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Original article

Patterns of resource exploitation in four coexisting globeflower fly species (*Chiastocheta* sp.)

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ABSTRACT

Life history and spatio-temporal patterns of resource utilisation were characterised in four *Chiastocheta* (Diptera: Anthomyiidae) species, whose larvae compete as seed predators on *Trollius europaeus* fruits. Interspecific co-occurrence was observed in 80% of the resource patches (= *Trollius* fruits) in the two communities studied. Isolated larvae from all species had a similar food intake, but differed in development time and size at emergence. Different species exhibit contrasting resource exploitation strategies with specific mining patterns and a partial temporal shift. Two species exhibited particularly singular strategies. *C. rotundiventris* escaped from strong interactions with other species because it was the first species to develop and the only one to exploit the central pith of *Trollius* fruits. The key role of this species as the main pollinator of the host-plant appears to be a by-product of constraints imposed by occupying a restricted niche. Although the resource is ephemeral due to seed dispersal, *C. dentifera*, the last species to oviposit, is not disadvantaged because it has a short development time and rapid food intake. The different patterns can partly explain the stability of *Chiastocheta* communities, but do not prevent competition to occur at high larval densities.

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1. Introduction

Ephemeral fragmented resources often support large numbers of species (Shorrocks, 1982; Toda et al., 1999) and offer a special opportunity for studying factors maintaining species diversity. Several mechanisms account for coexistence on such resources (cf., Richards et al., 2000) including spatio-temporal resource partitioning (Haigh and Maynard Smith, 1972; Tilman, 1994; Amarasekare, 2003) and life history variations (Amarasekare, 2003; Bonsall et al., 2004). Numerous theoretical studies and laboratory experiments have dealt with this topic, but far fewer studies have been conducted in the field because of the complexity of interactions that involve many species. In insect communities, several mechanisms are known to promote coexistence. For example

in dipteran communities, ecological isolation can be achieved through several levels of spatio-temporal heterogeneity (Shorrocks and Charlesworth, 1980), and patterns of interspecific associations among resource patches can be related to density-specific conditions (Sevenster and van Alphen, 1996; Krijger and Sevenster, 2001; Woodcock et al., 2002).

More generally, interspecific competition seems to be a key factor structuring insect communities exploiting ephemeral discrete resources (Hanski, 1987; Shorrocks, 1990; Krijger et al., 2001). This is the case for coexisting sister species that are specialised on a single resource. This includes several seed-predator insects such as globeflower flies (Pellmyr, 1989; Després and Jaeger, 1999), yucca moths (Pellmyr and Leebens-Mack, 2000), fig wasps (Weiblen and Bush, 2002; Molbo et al., 2003) and larch flies (Roques et al., 1995). In these systems, larvae of two or more species that are highly specialised on a host plant, develop by eating the seeds. In most cases, the ecological divergence between species may

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have arisen from competition on a limited resource (Després and Cherif, 2004). Several arguments support this hypothesis for the six European species of the genus *Chiastocheta* that coexist on the globeflower *Trollius europaeus* (Després et al., 2002; Ferdy et al., 2002). Studying the current differences in strategies of resource exploitation among sister species may help us to understand the selective pressures at the origin of the divergence, and the mechanisms that maintain species diversity. The coexistence of *Chiastocheta* species within *T. europaeus* populations is favoured by stronger intraspecific than interspecific competition among larvae (Després and Cherif, 2004). Such competition has been evidenced by a decrease in larval mass with increasing larval densities in a fruit (Després and Cherif, 2004). However, the mechanisms involved in species coexistence are not yet identified. Spatial egg distribution among fruits (= resource patches) does not fully explain coexistence (Johannesen and Loeschcke, 1996; Després and Jaeger, 1999), and additional mechanisms are expected on other spatio-temporal scales. Two mechanisms can be involved in promoting species coexistence: spatial partitioning of the fruit through different larval foraging patterns and temporal partitioning resulting from the shift in oviposition timing among species (Pellmyr, 1989).

In order to determine to what extent larval foraging strategies differ, we quantified larval life history and patterns of resource exploitation for each species. Our first objective was to test on isolated larvae whether the differences in mining patterns, that have been observed when larvae co-occur (Pellmyr, 1989), are intrinsic specific traits. The second objective was to determine the role of specific feeding patterns in spatial partitioning of the fruit. The third was to study the temporal patterns of fruit exploitation by larvae.

2. Material and methods

2.1. Biology of the *Trollius*/*Chiastocheta* association and studied sites

T. europaeus is a hermaphroditic, arctic-alpine species found above 700 m in the Alps. Each plant generally produces one yellow globe-shaped flower with 10–65 carpels containing

about 12 ovules each (Jaeger and Després, 1998). In the study populations flower lifespan was about 7 days, and the flowering period lasted about 3 weeks.

The globe-shaped corolla prevents any insect from entering into the flower, except small flies of the genus *Chiastocheta* which act as the exclusive pollinators (Pellmyr, 1989, 1992; Jaeger and Després, 1998). Females lay their eggs on carpels (cf., Fig. 1A for fruit organisation) and larvae develop on seeds throughout fruit maturation (about 3 weeks). At the end of their development, larvae exit from the fruit and drop into the soil where they overwinter as pupae. Six species that have different oviposition patterns coexist in the Alps. *Chiastocheta rotundiventris* Hennig lays eggs on the first two days of flowering. *C. setifera* Hennig, *C. trollii* Zetterstedt, *C. inermella* Zetterstedt and *C. macropyga* Hennig lay their eggs sequentially from the third to the last day of flowering, while *C. dentifera* Hennig oviposits after (Pellmyr, 1989; Després and Jaeger, 1999). Because they visit the flowers, the early ovipositing species behave as mutualistic pollinators, while late ovipositing species (that lay their eggs on developing fruits after flowering) behave more like parasites.

Larval strategies in resource exploitation were studied in two globeflower populations from the “Massif de la Chartreuse” (French Alps) separated by 2 km: Cherlieu (elevation 1000 m) and Som (elevation 1600 m). Because *C. inermella* and *C. setifera* were present at low abundances (less than 2% of the flies), they were not taken into account in our study.

2.2. Resource availability

In each population, the mean seed production per fruit before predation (gross seed production) was estimated on 50 fruits. It was calculated from five undamaged carpels per fruit, as the number of carpels multiplied by the mean number of seeds per carpel (Pellmyr, 1989). The mean number of ovules per fruit (i.e. unfertilised ovules or aborted seeds) was estimated with the same method. The percentage of fruits that had dehiscing carpels before larva exit, and the mean time between the beginning of dehiscence and larva exit, were calculated on 54 and 59 fruits in Cherlieu and Som, respectively. These fruits were taken from the pool used to study specific larval traits (see below).

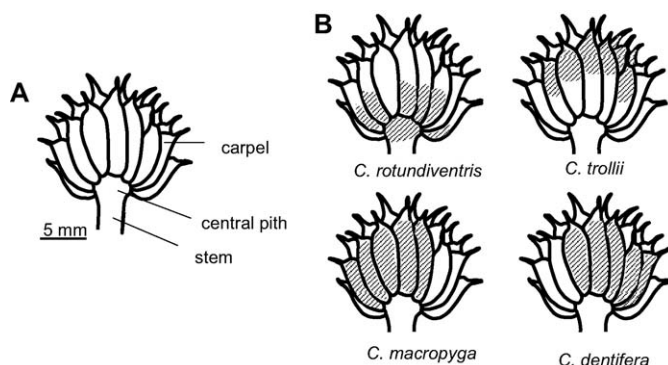


Fig. 1 – A. Mature polycarpic fruit of the globeflower *Trollius europaeus*. B. Foraging patterns of *Chiastocheta* larvae

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