



Local adaptation in oviposition choice of a specialist herbivore: The cinnabar moth



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ABSTRACT

Specialist herbivores feed on a restricted number of related plant species and may suffer food shortage if overexploitation leads to periodic defoliation of their food plants. The density, size and quality of food plants are important factors that determine the host plant choice of specialist herbivores. To explore how all these factors influence their oviposition behaviour, we used the cinnabar moth *Tyria jacobaeae* and the hybrids of a cross between *Jacobaea vulgaris* and *J. aquatica* as a study system. While defoliation by the cinnabar moth is common in the coastal area of The Netherlands, it is relatively rare in inland ragwort population. Ragworts contain pyrrolizidine alkaloids (PAs) and those that are found in coastal areas are rich in jacobine-like PAs while those that occur inland are rich in erucifoline-like PAs. We tested how the oviposition preference was influenced by plant size, nitrogen and water content and PA composition. We used cinnabar moth populations from a regularly defoliated area, Meijndel, and Bertogne, a rarely defoliated area. Our results revealed no effects of nitrogen or water content on oviposition preference. Moths from both populations laid larger egg batches on the plants rich in jacobine-like PAs. Moths from Meijndel preferred larger plants and spread their eggs over more egg batches that were, on average, smaller than those of Bertogne moths. These results suggest that Meijndel moths adopted a oviposition strategy to cope with potential defoliation.

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1. Introduction

Herbivorous insects face a green world as their food source. Generalist insect herbivores feed on a variety of different plant species. Specialist herbivores, in contrast, only feed on one or a restricted number of closely related plant species (Ali and Agrawal, 2012). This constitutes a great advantage for generalist herbivores that can benefit from an apparently unlimited availability and broad source of food while specialists depend on relatively scarce and easily depleted food sources of specialist herbivores (Bernays and Minkenberg, 1997). An advantage of specialist herbivores is that they are adapted to tolerate and use plant defences for their own benefit and on their host plants they suffer less from

interspecific competition (Krieger et al., 1971; Berenbaum et al., 1989).

Yet even then, specialist herbivores are more prone to suffer food shortage (Dempster and Lakhani, 1979). For example, as is common in predator-prey interactions, the overexploitation of a plant food source can lead to its complete defoliation resulting in a decline of its availability (Larvae, 1982; Kosola et al., 2001; Thalmann et al., 2003). This is followed by a crash of the herbivore population due to starvation (Dempster, 1971) which will however, recover in the following years when the populations of the food plant increase in numbers again (Gavloski and Lamb, 2000; Becklin and Kirkpatrick, 2006). Specialist herbivores have evolved oviposition strategies to avoid extinction. They can select larger plants (Kessler and Baldwin, 2002; Anthes et al., 2003) and adapt egg batch size to the features of the host plant (Pilson and Rausher, 1988). For example, if faced with a low plant density, the amount of eggs per plant will be larger as the search for scattered host plants is time-consuming and thus, costly.

Another key factor influencing the fecundity of herbivores is

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host plant quality (Awmack and Leather, 2002; Macel et al., 2002). For herbivores, plant quality is associated with its nutrient and water content as well as with the concentration of secondary metabolites (Coley and Barone, 1996; Coley et al., 2006). Plant quality strongly affects oviposition choice (Awmack and Leather, 2002). For example, larger egg batches are laid on high quality hosts since they can potentially support more offspring (Pilson and Rausher, 1988).

To investigate how the size and quality of food plants influence the oviposition behaviour of specialist herbivores, we used the cinnabar moth *Tyria jacobaeae* and the hybrids of a cross between *Jacobaea vulgaris* and *J. aquatica* as a study system. We used this system because in a F2 hybrid populations characteristics segregate independently and can therefore be studied against a common genetic background (Cheng et al., 2011). In coastal areas, ragwort density is high and defoliation by the cinnabar moth is common while inland ragwort density is lower and defoliation is rare. The content of pyrrolizidine alkaloids (PAs), a diverse but structurally-related group of secondary metabolites in ragwort, differs between the two areas. Coastal ragworts are often rich in jacobine-like PAs while those rich in erucifoline-like PAs are predominant in inland ragworts (Witte et al., 1992; Vrieling and Boer, 1999; Macel et al., 2004).

To test whether the different habitats of ragworts selected for different oviposition strategies of the cinnabar moth, we used moth populations from Meijendel, a regularly defoliated coastal area and Bertogne, a rarely defoliated inland area. From the hybrids system we choose genotypes rich in jacobine- or erucifoline-like PAs. We addressed the following questions: Is the oviposition preference of cinnabar moths related to the size of host plants and to the plant quality (PA concentration and composition, water content and nitrogen content)? If so, do cinnabar moths from Meijendel and Bertogne differ in their oviposition choices?

2. Materials and methods

2.1. Plant sources and growing

The genotypes used in the oviposition bioassay were propagated from a cross between *Jacobaea vulgaris* and *Jacobaea aquatica* that are maintained in tissue culture (Cheng et al., 2011). Both species are equally suitable as host plants for the cinnabar moth in laboratory rearings (Macel et al., 2002). Each hybrid was cloned to obtain replicated individuals. Clonal lines are hereafter referred to as 'genotypes'.

All the genotypes in this hybrid system reveal a large range in biomass and variation in PA concentration and composition (Cheng et al., 2011) of which we made use by selecting plants with different PA profiles. For this bioassay, 20 genotypes were selected from tissue culture. Cheng et al. (2011) measured for all the genotypes in tissue culture the different PA concentrations and shoot mass. Based on these data all the hybrid genotypes were sorted by the total amount of erucifoline-like PAs from the lowest to the highest. Considering also the total PA amount and fresh weight of shoots of the selected genotypes, 10 genotypes with high jacobine-like PAs and low erucifoline-like PAs were chosen, and another 10 genotypes were selected with low jacobine-like PAs and high erucifoline-like PAs concentration. Care was taken to keep the amount of PAs and shoot biomass between the two groups as similar as possible.

The 20 genotypes were cloned into 4 replicated individuals respectively. Plants were transferred to 0.8 L pots filled with a mixture of 95% sandy soil (collected from Meijendel), 5% potting soil (Slingerland Potgrond company, Zoeterwoude, The Netherlands) and 1.5 g/L Osmocote slow release fertilizer

(N:P:K = 15:9:11; Scott[®], Scotts Miracle-Gro, Marysville, Ohio, USA). They were grown in a climate room (relative humidity: 70%, light 16 h/dark 8 h, 20°C/20 °C regime) for 6 weeks and then transferred to a greenhouse with natural light one week before the start of the oviposition bioassay.

2.2. Herbivore origin and rearing

The cinnabar moth *Tyria jacobaeae* L., is a specialist univoltine herbivore that feeds mainly on common ragwort (*Jacobaea vulgaris*, formerly known as *Senecio jacobaea*) and a restricted number of other *Jacobaea* species (Macel et al., 2002; Vrieling, 2006). The life cycle includes 8 stages: egg, 5 larval stages, pupa, and adult. Moths emerge from the overwintering pupal stage at the beginning of May. Females lay eggs from mid May until mid June in egg batches on the undersides of the more basal leaves (Dempster, 1982). Eggs need about 4–20 days to hatch depending on the temperature (Rose, 1978). Larval stages 1 through 4 each last 4–5 days, while the fifth larval stage lasts 5–9 days (Karacetin, 2007). They pupate in cocoons on the ground, and spend the winter in the pupal stage before emerging as adult moths in the following year (Haccou and Hemerik, 1985).

The larvae of the cinnabar moth are completely dependent on ragwort as their food source (Dempster, 1971; Van Der Meijden et al., 1990). Late fifth instar larvae were collected in the coastal dunes of Meijendel (52°48'38"N, 4°41'7"E, The Netherlands) and in Bertogne (50°05'27"N, 5°40'29"E, Belgium) that are approximately 300 km apart. Dispersal of adult cinnabar moths are quite restricted. Rudd and McEvoy (1996) estimated dispersal of adults to be less than 500 m. We therefore assume that gene flow between the Meijendel and Bertogne populations is virtually absent. The larvae were kept in glass tubes until pupation; the pupae were then stored in a cold room for 10 months (light/dark, 16 h/8 h, 4 °C) (Zoelen and Kusters, 1986). After this, they were removed and sexed before hatching. They were placed in transparent plastic cages (70°70°50 cm) and kept at room temperature under natural light. Moths started to emerge after 2 weeks, and fed with water and honey. In total, 44 male and 44 female moths were selected from the Meijendel population and 34 male and 34 female moths from the Bertogne population; all were active and healthy.

2.3. Oviposition bioassay

The bioassay was conducted in 4 plastic cages (87 cm diameter, 1 m height) covered with gauze in a greenhouse. The setup was the same as that of Cheng et al. (2013). Each cage contained one clonal replicate of each of the high jacobine-like PA content genotypes and one of each of the high erucifoline-like PA content genotypes. An equal number of moths collected from the populations of Meijendel or from the populations of Bertogne were released into two separate cages each. Plants were watered every three days throughout the bioassay. The cages were rotated by 90° every 3 days to avoid position effects on oviposition. After 10 days, the moths were removed and the plants were harvested. Photographs of all the leaves with eggs were used to count the number of egg batches per leaf and the eggs per batch.

The fresh weight, diameter of the shoots and number of leaves were recorded. For PA and nitrogen determination, 2 leaves (from the fourth to eighth leaf) were collected, frozen with liquid nitrogen and lyophilized at –80 °C in a freeze dryer (Cryotheque[®], Sniders Scientific Company, Tilburg, The Netherlands) for 4 days. The samples were then ground to a fine powder and stored at –20 °C freezer until measurement. The remaining leaf material was dried in an oven at 50 °C for 4 days. The dry mass of the shoot was obtained by adding the mass of all the leaves. The water content (%)

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