Acta Oecologica 55 (2014) 15–22

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Host selection by the pine processionary moth enhances larval performance: An experiment

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ARTICLE INFO

Article history:
Received 7 December 2011
Accepted 28 October 2013
Available online 15 November 2013

Keywords:
Developmental plasticity
Maternal effects
Phenotypic plasticity
Preference-performance relationships

ABSTRACT

The development of a phytophagous insect depends on the nutritional characteristics of plants on which it feeds. Offspring from different females, however, may vary in their ability to develop in different host species and therefore females should place their eggs on host plants that result in the highest performance for the insect offspring. Causes underlying the predicted relationships between host selection and offspring performance may be: (1) a genetic association between larval ability to exploit particular hosts and the female insect's host preference; and (2) phenotypic plasticity of larvae that may be due to (a) maternal effects (e.g. differential investment in eggs) or (b) diet. In this work, we analyse the performance (i.e. hatching success and larval size and mortality) of the pine processionary (*Thaumetopoea pityocampa*) caterpillar developing in Aleppo (*Pinus halepensis*) or maritime (*Pinus pinaster*) pines. Larvae of this moth species do not move from the individual pine selected by the mother for oviposition. By means of cross-fostering experiments of eggs batches and silk nests of larvae between these two pine species, we explored whether phenotypic plasticity of offspring traits or genetic correlations between mother and offspring traits account for variation in developmental characteristics of caterpillars. Our results showed that females preferentially selected Aleppo pine for oviposition. Moreover, the offspring had the highest probability of survival and reached a larger body size in this pine species independently of whether or not batches were experimentally cross-fostered. Notably, the interaction between identity of donor and receiver pine species of larvae nests explained a significant proportion of variance of larval size and mortality, suggesting a role of diet-induced phenotypic plasticity of the hatchlings. These results suggest that both female selection of the more appropriate pine species and phenotypic plasticity of larva explain the performance of pine processionary caterpillars.

1. Introduction

Host selection by phytophagous insects is the result of the specificity of the insect species and of the morphological and chemical defences used by plants. Plant defences include morphological traits, such as thorns, spines, surface waxes, silica, trichomes, etc., and chemical traits such as phenolics, non-protein amino acids, and terpenoids, all of which reduce leaf digestibility or can be directly toxic to most herbivores (Bernays and Chapman, 1994; Schoonhoven et al., 1998). Herbivores, however, have evolved traits that allow them to counteract host defences and increase their feeding efficiency on host plants. These strategies include, detoxification mechanisms of plant compounds, morphological adaptations to avoid plant barriers, and the choice of non-defensive phenotypes (Karban and Agrawal, 2002). Moreover, some morphological traits of herbivores allow them to exploit particular host plants (Karban and Agrawal, 2002), as suggested by the striking correspondence between feeding morphologies of different species and the type of food ingested (Bernays, 1991); relationships that indicate an essential role of host selection in coevolutionary patterns.

Immature offspring of many insect species have limited movement capacity (i.e. Lepidoptera larvae) and, consequently, their appropriate development depends largely on the characteristics of host plants selected for oviposition by their mothers (Jaenike, 1978; Mayhew, 2001). Adaptive host selection for oviposition has been studied in many different herbivorous insect-plant systems (Jaenike, 1978; Ng, 1988; Thompson, 1988; Mayhew, 1997) by exploring the predicted positive relationship between female preference and offspring performance (growth and survival);

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1146-609X/$ – see front matter
http://dx.doi.org/10.1016/j.actao.2013.10.006

prediction that has received mixed support (Mayhew, 1997). Several ecological and behavioural factors have been proposed to explain the frequently detected mismatch in host selection (Thompson, 1988; Craig and Itami, 2008; Gripenberg et al., 2010). Females, for instance, might select the host plants that provide poor growth but good protection against predators or other natural enemies (Bernays and Graham, 1988). Females may also choose host plants that enhance their own fitness, which depends not on offspring performance alone, as demonstrated experimentally by Scheirs et al. (2000). A non-adaptive explanation is the possibility of real mistakes in host selection by females; i.e. when a female selects an inadequate plant for the development of their offspring (Larsson and Ekbom, 1995; Hódar et al., 2002).

The predicted relationship between host selection by females and offspring performance may be due to a genetic association between females' preferences and offspring ability to exploit the preferred host, or to phenotypic plasticity of the larvae. The evolution of plastic phenotypic traits allowing the optimal use of morphologically and chemically different plants is likely for phytophagous insects (Gold, 1979; Fry, 1989). Herbivorous larvae may alter their morphology and physiology by expressing the most appropriate phenotype to exploit the particular plant species where they grow (i.e. diet-induced phenotypic plasticity; see Hazel et al., 1990; Moczek, 1998). A genetic component of host preferences may also influence non-plastic traits of larvae, enhancing development in particular host plant. In this case, however, erroneous host selection by females would have disastrous consequences for their offspring. Thus, phenotypic plasticity of developing larvae and/or correct host selection by gravid females (i.e. genetic correlation between mother preferences for oviposition and offspring characteristics) may therefore be vital even for species using a single host species of plant because of intraspecific variation in host defences (Myszewski et al., 2002; Scriber, 2002).

The selection of different pine species by pine processionary moths (*Thaumetopoea pityocampa* Schiff.) has been previously explored (e.g. Mendel, 1988; Tiberi et al., 1999; Paiva et al., 2011), leading us here to study the preference of gravid females towards two of its commonly used host species: the Aleppo pine (*Pinus halepensis* Miller) and the maritime pine (*Pinus pinaster* Aiton). The aim of this article is to elucidate the consequences of host selection by females for larval performance and success. In this sense, by means of cross-fostering experiments of batches and larval silk nests, we seek to determine the relative importance that host selection and phenotypic plasticity of developing larva exert on offspring performance.

The hypothesis of optimal host selection in the pine processionary moth implies a relationship between preferences of the female moths and offspring performance. Thus, (i) Hatching success, survival, growth rate, and final caterpillar size should be higher in the preferred pine species (Prediction 1). Moreover, if the females' preferences are related to larval ability to exploit a particular host (because of either, a genetic correlation between adult and offspring traits or maternally induced phenotypic plasticity), (ii) larvae should perform much better in the pine species that the mother selected for oviposition than in the other pine species (Prediction 2). (iii) Based on diet-induced plasticity, if larvae plastically adapt traits related to host exploitation, a change of partially developed nests from one tree species to another should decrease larval growth and survival (Prediction 3). Finally, diet-induced phenotypic plasticity in larval development may also allow optimization of traits that enhance individual host exploitation. In this case, (iv) the change of individual pine should explain, at least partially, the effects of cross-fostering experiments of larval nests (Prediction 4).

2. Materials and methods

2.1. Study area

The fieldwork was conducted in the high-altitude plateau of Hoya de Guadix (37°18′N, 3°11′W), Spain, at approximately 1000 m a.s.l., under a semi-arid climate. In this area, there are two pine species susceptible of pine-processionary moth attacks, the Aleppo pine and the maritime pine, though the former is the most abundant, representing around 90% of individuals. The trees are quite regularly distributed (i.e. spacing of c. 4–5 m) within the study area, with the maritime pines usually being surrounded Aleppo pines, which are more abundant (c. 9:1). Our study zone is a young forestation area (25 year old) of 118.9 ha. The trees average 4 m in height with a tree density of around 625 trees per ha. The terrain is steep (12.7% in average) with a predominantly east-west orientation. To standardize the conditions of exposure to sunlight and rainfall, we used only pines located in plain areas.

2.2. Study species

Larvae of the pine processionary moth feed on *Pinus* and *Cedrus* needles (Devkota and Schmidt, 1990) throughout the Mediterranean region and southern Europe, implying a serious socioeconomic impact, due not only to major economic losses on pine plantations (Buxton, 1983; Kanat et al., 2005; Gatto et al., 2009), but also because processionary larvae from the 3rd instar onwards posses urticating hairs (Lamy, 1990; Pérez-Contreras and Tierno de Figueroa, 1997; Vega et al., 2000), which can provoke important public health problems. Pine processionary moth females lay their eggs in a single batch and, in our study population, prefer host plants of rapid growth and with the longest needles for oviposition (Pérez-Contreras et al., 2008). Other authors suggest that the female moth is able to select its host by following visual (Démolin, 1969) or olfactory cues (Paiva et al., 2011), or even at random due to the eruptive population dynamics of this species (Hódar et al., 2002). The number of eggs per batch is highly variable (reviewed in Schmidt et al., 1999), fluctuating among regions and years (Arnaldo and Torres, 2006); in our study population numbers varied between 77 and 263 eggs (Pérez-Contreras and Soler, 2004). Adult females of the pine processionary moth have a very short life of typically one night (Stastny et al., 2006) and disperse on average 300 m from pupation sites (Démolin, 1969). Adult males, on the other hand, live longer and appear to fly greater distances than do females (Démolin, 1969). The eggs of the pine processionary moth hatch after 5–6 weeks (Schmidt, 1989), the larvae feed on needles, and their development involves five instars.

The Aleppo pine is a species widely distributed throughout Central and Southern Europe. This species is quite resistant to the drought and can grow in soils extremely poor in nutrients (López-González, 1982). The maritime pine has a more reduced distribution than the Aleppo pine, being more often present in rainy areas and less resistant to drought and frost than is Aleppo pine. The needles of Aleppo pine are softer and less fibrous (Franco, 1986), with a lower amount of resin than those of the maritime pine. Thus, the Aleppo pine would *a priori* be considered the more appropriate host for developing larvae of processionary pine.

2.3. General procedures

In the study population, we selected four different groups of pines that were used for different purposes (see Appendix). The first one included 200 randomly selected pines of the mixed plantation reflected relative abundance of the two pine species in the study area [18 maritime pines (9%) and 182 Aleppo pines (91%)].