relationship with Lepidoptera larvae is thought possible. However, *V. modesta*, a denizen of sand dunes from June to September, has been bred from the cells of the solitary bee *Osmia aurulenta* nesting in empty snail shells (O'Toole, unpubl. data). *Thyridanthrax fenestratus* has been seen 'shadowing' females of the large hunting wasp *Ammophila sabulosa* in the New Forest.

The cocoons of wood ants (*Formica* spp.) are parasitized by two species of phorid, *Aenigmatias brevisfrons* and *A. lubbocki*. The females of these flies are wingless, flattened in shape and resemble small cockroaches. Both sexes can be found in the galleries of *Formica* nests, though the two species are quite rare.

The remaining families in this section have in common the larval habit of feeding on the host's food store, either paralysed insect prey in the case of sphecid wasps, or honey and pollen in the case of solitary bees. The drosophilid *Cacoxenus indagator* is typical. It lives in the nests of solitary bees, especially species of *Osmia*. Both sexes frequent the immediate area of the host's nest. The female waits around until the female bee leaves the nest and then enters and lays one or more eggs in the cell that is currently being provisioned. It has been noted that when the *Cacoxenus* leave the nest of *Osmia rufa*, the tips of their abdomens are often dusted with pollen, indicating that they oviposit directly into the host's food store. Up to 28% of *O. rufa* nests may be infested with *Cacoxenus*.

The females of Sarcophagidae and Anthomyiidae which parasitise wasps and bees also loiter in the nest sites of the hosts, waiting for the female wasps or bees to leave on foraging trips. Some species such as the sarcophagid *Amobia signata* specialize in parasitising solitary wasps, while others, such as the anthomyiid *Leucophora personata* restrict themselves to solitary mining bees (Appendix 5). There are two sub-families of the Sarcophagidae specializing in aculeates, the largest being the Miltogramminae (*Amobia*, *Miltogramma*, *Senotainia*, *Pterella*, *Metopia* and *Ptychoneura*), with most species associated with ground-nesting aculeates as considered below. In the Macronychiinae, *Macronychia griseola* has been recorded from the ground-nesting *Oxybelus*, but *M. unguans* has been reared from the fly-hunting wasp *Ectemnius cavifrons* which is wood-nesting and *M. polyodon* has been associated also mainly with wood-nesting aculeates.

Two species of sarcophagid, *Miltogramma punctatum* and *Metopia argyrocephala* are remarkable in that they readily parasitise both wasps and bees, so that the larvae must be capable of coping with either insect prey in wasps' nests, or pollen and honey mixtures in the nests of bees. It would be interesting to check if the larvae really do feed on the food store or whether they feed on the host larvae. With the exception of one species, all the sarcophagids which parasitise aculeates are larviparous. The exception is *Senotainia conica* which lays its eggs on an adult female wasp as it carries its prey back to the nest. Presumably the larva of the fly detaches itself from the wasp and lives on the stored insect prey. Aculeates have

been found with Diptera eggs attached to their bodies, usually the sides of the thorax. All but two of the species were crabronine wasps and most were female. The identity of the Diptera eggs was uncertain but possibly they belonged to *Senotainia conica*, one of two species of sarcophagid frequenting one of the sites concerned.

The anthomyiid *Eustalomyia*, with four attractive grey and black species, may be found near the entrances of solitary wasp nests in dead wood. The larva consumes the host's prey, which is often adult Diptera.

Flies as Commensals of Aculeates - Braulidae - Milichiidae (Appendix 6)

The Braulidae comprises one genus, *Braula*, with two species, both of which are associated with bees. *B. caeca* is a cosmopolitan commensal of honeybees and the louse-like, wingless adults are often found attached to worker and queen bees. There are no claws, but the bristles of the tarsal combs are well-adapted for clinging to the body hairs of bees. Previously thought to be parasites, braulids are now known to be commensals, the adults feeding on honey as it is regurgitated by worker bees. The eggs are laid in the brood comb of the bee and the larvae feed on the food presented to the bee larvae. Little harm seems to be done to the bees and pupation takes place in a small burrow excavated in the wall of the host's cell. *Desmometopa sordidum* (Milichiidae), which is phoretic on hive bees, consumes the collected pollen.

#### Further Reading

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#### APPENDIX 1. RECORDS OF DIPTERA PREDATORY ON ACULEATE HYMENOPTERA.

ASILIDAE: *Asilus crabroniformis*, *Vespula germanica*, *Andrena fulva*, *Apis mellifera*; *Dysmachus trigonus*, *Pompilus cinereus*; *Eutolmus rufibarbis*, *Lasius niger*; *Machimus atricapillus*, *Myrmica rubra*, *M. ruginodis*, *Lasius niger*, *Ancistrocerus trifasciatus*, *Lasioglossum smeathmanellum*; *Pamponerus germanicus*, *Lasioglossum calceatum*; *Philonicus albiceps*, *Formica fusca*, *Andrena sp.*; *Laphria marginata*, *Myrmica ruginodis*, *Formica rufa*; *Dioctria baumhaueri*, *Diodontus minutus*, *Entomognathus brevis*, *Lasioglossum fulvicorne*; *D. linearis*, *Lasius niger*, *Formica fusca*; *D. oelandica*, *Andrena minutula*, *Lasioglossum lativentris*; *D. rufipes*, *Formica fusca*; EMPIDIDAE: *Empis opaca*, *Nomada marshamella*; SCATHOPHAGIDAE: *Scathophaga stercoraria*, *Lasius flavus*, *Mellinus arvensis*.

APPENDIX 2 RECORDS OF DIPTERA SCAVENGING IN THE NESTS OF ACULEATE HYMENOPTERA N.B. The larvae of Volucella (Syrphidae), Fannia (Fanniidae), Achantiaptera and Muscina (Muscidae), although primarily scavengers, may occasionally feed on larvae, pupae and weakened adults of their hosts, especially towards the end of the season.

TRICHOCERIDAE: *Trichocera hiemalis*, *T. regulationis*, *Vespula*; TIPULIDAE: *Ctenophora bimaculata*, *Vespula*; CERATOPOGONIDAE: *Forcipomyia braueri*, *Formica fusca*; *F. myrmecophila*, *Formica rufa*, *F. exsecta*; *Atrichopogon lucorum*, *Lasius brunneus*; MYCETOPHILIDAE: *Docosia gilvipes*, *Vespula*; SCIARIDAE: *Platostociara brachyptera*, *Lasius alienus*; *P. vanderwieli*, *Vespula*. *Scatopsiara vivida*, *Vespula*; SCATOPSIDAE: *Colobostema nigripenne*, *Lasius fuliginosus*, *Formica rufa*; *Holoplaga richardsi*, *Lasius fuliginosus*; *Scatopse notata*, *Vespula*; PHORIDAE: *Megaselia longicostalis*, *Lasius fuliginosus*, *Formica fusca*; *M. pulcariarum*, *Formica rufa*; *M. giraudi*, *Formica exsecta*, *Dolichovespula norvegica*; *M. minor*, *Lasius fuliginosus*; *M. rufipes*, *Vespula*; *M. aequalis*, *Lasius fuliginosus*, *L. brunneus*; *M. ciliata*, *L. fuliginosus*, *L. brunneus*; *M. conformis*, *Myrmica laevinodis*; *M. fungivora*, *Lasius fuliginosus*; *Conicera pauxilla*, *Vespula germanica*; *Diploneura concinna*, *Vespula germanica*; *D. funebris*, *Vespula*; *Triphleba lugubris*, *Vespula vulgaris*; *Gymnoptera longicostalis*, *Vespula*; *G. vitripennis*, *Bombus*; *Phora aterrima*, *Lasius fuliginosus*; PLATYPEZIDAE: *Protoclythia modesta*, *Vespula*; SYRPHIDAE: *Microdon devius*, *Lasius fuliginosus*, *Formica rufa*, *F. sanguinea*, *F. fusca*; *M. eggeri*, *Lasius niger*; *M. mutabilis*, *Myrmica ruginodis*, *Lasius niger*, *Formica fusca*, *F. lemani*; *Volucella bombylans*, *Vespula vulgaris*, *V. germanica*, *Bombus*; *V. inanis*, *Vespula vulgaris*; *V. pellucens*, *Vespula vulgaris*, *V. germanica*, *V. rufa*; *V. zonaria*, *Vespula vulgaris*, *V. germanica*; HELEOMYZIDAE: *Tephrochlamys laeta*, *T. rufiventris* var. *canescens*, *Vespula*; SEPSIDAE: *Themira lucida*, *Vespula vulgaris*; SPHAEROCERIDAE: *Leptocera caenosa*, *Vespula germanica*; *L. claviventris*, *Vespula vulgaris*; *L. clunipes*, *Lasius brunneus*; *L. flavipes*, *Vespula*; *L. fungicola*, *Lasius fuliginosus*, *Formica rufa*, *Vespula germanica*; *L. heteroneura*, *Vespula*; *L. moesta*, *Vespula germanica*; *L. palmata*, *Vespula vulgaris*, *V. germanica*; *L. rufilabris*, *Formica fusca*; MILICHIIDAE: *Phyllosoma equitans*, *Lasius fuliginosus*; *P. formicae*, *Formica rufa* (as *donisthorpei*), *Lasius fuliginosus*; *Milichia ludens*, *L. fuliginosus*; FANNIIDAE: *Fannia canicularis*, *Vespa crabro*, *Vespula germanica*, *Bombus*; *F. coracina*, *Vespula*; *F. fuscata*, *Vespula vulgaris*, *F. hamata*, *F. scalaris*, *Vespula*; *F. vesparia*, *Vespula germanica*; MUSCIDAE: *Achantiaptera rohrelliformis*, *Vespula vulgaris*, *V. germanica*; *Muscina pabulorum*, *Vespula rufa*; *M. stabulans*, *Vespula germanica*; *Phaonia populi*, *Vespula*.

#### APPENDIX 3. RECORDS OF DIPTERA WITH LARVAE PARASITIC ON ADULT ACULEATE HYMENOPTERA.

PHORIDAE: *Pseudacteon brevicauda*, *Myrmica ruginodis*; *Pseudacteon formicarum*, *Myrmica lobicornis*, *Tapinoma erraticum*, *Lasius fuliginosus*, *L. niger*, *L. alienus*, *L. flavus*, *Formica sanguinea*; *Megaselia* sp., *Bombus terrestris*; CONOPIIDAE: *Conops ceriaeformis*, *Bombus muscorum*; *C. flavipes*, *C. quadrifasciatus*, *Bombus lapidarius*; *Leopoldius brevisrostris*, *Vespula*; *Physocephala nigra*, *Bombus muscorum*; *P. rufipes*, *Bombus terrestris*, *B. lucorum*, *B. lapidarius*, *B. pratorum*, *B. hortorum*, *B. ruderarius*, *B. sylvarum*, *B. pascuorum*; *Zodion cinereum*, *?Halictus rubicundus*; *Thecophora atra*, *T. fulvipes*, *Halictus*, *Lasioglossum*; *Sicus ferrugineus*, *Bombus terrestris*, *B. lapidarius*, *B. hortorum*, *B. pascuorum*.

#### APPENDIX 4. RECORDS OF DIPTERA WITH LARVAE PARASITIC ON THE EGGS OF ACULEATE HYMENOPTERA

SARCOPHAGIDAE: *Ptychoneura cylindrica*, *Pemphredon lugubris*, *Crossocerus capitatus*; *P. rufitarsis*, *Rhopalum coarctatus*, *R. clavipes*.

#### APPENDIX 5. RECORDS OF DIPTERA WITH LARVAE PARASITIC ON LARVAL ACULEATE HYMENOPTERA

BOMBYLIIDAE: *Bombylius major*, *Andrena labialis*, *A. bicolor*, *A. chrysoseles*, *A. clarkella*; *B. minor*, *Colletes daviesanus*; *Thyridanthrax fenestratus*, *Ammophila sabulosa*; *Villa modesta*, *Osmia aurulenta*; PHORIDAE: *Aenigmatias brevifrons*, *Formica rufibarbis*; *A. lubbocki*, *Formica fusca*, *F. transcaucasica*; DROSOPHILIDAE: *Cacoxenus indagator*, *Anthophora acervorum*, *Osmia rufa*, *O. aurulenta*; TACHINIDAE: *Gonia divisa*, *Anthophora*, *Bombus terrestris*; *G. picea*, *Anthophora retusa*, *A. acervorum*, *B. terrestris*; SARCOPHAGIDAE: *Amobia signata*, *Odynerus spinipes*, *Ancistrocerus nigricornis*, *Pemphredon lugubris*, *Trypoxylon figulus*, *T. attenuatum*, *Ectemnius lapidarius*; *Miltogramma germari*, *Anthophora bimaculata*; *M. punctatum*, *Podalonia viatica*, *Trypoxylon figulus*, *Colletes succinctus*, *C. fodiens*, *C. daviesanus*, *C. halophilus*; *Senotainia conica*, *Tachysphex unicolor*, *Oxybelus uniglutinis*, *Crabro peltarius*, *Mellinus arvensis*, *Argogorytes fargeii*, *Phylanthus triangulum*; *Pterella grisea*, *Cerceris rybyensis*, *C. arenaria*; *Metopia argyrocephala*, *Ammophila sabulosa*, *Oxybelus uniglutinis*, *Crabro peltarius*, *Phylanthus triangulum*, *Cerceris rybyensis*, *Colletes succinctus*, *C. daviesanus*, *Andrena barbilabris*; *Macronychia griseola*, *Oxybelus uniglutinis*; *M. polyodon*, *Crossocerus elongatulus*, *C. capitatus*, *Ectemnius lapidarius*, *E. rubicola*, *Bombus terrestris*; *M. unglans*, *Ectemnius cavifrons*; *Brachicoma devia*, *Dolichovespula sylvestris*, *Bombus terrestris*, *B. lucorum*, *B.*