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Effects of host-plant population size and plant sex on a specialist leaf-miner

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ABSTRACT

Animal population density has been related to resource patch size through various hypotheses such as those derived from island biogeography and resource concentration theory. This theoretical framework can be also applied to plant–herbivore interactions, and it can be modified by the sex of the host-plant, and density-dependent relationships. Leaf-miners are specialised herbivores that leave distinct traces on infested leaves in the form of egg scars, mines, signs of predation and emergence holes. This allows the life cycle of the insect to be reconstructed and the success at the different stages to be estimated. The main stages of the leaf-miner *Phytomyza ilicis* were recorded in eleven populations of the evergreen host *Ilex aquifolium* in Denmark. Survival rates were calculated and related to population size, sex of the host plant, and egg and mine densities. Host population size was negatively related to leaf-miner prevalence, with larger egg and mine densities in small populations. Percentage of eggs hatching and developing into mines, and percentage of adult flies emerging from mines also differed among host populations, but were not related to population size or host cover. Feeding punctures left by adults were marginally more frequent on male plants, whereas egg scars and mines were more common on females. Overall survival rate from egg stage to adult emergence was higher on female plants. Egg density was negatively correlated with hatching, while mine density was positively correlated with emergence of the larvae. The inverse effects of host population size were not in line with predictions based on island biogeography and resource concentration theory. We discuss how a thorough knowledge of the immigration behaviour of this fly might help to understand the patterns found.

1. Introduction

Animal population density has been related to resource patch size through diverse hypotheses leading to different predictions. Island biogeography (MacArthur and Wilson, 1967), density compensation phenomenon (MacArthur et al., 1972), resource concentration theory (Root, 1973), and mixed hypotheses derived from them, have been interpreted and applied broadly to a variety of spatial scales and taxa. This includes plant–herbivore interactions, suggesting a diversity of factors and conditions acting at the same time, and influencing animal population densities (see reviews by Connor et al., 2000; Gaston and Matter, 2002). (1) According to island biogeography, herbivore abundance is expected to increase linearly with the population size of the host plant, such that density should be constant with area (MacArthur and Wilson, 1967). (2) Following from this, the density compensation hypothesis accounts for observations that the accumulated density of herbivore species on small islands or habitat patches equals that of a larger island or habitat patch. Since total number of species is expected to be lower in smaller islands, the average population density of each species should be greater on smaller islands or patches if herbivore density would be independent of island size (MacArthur et al., 1972). (3) Related to these theories, but only focusing on plant–animal interactions, the 'resource concentration hypothesis' (Root, 1973) describes an insect–plant feedback mechanism whereby "herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands", suggesting that small host populations are difficult for a specialist herbivore to detect, which, eventually, might lead to disproportionally lower densities of the specialist in these small populations. (4) The 'trophic-level hypothesis of island biogeography' takes this idea further, setting it into a food web framework. It suggests that organisms in a relatively higher trophic position in the food web (specialist herbivores in this case) may suffer more from reduction in habitat area and isolation of populations than organisms in

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a lower trophic position (their hosts in this case) (Holt, 1996; Carlsson-Granér and Thrall, 2002). This could be caused by inverse density effects leading to a loss of genetic variability and demographic stochasticity.

These hypotheses (with the exception of the density compensation hypothesis when considering individual species) predict a neutral or positive relationship between host-plant population size and herbivore density, whereas empirical results on effects of plant population size are equivocal: Small plant population size has been related to low densities of pollinators or fruit dispersers, which reduces plant reproductive success (Olesen and Jain, 1994; Kearns et al., 1998). Small plant populations have also been associated with lower incidence of seed predation and diseases, which would increase plant fitness (Kéry et al., 2001; Colling and Matthies, 2004). However, there are also several studies that failed to find any effect of plant population size (Benitez-Malvido, 1998) or reported negative correlations (Dooley and Bowers, 1998; reviewed by Bowers and Matter, 1997; Bender et al., 1998; Debinski and Holt, 2000).

Immigration behaviour has been proposed as an additional factor influencing the effects of plant population size on plant–animal interactions, in order to explain apparently contradictory results (Bowman et al., 2002). This hypothesis considers the probability of patch interception as proportional to a linear patch dimension rather than to patch area. Since patch area increases quadratically with its linear dimension, the number of immigrants per unit area would decrease with increasing patch size, leading to a negative relationship between host patch size and the population density of a specific herbivore. An exception could be organisms with active searching behaviour which enables them to detect a preferred habitat or resource from some distance (Bowman et al., 2002). There are other factors besides immigration that can affect density (i.e. birth, death, emigration), and these may also differ with patch size, resulting in a different final pattern. The hypothesis therefore applies particularly to situations in which immigration is the dominant process, and should be treated with caution in other cases. Nevertheless, it is frequently suggested that immigration has important effects on population density in habitat fragments, even for established populations (Fahrig and Paloheimo, 1988; Bowman et al., 2002 and references therein).

In dioecious plant species effects of population size might be modified by the sex ratio of the host. This is due to sexual differences in plant palatability, with the larger reproductive allocation in females forcing them to grow slower, with higher leaf concentration of carbon-based secondary metabolites (Reekie and Bazzaz, 1987a) and lower nitrogen concentration (Reekie and Bazzaz, 1987b; reviewed by Ågren et al., 1999; Cornelissen and Stiling, 2005). Empirical studies have shown that male plants are often more damaged by herbivores, although the mechanism is not yet completely clear. Moreover, if there is a sexual difference in food quality, then herbivores should perform better on the preferred sex. However, the only two studies that have compared herbivore performance in dioecious plants do not support this hypothesis, although the herbivores showed a clear preference for male leaves (Krischik and Denno, 1990; Strauss, 1990). However, these studies only considered one aspect of the life cycle of the herbivore, i.e. adult fecundity in the first study, and larval growth and survival in the second. To add some more complexity, any gender-biased activity of the herbivore and any population size effect may be modulated by the density dependence of the insect population.

The relative effects and potential interactions of host population size, plant sex and density dependence of a monophagous herbivore have not been studied before, and are the aim of our study. We will focus on the monophagous holly leaf-miner (*Phytomyza ilicis* Curtis, Diptera: Agromyzidae) and its host plant, the European holly (*Ilex aquifolium* L., Aquifoliaceae; Cameron, 1939). Macroecological variation (Brewer and Gaston, 2002), population dynamics (Valladares and Lawton, 1991; Brewer and Gaston, 2003), and abiotic factors controlling this interaction are well understood (Klok et al., 2003). There is also some evidence that egg and mine density can limit the final success of the leaf-miner (Valladares and Lawton, 1991; Eber, 2004). However, nothing is known about potential effects of population size and sex of the host plant on final density. In this paper we test the following hypotheses: (1) leaf-miner density is lower in small populations of the host plant; (2) the leaf-miner prefers male plants; (3) leaf mining is less successful in females; and (4) low egg and mine densities lead to increased hatching and higher larval emergence rates.

2. Material and methods

2.1. Leaf-miner

Leaf-miners are immature stages of moths, beetles, flies or sawflies that feed on tissue between the upper and lower surface of leaves (Needham et al., 1928; Connor and Taverner, 1997). They usually cause little damage, but some species are pests on ornamental shrubs and trees (Weintraub and Horowitz, 1995; Eber et al., 2001; Salvo and Valladares, 2007). Leaf-miners leave characteristic signatures on infested leaves in the form of egg scars, mines, signs of predation and emergence holes. This allows reconstruction of the life cycle of the insect and estimation of their success at the different stages, especially on evergreen hosts. Monophagous leaf-miners can also be used for studying plant–herbivore interactions over large areas (Brewer and Gaston, 2002, 2003; Gaston et al., 2004).

The holly leaf-miner (*P. ilicis* Curtis, Diptera: Agromyzidae) is a small fly, which is a specialist herbivore on the dioecious evergreen European holly (*I. aquifolium* L., Aquifoliaceae; Cameron, 1939). The insect is monophagous, and thus its geographical range and local distribution are limited by the presence of the host species. The leaf-miner has the following main developmental stages: In summer, adult females damage leaves with their ovipositors, causing small punctures from which sap exudes. Both males and females feed on leaf sap, and after healing the puncture looks like a pock mark; large numbers of punctures lead to stunted or twisted leaves. At the same time, females lay eggs in the midrib of young leaves, resulting in another type of scar. In late summer, the maggots eat and form mines from the midrib to other central parts of the leaf. The larvae pupate in March, and in late May until early June new adults emerge, leaving round holes of around 1 mm diameter.

Some maggots become parasitized, and their mines remain small and undeveloped; the most common parasitoid is *Chrysocharis gemma* (Hymenoptera: Eulophidae; Eber et al., 2001). Some larvae are eaten by birds, resulting in open mines with a V-form mark. Maggot death due to parasitoids can happen at any stage of larval development, while bird predation occurs most often in late spring. The dispersing adult flies cover distances of at least several hundred meters (Eber, 2004).

2.2. Host plant

I. aquifolium is a shrub or small tree (<25 m height, <250 years) that occurs sparsely but usually gregariously in deciduous forests of western and southern Europe (Peterken, 1966). Its north-eastern border in Denmark has been associated with winter frost (Iversen, 1944; Peterken and Tubbs, 1965; Walther et al., 2005). Naturally, the species is most common in old-grown beech forests on moist, nutrient-rich soils (Lawesson, 2000; Arrieta and Suárez, 2004), but it is also found in other forest types suggesting a relatively broad habitat niche (Bañuelos et al., 2004). Seeds are dispersed mainly by