

Ecology and biology of *Euphranta connexa* (Fabr.) (Diptera: Tephritidae) - a seed predator on *Vincetoxicum hirundinaria* Med. (Asclepiadaceae)

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The distribution, biology and ecology of *Euphranta connexa* (Fabr.), a tephritid fruit fly attacking the seeds of the perennial herb *Vincetoxicum hirundinaria* Medicus (Asclepiadaceae), is described based on observations in Sweden, Finland and Denmark. The female oviposits in developing fruits, where the larva subsequently feeds on the immature seeds. The insect occurs in most places where the host plant grows, often attacking close to 100% of available fruits. Usually one, but sometimes two or more larvae leave the fruit in late summer to pupate in the soil. There is one generation per year. Several parasitoid species attack *E. connexa* larvae, of which *Scambus brevicornis* (Gravenhorst) (Ichneumonidae), a highly polyphagous species, is most common and *Bracon picticornis* (Wesmael) (Braconidae) second most common.

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Introduction

Euphranta connexa (Fabr.) is a tephritid fruit fly, the larva of which feeds on the immature seeds of the perennial herb *Vincetoxicum hirundinaria* Med. (Asclepiadaceae). It has been the subject of population dynamics studies (Solbreck and Silén-Tullberg 1986, Solbreck unpubl.) but otherwise little has been published on its biology and ecology, except for the paper by Janzon (1982). The aim of the present paper is to summarize available information on its distribution, biology and ecology in the Nordic countries.

Euphranta Loew 1862 is a species-rich genus of mainly Oriental-Australian distribution, in Europe represented only by two species, *E. (Euphranta) connexa* (Fabr.), and *E. (Rhacochlaena)*

toxoneura (Loew) (Hendel 1949, Foote 1984, Merz 1994, Rikhter 1989). The adult of *E. connexa* is black and yellowish, 5.5-7 mm long and easily recognized in the field by its typical wing markings with a large forward pointing U-shaped mark on the outer half of the wing (Fig. 2A) (Hendel 1949, Foote 1984, Merz 1994). The egg is slightly sickle-shaped and about 0.9x0.2 mm with a pointed tip (figure in Janzon 1982). The fully developed larva (3rd instar) is 6.3-10.0 mm long (Fig. 2D, E) (Dirlbek and Dirlbek 1962, Janzon 1982). Janzon (1982) provided a detailed description of larval morphology. The puparium is pale to medium brown, 4.3-5.8 mm long (Janzon 1982).

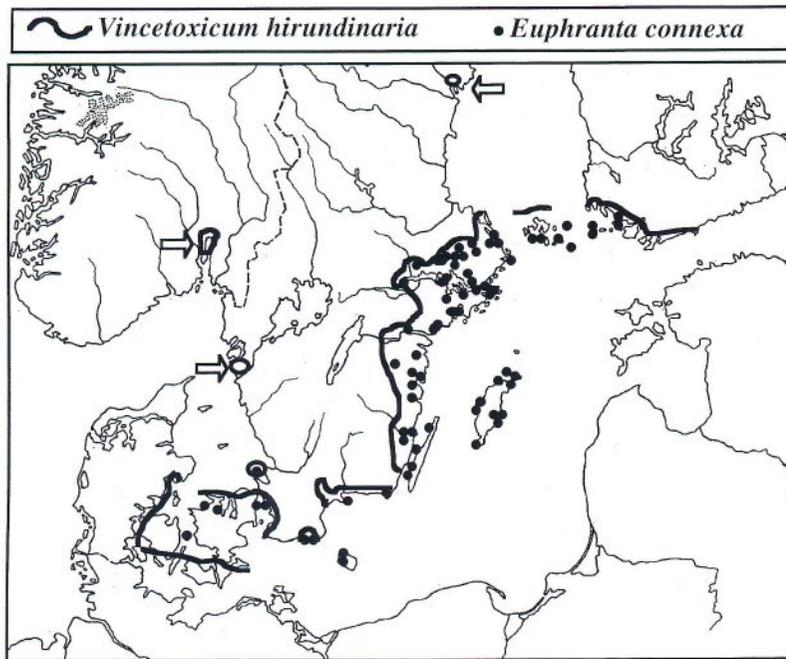


Fig. 1. Finds of *E. connexa* (dots) in the Nordic countries. The distribution of *V. hirundinaria* is delineated by the thick line. Notice the isolated outposts (arrows) of the plant around Oslo, north of Göteborg, and at Sundsvall on the north Baltic coast of Sweden. Based upon published finds, museum specimens, and the author's own finds.

Utbredning av *E. connexa* (punkter) i de nordiska länderna i relation till tulkörtens utbredning (angiven med gränslinje). Observera de isolerade tulkörtslokaler (pilar) vid Oslo, norr om Göteborg samt i Sundsvall som alla saknar *E. connexa*.

Host plant and distribution

The larva of *E. connexa* is strictly monophagous on *V. hirundinaria* in the Nordic countries where no other Asclepiadaceae species occur. Literature records from other areas also mention *V. hirundinaria* (Buhr 1964, Hendel 1949, Dirlbek and Dirlbek 1962, Janzon 1982, Merz 1994, Rikhter 1989, Wahlgren 1919) or just *Vincetoxicum sp.* (Richter 1960) as the host plant.

E. connexa is found in central and northern Europe as well as in the European part of the former USSR. It is uncommon in the Mediterranean region, and it does not occur on the British Isles (Rikhter 1989, Foote 1984, Hendel 1949, Merz 1994). Among the Nordic countries *E. connexa* has been recorded from Finland (Hackman 1980), Sweden (Hedström 1995, Jansson 1922, Ringdahl 1941, Wahlgren 1919) and Denmark (Henriksen and Tuxen 1944). In Sweden it

has recently been listed from five provinces, Sk, Öl, Go, Sö and Up (Hedström 1995).

Although the number of museum specimens and published find records of *E. connexa* is limited, the species is actually rather common. A systematic search for the insect has resulted in numerous new finds (Fig. 1) and four new provincial records from Sweden (Bl, Sm, Ög and Vs - a list of localities is available upon request from the author.). The geographical distribution of *E. connexa* closely follows that of the host plant. It is striking how efficient *E. connexa* has been to establish itself even in isolated localities on the very fringes of its host plant's distribution, for example along the coast of Skåne (Sk), at Hjälmare kanal (Vs), along the coast of Uppland (Up), on the Åland islands (Al) and in the southwest of mainland Finland (Ab) (figure 2).

However, there are three very isolated out-

posts of *V. hirundinaria* in the Nordic countries where *E. connexa* evidently is absent. In Sundsvall in northern Sweden (where *V. hirundinaria* was introduced in 1901) and around Oslo large numbers of pods have been sampled without any signs of *E. connexa* larvae. A very small stand of *V. hirundinaria* north of Göteborg (Nordre Älv) was visited in July 1990. It had no pods, and it is unlikely that *E. connexa* occurs there.

The host plant, *V. hirundinaria*, is in most cases patchily distributed in the landscape. The plant is very long-lived and plant patches are accordingly very stable over time. Nevertheless, from the insect's point of view, the plant provides a rather unstable resource, because seed pod production varies much from year to year in response to weather conditions (Solbreck and Sillén-Tullberg 1986, Solbreck unpubl.). Total seed crop failures are fairly common in small patches causing local extinctions of *E. connexa*. However, recolonization is usually rapid in succeeding years when new pods appear (Solbreck and Sillén-Tullberg 1986, Solbreck unpubl.). These observations suggest that *E. connexa*, like many other tephritid flies (Dempster et al 1995, Eber and Brandl 1994, Jansson 1992, Schlumprecht 1989), has considerable migratory ability.

General biology

During sunny summer days the adult flies can be found on *V. hirundinaria* plants, running around, basking (Fig. 2A, following page), feeding, courting or ovipositing (Fig. 2B), whereas in cool and rainy weather flies hide under the leaves of the host plant. Adults feed by licking leaf surfaces or sucking nectar in *V. hirundinaria* flowers. Flower visits are brief and one rarely sees *E. connexa* among the numerous insect species visiting *V. hirundinaria* flowers for nectar. The fly does not contribute to pollination of the host plant, since on no occasion have I found *V. hirundinaria* pollinia on adults.

Courting takes place on host plant leaves. The male circles the female with vibrating wings. He eventually "kisses" the female, evidently giving her a food gift. Such delivery of nuptial gifts is known from a few other species of tephritids (Freidberg and Kugler 1989). After the male has delivered his gift he jumps on top of the female

to initiate copulation. The few copulations observed have been of short duration being terminated within 5-10 seconds.

Females emerge from puparia with undeveloped ovaries, as many tephritids do (Fletcher and Prokopy 1991). The time it takes for individual females to develop mature eggs is unknown, but a couple of weeks following the first appearance of adults most females have chorionated eggs. Females may contain up to 60 mature (chorionated) eggs (for 16 dissected females with eggs mean number of eggs was 29, range 2-60).

Females oviposit in immature fruits of *V. hirundinaria*. Fruits are attacked in all stages of maturation from just initiated (a few mm long) to fully grown (usually 50-70 mm), as long as they have a soft and green wall and white and soft seeds. The female, usually hanging upside down (Fig. 2B), bores a hole in the fruit wall with the tip of her abdomen, and inserts one egg, which is deposited on the inside of the fruit wall. Egg laying usually lasts about 30-60 s. Egg laying results in a permanent scar (Fig. 2C) in the pod wall, and the number of egg scars provides a good measure of the number of eggs deposited in the fruit.

After oviposition the female zig-zags or moves spiral-wise around the fruit dragging the tip of her abdomen along the pod wall, an activity which usually lasts about 5-15 s. During this behaviour the female evidently deposits a marking pheromone, a common habit among tephritids (Fletcher and Prokopy 1991, Roitberg and Prokopy 1987, Averill and Prokopy 1989). However, marking does not always prohibit later ovipositions in the same pod. In years when the ratio of adult flies to pods is high females neglect previous egg layings, and numerous eggs may then be deposited in the same fruit (Solbreck unpubl.). In a few cases I have found more than 30 eggs in a single fruit. Usually, however, there is only one or a few eggs per fruit.

The larva feeds on and tunnels through the soft immature seeds in the developing fruit (Fig. 2D). When the larva is fully grown it bores through the fruit wall (Fig. 2E), or leaves the fruit through the ruptured wall if the fruit is mature, and then pupates in the soil. According to Hendel (1949) pupation may also take place in

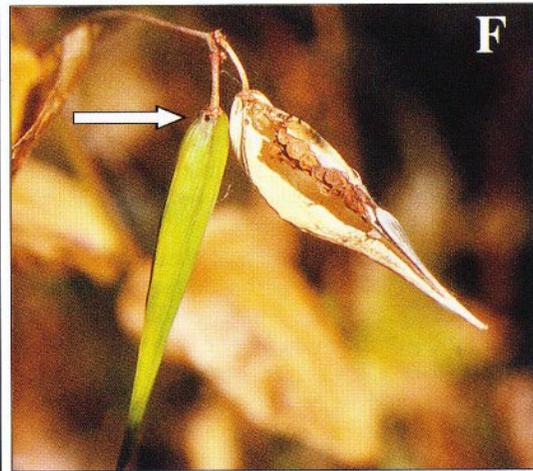
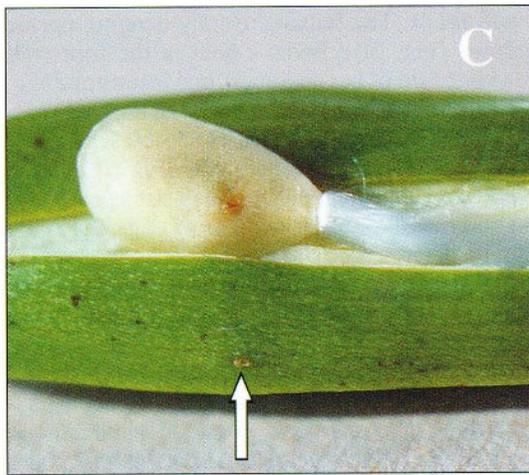
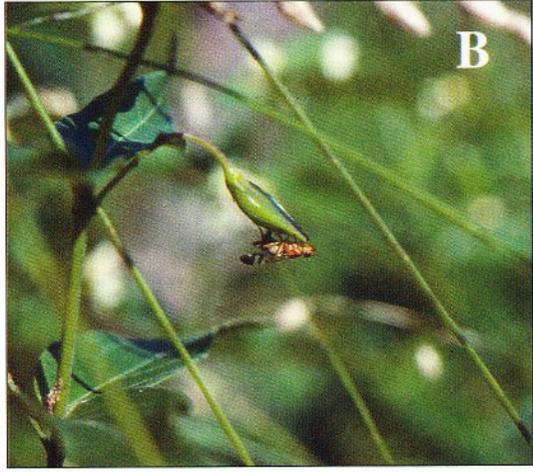


Fig. 2. A) Female *E. connexa* on a *V. hirundinaria* leaf. B) Female ovipositing in immature fruit of *V. hirundinaria*. C) Oviposition mark on fruit wall (arrow) and initial damage to seed by newly hatched larva. D) Last instar larva in opened fruit. E) Larva leaving fruit for pupation in the soil. F) Two fruits attacked by *E. connexa* larvae. The fruit to the right is open and dry showing partly destroyed seeds clogging together. The left fruit is still green and unopened but it has an exit hole at the base (arrow). All photos Christer Solbreck.

2A) Hona av *E. connexa* på blad av tulkört. B) Hona lägger ägg i o mogen tulkörtsfrukt. C) Äggläggningssmärke (pil) i fruktväggen samt gnag (brun fläck) av nykläckt larv i omoget tulkörtsfrö. D) Sista stadiets larv bland söndergnagda frön. E) Färdig larv som lämnar tulkörtsfrukt för att förpuppa sig i marken. F) Två angripna tulkörtsfrukter. Den vänstra är oöppnad men visar ett utgångshål vid fruktens bas (pil). Den högra frukten är öppnad men fröresterna är hopklibbade och sitter fast i frukten.

the fruit, but this is unusual in Sweden.

Attacks by *E. connexa* on *V. hirundinaria* can usually be ascertained long after the larvae have left the fruits. Holes through the seeds or exit holes in the fruit wall are reliable signs of *E. connexa* attack (Fig. 2F). (A hole may also be made by a parasitoid, like *Scambus brevicornis*, see below, which has earlier devoured an *E. connexa* larva.) The seeds in attacked fruits usually clog together and remain attached to the fruit wall (Fig. 2F) during the autumn and sometimes until next summer. Even after the seed remains have been weathered away many fruit walls remain as flags on the durable dry plant stalks. Hence, presence of *E. connexa* can sometimes be determined up to one year after larvae have left the plant on the basis of old "fruit flags" with exit holes.

Larval feeding does not change the exterior of the fruit (Fig. 2F). It has been claimed that *E. connexa* causes a gall-like swelling and undulation of the fruit wall (Buhr 1964, Coulianos and Holmåsén 1991), but this is a misunderstanding. The mentioned symptoms are caused by the gall midge *Contarinia asclepiadis* Giraud, which feeds in the fruit wall. The mistake is easily made because the gall midge usually occurs in fruits also attacked by *E. connexa*. This gall midge is, however, very rare in Sweden (Widenfalk and Solbreck unpubl.).

Phenology and voltinism

E. connexa has one generation per year (Hendel 1949, Merz 1994). Adults occur during a large part of the summer; mainly a result of the flies being rather long-lived. In Eastern Sweden flies usually start to emerge in late June or early July with a peak in adult density in mid July. Fly

density then gradually tapers off until late August to early September, when the last flies are seen. There are, however, large variations in phenology between years, particularly with regard to first appearance of flies. These yearly variations are illustrated by population transect data from Tullgarn (Sö) during a "normal" year (1989), a year with unusually warm weather in April and May (1992), and a year with a cool summer (1991) (Fig. 3).

Most eggs are laid during July when young fruits appear, but in cool summers egg laying starts later and may continue even into the first days of September. Larvae usually leave the fruits during August and September to pupate in the soil. There is, however, considerable variation in the timing of this event. In sunny summers larvae may leave fruits already in July, whereas after cool summers many fruits may still contain larvae in October. Although these late larvae will survive the first moderate frosts, many will undoubtedly be unable to finish development and hence will eventually perish.

It is not uncommon for tephritid flies to overwinter more than one year. However, this does not seem to be the case with *E. connexa*. In the autumn of 1997 56 puparia were caged under natural hibernation conditions at Uppsala. All surviving puparia (33) produced adult flies in mid July the following year. The experiment was repeated in 1998/99 when all surviving pupae (8) also emerged after one winter.

Resource exploitation and competition

Attack rates by *E. connexa* on *V. hirundinaria* fruits are usually high, and it is not uncommon that close to 100 percent of the fruits in a plant patch harbour *E. connexa* larvae (Solbreck and

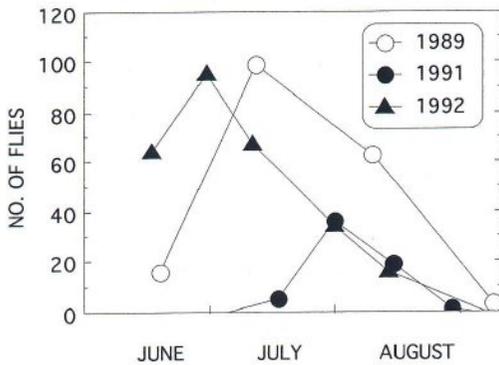


Fig. 3. Phenology of adult *E. connexa* at Tullgarn (about 50 km SSW of Stockholm) during three years with different weather conditions. Sampling was made by walking transects through seven host plant patches (totalling about 450 m² of plant covered ground) counting all flies observed.

Fenologi hos *E. connexa* under ett normalår (1989), ett år med varm försommar (1992) och ett med kall sommar (1991). Punkterna visar antal vuxna flugor observerade under linjetaxering på sju tulkörtslokaler vid Tullgarn (SÖ). Den totala taxerade ytan var ca 450 m².

Sillén-Tullberg 1986, Solbreck unpubl., Sterner 1922). However, densities of fruits vary much between years (more than two orders of magnitude) and as a result of this *E. connexa* densities also vary much. Very low attack rates, down to about 10 % of the fruits attacked, occur when a good crop year is preceded by a year with very few fruits (Solbreck and Sillén-Tullberg 1986, Solbreck unpubl.).

On average about one puparium is produced per attacked fruit (mean for 1986 to 1991 yearly means is 0.98 with a range of 0.55-1.47, N=212-554). A single *E. connexa* larva destroys a major proportion of the seeds in a fruit. With two or three old larvae all seeds are consumed in an average sized fruit. Only rarely are more than two or three puparia produced in a fruit, the largest number observed being six. With increasing density puparia become considerably smaller (Solbreck unpubl.). In some years the number of eggs per fruit (see above) is very much higher than the number of puparia a fruit can produce, causing strong intraspecific competition bet-

ween larvae in the fruit (Solbreck unpubl.).

In addition to the direct damage caused by larval tunnelling through seeds there is also a secondary damage inflicted on seeds by fungi invading attacked fruits. They often destroy those seeds not immediately killed by *E. connexa* larvae. Furthermore, the clogging together of seeds in attacked fruits seriously impairs the dispersal of any seeds that may survive insect and fungal attacks.

The lygaeid bug *Lygaeus equestris* (L.) is the only other seed feeding insect on *V. hirundinaria* in the Nordic countries. It feeds on the ovulae in the flowers, on seeds in developing fruits and on mature seeds (Solbreck 1995). However, there is no evidence of *L. equestris* affecting fruit density or destroying a substantial proportion of seeds during the seed maturation period when *E. connexa* inhabits the fruits (Solbreck unpubl.). (Old seeds on the ground seems to be the limiting resource for *L. equestris* (Solbreck 1995)). Hence, whereas intraspecific competition is often strong in *E. connexa*, interspecific competition from other seed feeders seems negligible.

Enemies

In a few cases I have seen sunbasking or ovipositing adults of *E. connexa* being attacked by predators. On one occasion a *Vespa* species was observed feeding on an adult, and in seven cases spiders were predators; *Misumena vatia* Clerck (Thomisidae) adults in four cases, a juvenile *Dolomedes fimbriatus* (Clerck) in one case, and unidentified species in two more cases. The spiders not only captured the flies but also ate them. (This is in contrast to the situation with *L. equestris*, the other seed predator on *V. hirundinaria*, which is sometimes caught in spiders' webs. It is obviously unpalatable to spiders because they do not consume it.)

Larvae of *E. connexa* are attacked by several species of parasitoids (table 1). I have reared seven species of parasitic Hymenoptera from *V. hirundinaria* fruits with *E. connexa* larvae (table 1). By far the most common parasitoid on *E. connexa* in Sweden is *Scambus brevicornis* (Gravenhorst) (Ichneumonidae), a highly polyphagous ectoparasitoid (Aubert 1969, Janzon

Table 1. Hymenoptera species hatched from *V. hirundinaria* fruits with *E. connexa* larvae. (Sweden)

Family	Species	Habits
Ichneumonidae	<i>Scambus brevicornis</i> (Gravenhorst)	Highly polyphagous.
Braconidae	<i>Bracon picticornis</i> (Wesmael)	Polyphagous. Reported from symphytans, cerambycids and a gall midge (Shenefelt 1978).
Pteromalidae	<i>Pteromalus helenomus</i> (Graham)	Host unknown (K.J. Hedqvist in litt.).
	<i>Stenomalina muscarum</i> (L.)	Recorded from several species of Agromyzidae and from <i>Chlorops</i> (Chloropidae) (Graham 1969).
Eurytomidae	<i>Eurytoma curculionum</i> Mayr	The genus has a wide host spectrum, phytophagous species as well as parasitoids of cecidomyids and other insects.
Eupelmidae	<i>Macroneura vesicularis</i> (Retzius)	Highly polyphagous on flies, beetles and symphytans. Often hyperparasitoid (C. Hansson in litt.).
Ceraphronidae	<i>Aphanogmus</i> sp.	

1982). Certain years up to about 30% of fruits may harbour *S. brevicornis* larvae, but in most years rates of parasitism are considerably lower. The second most common species, although usually an order of magnitude less common than *S. brevicornis*, is *Bracon picticornis* (Wesmael) (Braconidae). It is probably also polyphagous (Shenefelt 1978). I have observed females of both species ovipositing in fruits of *V. hirundinaria* by boring their ovipositor through the fruit wall. Both *S. brevicornis* and *B. picticornis* are widely distributed in Sweden and I have found them attacking *E. connexa* in all parts of its distribution range.

The remaining species in table 1 I have only occasionally encountered as they emerged from fruits brought to the laboratory. The number of parasitoid species notwithstanding, parasitoids obviously have small effects on *E. connexa* densities, which are largely resource controlled (Solbreck unpubl.).

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Sammanfattning

Tulkörtsborrflugan (*Euphranta connexa* (Fabr.)) lever som larv på tulkörtens (*Vincetoxicum hircundinaria* (Med.)) frön. I Norden förekommer den nästan överallt där värdväxten finns (figur 1, 2), och den angriper ofta en mycket stor andel av tulkörtens frukter. Flugan uppträder vanligen från mitten av juni fram till augusti (figur 3). Uppvaktning och parning sker på tulkörtens blad. Hanen rör sig runt honan med vibrerande vingar och överröcker en födogåva före parningen. Honan lägger ägg i gröna mjuka tulkörtsfrukter. Vid varje äggläggningstillfälle borrar ett ägg in under fruktskalet, och efteråt markeras äggläggningen genom att honan cirklar runt frukten med ägglägningsröret tryckt mot fruktskalet. Larverna äter och borrar igenom de vita omogna fröna varvid de flesta fröna förstörs. När larven är fullvuxen, vanligen i slutet av juli och augusti, borrar den sig ut genom fruktväggen och faller till marken där den förpuppas. Den övervintrar en gång.

En viss predation förekommer på vuxna flugor, framför allt från krabbspindlar. Flera arter parasitsteklar angriper larverna, av vilka *Scambus brevicornis* (Gravenhorst) (Ichneumonidae) är vanligast och *Bracon picticornis* (Wesmael) (Braconidae) näst vanligast. Fienderna har emellertid ingen nämnvärd effekt på flugpopulationen som begränsas av tillgången på tulkörtsfrukter.