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Larval morphology and feeding patterns of four *Cheilosia* species (Diptera: Syrphidae) associated with *Cirsium palustre* L. Scopoli (Compositae) in Scotland

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Four species of *Cheilosia* (Diptera: Syrphidae) were reared from *Cirsium palustre* in Scotland. The third-stage larva is similar in all four species but each can be recognized by the form of the posterior respiratory process. A modified prothorax and thickened bands of spicules on some of the segments may characterize the plant-boring type of *Cheilosia* larva. The univoltine *Cheilosia grossa* oviposits in batches on young stems. With three or more larvae per plant the tip of the stem is killed. The plant responds by producing a mass of basal stems in which larvae subsequently feed. *Cheilosia fraterna* and *Cheilosia proxima* do not oviposit in batches and are bivoltine. *Cheilosia fraterna* attacks mature stems and rosettes. *Cheilosia proxima* attacks only rosettes. *Cheilosia albipila* was reared only six times, from stems collected in July. Rates of parasitism were low and only two parasitoid species were recorded.

Keywords *Cheilosia*, *Cirsium palustre*, thistle, larval morphology, feeding pattern, life histories.

Introduction

Although species of *Cheilosia* are common and widespread in many regions of the world, they are biologically poorly known. The few verified rearing records indicate that larvae are phytophagous (Lundbeck, 1916; Hering, 1957; Smith, 1979). However, few descriptions of larvae have appeared since Smith (1979) stated that descriptions were available for fewer than 7% of the 130 or so Palaearctic species. The number of species has been revised to 286 (K. G. V. Smith, personal communication).

A number of species seem to feed as larvae on species of *Carduus* and *Cirsium* (Stubbs and Falk, 1983). *Cheilosia* larvae were common in stems and roots of *Cirsium palustre* (L.) Scopoli in Dunbartonshire, Scotland in 1984. From these, in April and May 1985, adults of *Cheilosia albipila* Meigen, *Cheilosia fraterna* (Meigen), *Cheilosia grossa* (Fallén) and *Cheilosia proxima* (Zetterstedt) were obtained. Although rearing records from *C. palustre* have been published for *C. albipila* (Andrews, 1944), *C. fraterna* (Stubbs, 1980) and *C. grossa* (Nurse, 1910), few biological data are recorded and only the larva of *C. grossa* has been described (Dušek and Láska, 1962).

Methods

To see if there was any relationship between the life-cycles of the flies and their food plant, the phenology of *C. palustre* was recorded by counting, at approximately fortnightly intervals from May to October 1985, the number of plants in two 30 × 30m plots in fields used for stock grazing in Dumbartonshire, Scotland. The length of stems and diameter of rosettes were recorded and the development of flowers monitored. The plots were 300m apart and separated by a strip of coniferous woodland. At the same time growth and development of *C. palustre* populations was monitored intermittently at other sites in S. Scotland.

Life-histories of the flies were recorded in the same fields. At approximately fortnightly intervals from May to October 1985, each *C. palustre* plant in three arbitrarily selected 10 × 10m plots was examined for the presence of eggs and larval entry holes. Each plant was split open and larval feeding tracks (= tunnels) recorded. Larvae were removed from the plant and placed individually in 10–15cm long, hollow sections of *C. palustre* stem for subsequent rearing. In the laboratory each larva was identified and its stage of development recorded.

Infested plants, in a soil core, were taken to the laboratory for detailed observations of larval feeding behaviour. Plants were partially split to find and identify larvae and then examined daily until puparia formed. Plants were held together with wire and kept outdoors in unsealed plastic bags. To confirm details of feeding behaviour, *C. palustre* plants ($N = 70$) were regularly dissected at other sites in S. Scotland.

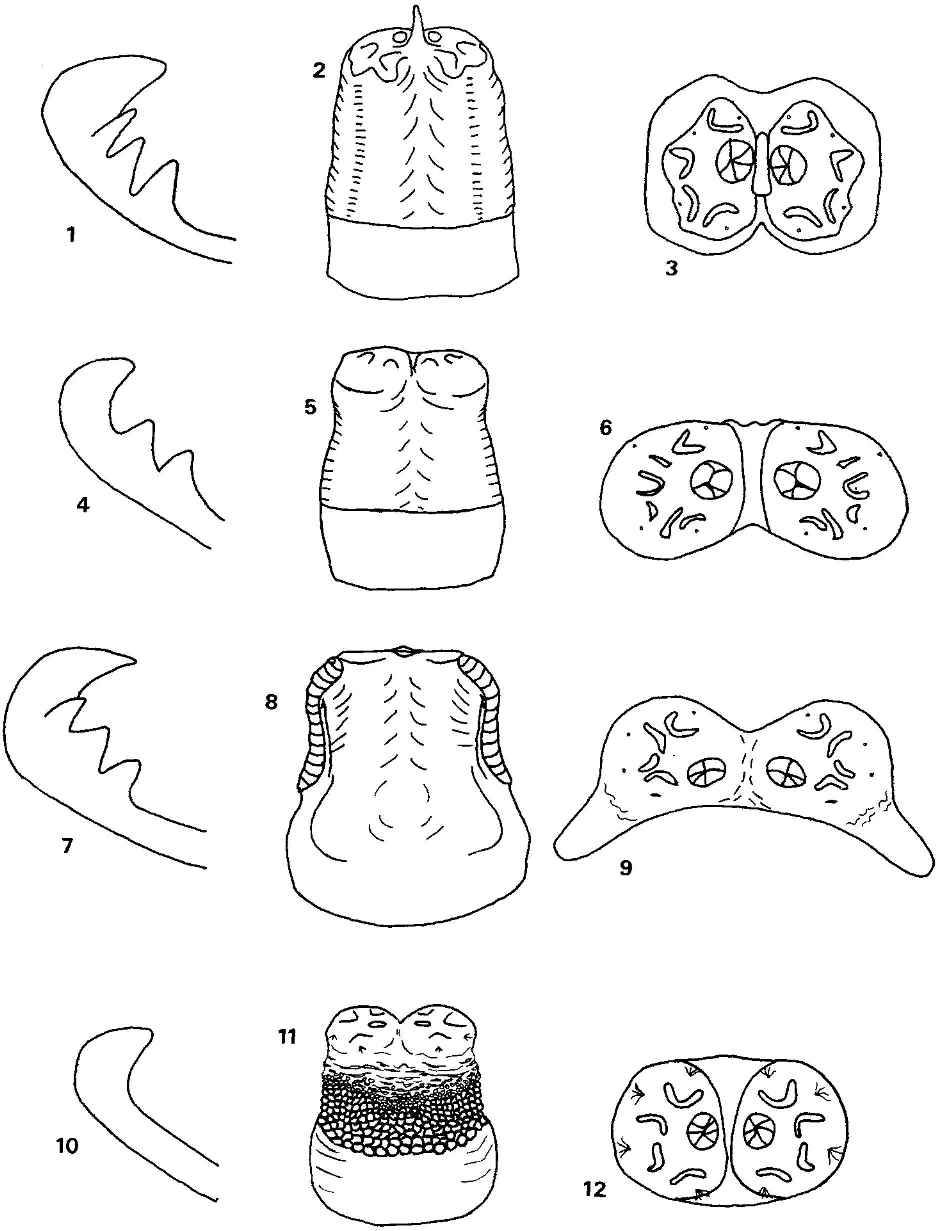
Results

Description of the third-stage larva

Cheilosia albipila. Length 15–18 mm; width 3 mm: oval in cross-section; tapering from metathorax to head, truncate posteriorly; white to pale brown; integument covered in backwardly directed pale orange spicules which are less dense in the transverse folds of each segment; spicules thickened, sclerotized and blunt-tipped on lateral and ventral margins of the thorax; on lateral and ventral margins of the abdomen each segment with two transverse folds, meso- and metathorax with one fold; prothorax greatly modified, elongate with a broad, shining, sclerotized, square-shaped region between the anterior spiracles and delimited laterally by longitudinal grooves; chaetotaxy – prothorax with 11 pairs of sensilla, meso- and metathorax nine pairs, abdominal segments 1–7 10 pairs, anal segment seven pairs; three pairs of lappets; ventral pair of lappets larger than the rest; one large and three smaller pairs of black mouth hooks (Fig. 1); posterior respiratory process (Fig. 2): length, 1.5–2 mm; width at tip, 0.8 mm; basal third clear, shining pale brown, apical two-thirds pale brown and nodulated; constricted just before tip; conspicuous projection between the spiracular plates (Fig. 2); four pairs of curved spiracular slits (Fig. 3).

Cheilosia fraterna. Length 10–12 mm; width 3 mm; oval in cross-section; tapering from metathorax to head, truncate posteriorly; white to creamy-white; integument covered in short translucent spicules, those on the lateral and ventral margins of the thorax and abdomen tending to be denser, thicker, sclerotized and dark brown; abdomen dorsally and ventrally with two transverse folds per segment, meso- and metathorax with one fold; prothorax modified, elongate with a broad, thickened, square-shaped region between the anterior spiracles and delimited laterally by longitudinal grooves; chaetotaxy – prothorax with 11 pairs of sensilla, meso- and metathorax nine pairs, abdominal segments 1–7 10 pairs, anal segment seven pairs; three pairs of lappets; middle pair of lappets smaller than the rest; three pairs of approximately equal-sized black mouth hooks (Fig. 4); posterior respiratory process (Fig. 5): length 1.5–2 mm long; width at tip 0.8 mm; basal third clear, shining pale brown then slightly nodulated to tip; spiracular slits indistinct and variable in shape (Fig. 6); projection between the spiracular plates absent.

Cheilosia grossa. Length 12–15 mm; width 3 mm; sub-rectangular in cross-section; tapering from metathorax to head; truncate posteriorly; white to creamy-white;



FIGS 1–12. Third stage *Cheilosia* larvae. 1–3, *Cheilosia albipila* Meigen: 1, mouth hooks, lateral view; 2, posterior respiratory process (p.r.p.), anterior view; 3, p.r.p., dorsal view. 4–6, *Cheilosia fraterna* (Meigen): 4, mouth hooks, lateral view; 5, p.r.p., anterior view, 6, p.r.p., dorsal view. 7–9, *Cheilosia grossa* (Fallén): 7, mouth hooks, lateral view; 8, p.r.p., anterior view; 9, p.r.p., dorsal view. 10–12, *Cheilosia proxima* (Zetterstedt): 10, mouth hooks, lateral view; 11, p.r.p., anterior view; 12, p.r.p., dorsal view.

integument covered with short translucent spicules, those on the lateral and ventral margins of the thorax and dorsally on the prothorax, thicker, sclerotized, blunt-tipped and dark brown; abdomen dorsally and ventrally with two transverse folds per segment; meso- and metathorax with one fold; prothorax elongate with a broad, lightly sclerotized region between the anterior spiracles and delimited laterally by longitudinal grooves; chaetotaxy – prothorax with 11 pairs of sensilla, meso- and metathorax nine pairs, abdominal segments 1–7 10 pairs, anal segment seven pairs; three pairs of lappets; dorsal pair of lappets larger than the rest; one large and three smaller pairs of black mouth hooks (Fig. 7); posterior respiratory process (Fig. 8); length 1·5–2·0 mm; width at tip 0·9 mm; red-brown with conspicous raised lateral margins; three to four pairs of indistinct curved, spiracular slits (Fig.9).

Cheilosia proxima. Length 9 mm; width 1·5–2·5 mm; oval in cross-section; tapering from metathorax to head; truncate posteriorly; creamy-white to pale brown; integument covered in short, blunt-tipped spicules; dorsal and ventral margins of the abdomen with two transverse folds per segment, meso- and metathorax with one fold; prothorax elongate with a broad, clear, region between the anterior spiracles and delimited by longitudinal grooves; chaetotaxy – prothorax with 11 pairs of sensilla, meso- and metathorax nine pairs, abdominal segments 1–7 10 pairs, anal segment seven pairs; two pairs of equal-sized lappets; one pair of black mouth hooks (Fig. 10); posterior respiratory process (Fig. 11): length 1·5 mm; width at tip 0·6 mm; basal third wider than rest and lightly nodulated; middle third with large nodules; distal third lightly nodulated and striated; construction just before tip; four pairs of curved spiracular slits; four pairs of plumose inter-spiracular setae (Fig. 12).

Phenology of Cirsium palustre

At the beginning of spring above-ground populations consisted of rosettes up to 25 cm in diameter. Single stems developed from the largest (> 15 cm diameter) of these and stem production continued until late June (Fig. 13). By mid-July most stems had finished growing and many had started to flower. Rosettes were more abundant than stems throughout the sampling period (Fig. 13). In winter, stems died and broke up.

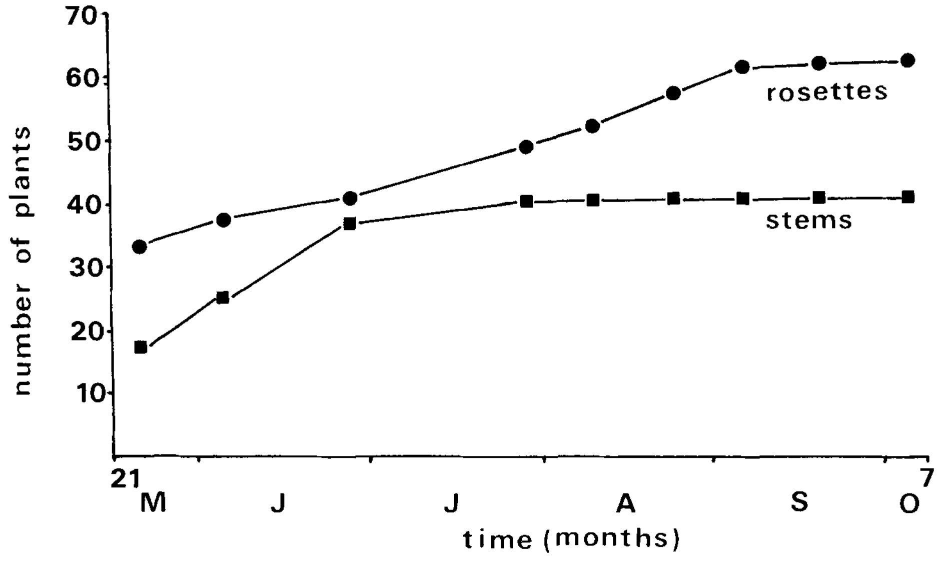


FIG. 13. Numbers of stems and rosettes of *Cirsium palustre* in two 30 × 30 m plots from 23 May to 4 October 1985.

Feeding mechanism of the third-stage larva

To feed, the larva scraped the mouth hooks against the plant in front of it. This loosened small fragments of tissue, some of which were eaten. This basic technique was used by all four species. Unconsumed fragments, which often accumulated in front of a larva, did not block the tunnel because, as the larva moved forward, they were rolled out of the way between the sides of the tunnel and the larva.

Life-histories

Cheilosia albipila. Only six larvae of this species were recorded. All were encountered as third-stage larvae tunnelling in the basal region of stems in July. They occurred solitarily and adults emerged in May of the following year, having overwintered as puparia.

Cheilosia fraterna. Eggs first appeared in late June near the tip of the upper surface of leaves on stems and rosettes but only those with a well-developed core of leaves, i.e., those about 10 mm in diameter. There was one egg per leaf ($N = 47$). On hatching, the larva tunnelled into the protuding mid-vein of the leaf about 3 cm from its base.

Having arrived in the stem, larvae tunnelled towards the roots. Sometimes tunnels ended if the hollow part of the stem was breached, in which case tunnelling resumed at the base of the plant. In rosettes larvae tunnelled in a spiral around the core down towards the roots. Inside the main root larvae excavated an irregular-shaped cavity.

On 25 July 1985 the first empty, but obviously tunnelled, plants were encountered. In the soil surrounding these plants puparia were found. The proportion of adults that emerged from these puparia decreased towards the end of August (Fig. 14). Adults emerged from the remaining puparia in the following year. In early September eggs and first-stage larvae were recorded again, having been absent since mid July. By the end of September only third-stage larvae remained in plants. From mid October no larvae were found in plants.

From 25 July to 6 September, the main period of infestation, numbers of larvae in rosettes versus stems were inversely related to their relative abundance (chi square $= 1{\cdot}07$, $P < 0{\cdot}0001$), with 42·2% of rosettes ($N = 161$) infested and 65·9% of stems ($N = 91$). Furthermore, there were significantly more larvae per stem than rosette (means $2{\cdot}21 \pm 1{\cdot}4$, range 1–6 and $1{\cdot}8 \pm 0{\cdot}4$, range 1–2 respectively, $t = 2{\cdot}98$, $P < 0{\cdot}005$). Stems varied in length (mean $91{\cdot}4 \pm 20{\cdot}3$, range 34–148 cm). However, no significant relationship was obtained between presence of larvae and stem length ($P > 0{\cdot}10$).

One parasitoid species was reared from stem-feeding larvae (*Bracon* sp., Hymenoptera: Braconidae). This was a gregarious species with two to five progeny per host. Only four host larvae were parasitized. Adult parasitoids overwintered in their cocoons and emerged in July.

Cheilosia grossa. Eggs first appeared in early May on the tips of young stems. They usually occurred in batches (mean size $4{\cdot}22 \pm 1{\cdot}8$, range 1–9, $N = 27$), On hatching larvae entered the growing point of the stem and tunnelled downwards.

However, in plants with three or more larvae, tunnelling stopped after about 3 cm. By this time larvae had developed to the late second or early third stage. Larvae left the tunnel and, by moving externally down the plant, re-entered the stem via longitudinal slits or holes just above a leaf base. Each larva made its own slit and tunnelled to the base of the plant.

With three or more larvae present the growing point was usually killed. The plant responded in a characteristic manner by producing up to nine basal stems. These produced flowers and each resembled a normal flowering stem. The aborted stem

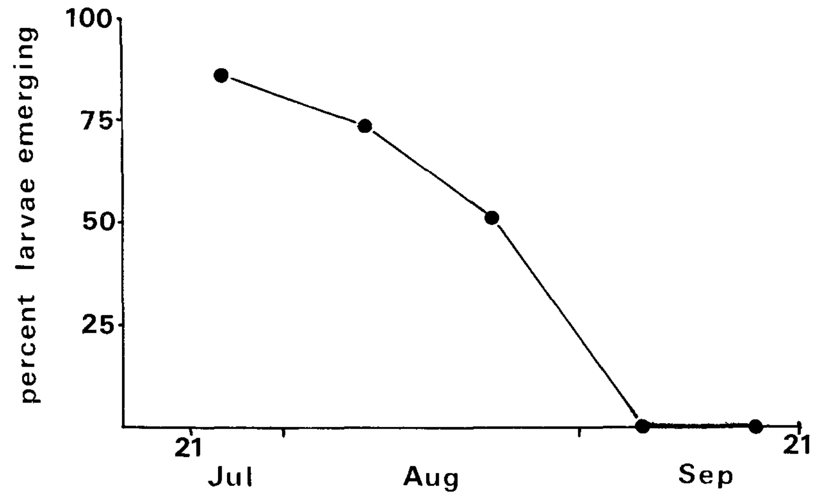


FIG. 14. Percentage adult emergence from *Cheilosia fraterna* puparia collected during the period 25 July to 18 September 1985.

sometimes grew a few centimetres from its base but no flowers were produced. Larvae tunnelled along the basal regions of these extra stems as well as the aborted main shoot. In plants with only one or two larvae, growing points were not killed and stems appeared to develop normally.

Obviously tunnelled but empty plants were first recorded on 22 August with larvae and puparia in the soil surrounding them. By mid October all larvae had left their plants. In the following year adults emerged from April to June from overwintered puparia.

From 23 May to 25 June, mean density of stems in the 10 × 10 mm plots was 14·0 ± 2·6, range 9–17. Mean percentage infestation was 60·3 ± 9·7, range 53·5–84·6.

One species of parasitoid was reared, *Phygadeuon grossae* Horstmann (Hymenoptera: Ichneumonidae). It was a solitary larval-pupal parasitoid that emerged in late July to mid August from overwintered host puparia. Parasitized puparia were narrower than non-parasitized individuals. Only five larvae were parasitized.

Cheilosia proxima. Larvae of this species first appeared in late June. They were only recorded in rosettes with a well-developed central core, i.e., rosettes of about 10 cm diameter.

Larvae tunnelled in a spiral towards the roots. However, larvae did not tunnel into the main root. Third-stage larvae were found externally among the lateral roots beneath the plant. First-stage larvae were again recorded in late August and September. By mid October no larvae were left in rosettes but puparia were found in the surrounding soil.

From 25 July to 6 September mean density of rosettes with a diameter of 10 cm or more in the plots was 18·3 ± 6·5, range 2–27. Mean percentage infestation was 13·3 ± 2·9, range 0–19·6. The only parasitoid reared was a single female *Phygadeuon* sp.

Discussion

The third-stage larvae of all four species were similar in shape and form. They had similar patterns of sensilla, transverse folds and thickened spicules. They all had lappets and a modified prothorax. Yet the different species could be separated by the form of the posterior respiratory process. They can be separated from other syrphid larvae with mouth hooks, in having sensilla with more than one seta (*Merodon* larvae have one seta per sensillum; Hartley, 1961), the absence of bilobed lappets (*Eumerus* larvae have at least one pair of bilobed lappets; Hartley, 1961) and the posterior respiratory process longer than broad (*Portevinia maculata* (Fallén) has a broader than long posterior respiratory process; Speight, 1986).

There were also similarities in larval life-histories. All four species tunnelled towards the roots and third-stage larvae spent most time there. At the base of the plant they are close to pupation sites in the soil. Possibly stems, away from the base, are too narrow for tunnelling by these relatively large larvae. The advantage of pupating in the soil as opposed to staying in the plant is that larvae avoid becoming exposed and avoid a saprophytic environment when food plants break up and decay during winter.

The modified prothorax and thickened spicules are probably adaptations to tunnelling. In particular, the sclerotized part of the prothorax may help prevent excessive wear as the rasping feeding action repeatedly forces this area against the plant. The spicules probably provide grip against the sides of the tunnel during locomotion and prevent the larva from slipping backwards when rasping for food.

Adaptation of *Cheilosia* larvae to particular situations is reflected by a variety of morphological forms within the genus. A modified prothorax and thickened spicules may characterize the tunnelling type of larva. The lack of these features and absence of lappets may characterize the leaf-mining type, as revealed by an examination of *Cheilosia semifasciata* (Becker) puparia from leaf mines on *Umbilicus rupestris* (Salisbury) Dandy. Extreme specialization occurs in the larvae of *Cheilosia morio* Zetterstedt (Tragardh, 1923) and *Cheilosia alaskensis* Hunter (Burke, 1905). These larvae live in resin-filled chambers excavated from bark beetle tunnels and have developed, like Eristalini (Diptera: Syrphidae), an elongate breathing tube to keep them in contact with the outside air.

In attacking stems at an early developmental stage *C. grossa* larvae alter the growth form of the plant to their own advantage. By killing the growing tip, the food supply is increased because the plant produces a mass of basal stems in which larvae subsequently feed. Batching of eggs, which was only recorded in *C. grossa*, is probably facilitated by this effect. Although similar to gall formation, the effect differs in that *C. grossa* takes advantage of a generalized response of the plant to loss of apical dominance, rather than inducing a specialized growth form like a gall. Further, unlike many gallicolous insects which tend to be food-plant specific (Ananthakrishnan, 1984), *C. grossa* induces the response in other plant species. For example, van Leeuwen (1983) records it in *Cirsuim vulgare* (Savi) Tenore. I have seen it in this species and *Carduus tenuiflorus* Curtis in Scotland. The reasons why *C. grossa* larvae exit from the stem tip instead of tunnelling through it are unclear. The cause may be crowding, as it only occurred when three or more larvae were present. With one or two larvae, the stem tip was not killed and no multi-stemmed plants occurred. However, in such cases it is probably unnecessary to increase the food supply.

In contrast, the life-cycle of *C. fraterna* began when stems were almost fully grown so this species is unable to affect the plant in the same way. However, by appearing when plants have matured, a maximum quantity of food is available for exploitation. Larvae also occurred in rosettes, although significantly more stems were infested than rosettes. An advantage of including rosettes is that the range of food plants is broadened. Unlike *C. grossa*, *C. fraterna* had a partial second generation. Its partial nature is suggested by the decreasing rate of adult emergence towards autumn (Fig.

14). Thus the second generation comprises individuals from early in the life-cycle.

Cheilosia proxima occurred at about the same as *C. fraterna*. It was only recorded in rosettes but, unlike *C. fraterna*, was not found inside the main root. *Cheilosia proxima* was the smallest species studied and so may not need extra food from inside the root. It may, however, graze externally, although this was not adequately confirmed. Like *C. fraterna*, *C. proxima* had a second generation.

Cheilosia albipila was the rarest of the four species. Although larvae occurred singly in plants from Scotland, when *C. palustre* samples from Bayreuth, FR Germany were analysed larvae were common and gregarious (mean number per plant 3·95 ± 1·23, range 2–6, based on 11 plants). In Scotland, *C. albipila* may be near the limit of its range which may account for these differences.

The three commonest *Cheilosia* species are largely separated from each other by temporal and spatial characteristics (Table 1). Furthermore, third-stage larvae were not aggressive towards one another, either intra- or inter-specifically, when experimentally crowded in stem sections. Negative interactions may occur, however, between rosette-feeding species and *C. grossa* if, subsequently, rosettes are unable to produce stems in the following year. No evidence for this was sought. In contrast, *C. grossa* could benefit *C. fraterna* by increasing stem production via loss of apical dominance. Indeed, C. fraterna larvae were sometimes found in *C. grossa* induced multi-stemmed plants.

Table 1. Summary of differences between *Cheilosia* species associated with *Cirsium palustre*.

Cheilosia species	Generations (no.)	Oviposition period	Mean no. eggs/leaf ± S.D.	Larval feeding sites		
				Stem	Rosette	Root
C. albipila	1		1·0* 3·95 ± 1·23†	X		
C. fraterna	2	(i) June to early July (ii) September	1·0	X	X	X
C. grossa	1	April to early June	4·22 ± 1·8	X		X
C. proxima	2	(i) June to early July (ii) Late August to September	1·0		X	

*Based on samples from Dunbartonshire, Scotland.
†Based on samples from Bayreuth, FR Germany.

These four *Cheilosia* species are not the only ones associated with *C. palustre*. In Italy *Cheilosia cyanocephala* Loew and *Cheilosia vulpina* (Meigen) have been reared from *C. palustre* (Dunn, personal communication). These two species are more common in S. Britain than Scotland (Stubbs and Falk, 1983). In addition, all four species studied here have been reared from species of *Cirsium* and *Carduus* other than *C. palustre* (Lundbeck; 1916, Dušek and Láska, 1962; Smith, 1979; Dunn, personal communication). There are also rearing records of other species, *Cheilosia mutabilis* (Fallén) (Rossi, 1848) and *Cheilosia variabilis* (Panzer) (Kaltenbach, 1874), from *Carduus* species. Thus there is a large community of *Cheilosia* species associated with *Cirsium* and *Carduus* thistles with apparantly few plant-specific species. Geographical factors may be important in determining the size of the community and perhaps, as in the case of *C. albipila*, some of its characteristics.

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