

# Host-plant use in the range expansion of the pine processionary moth, *Thaumetopoea pityocampa*

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**Abstract.** 1. During range expansions of phytophagous insects, secondary or novel hosts may allow colonisation of areas without primary hosts. Because plant species often differ in their relative attractiveness and suitability for insects, insect preference for, and performance on, these hosts can determine recruitment potential in the current and future expansion areas.

2. This study explores the relative roles of female preference and larval performance in an important pine defoliator, *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Lepidoptera, Notodontidae), which colonises three *Pinus* species at its current range margin in the Italian Alps: *P. nigra* (primary host), *P. sylvestris* (secondary host), and *P. mugo* (novel host).

3. Host use patterns in multiple insect populations were studied through choice and no-choice oviposition experiments in cages, field surveys of mixed stands, and laboratory and field monitoring of larval growth and mortality. It was predicted that a specific life-history trait – time limitation of short-lived females to lay a single batch of eggs – would act as a component of female performance, and lead to similar rates of host acceptance in no-choice settings.

4. In the choice experiment, *P. nigra* was accepted the most frequently while *P. sylvestris* was accepted the least frequently, confirming nest density patterns in the field. Contrary to prediction, females remained discriminating in no-choice settings in spite of time limitation. In contrast, relative growth rate (RGR) and mortality of larvae did not differ significantly among the three hosts, highlighting a discrepancy between female preference and larval performance.

5. Recruitment potential of *T. pityocampa* in future expansion into stands of *P. sylvestris* and *P. mugo* is evaluated by combining host quality, conservatism in oviposition behaviour, habitat suitability, and the opportunity for local adaptation.

**Key words.** Female longevity, host plants, host preference, larval performance, life history, oviposition, *Pinus nigra*, *Pinus sylvestris*, *Pinus mugo*, range expansion.

## Introduction

Many organisms depend on a single, or select few, species for food or other resources, with their distributions at least in part

dictated by the availability of other species. For instance, specialised and oligophagous insect herbivores occur in regions that coincide with the geographic ranges of their host plant(s) (Koizumi *et al.*, 1999), and their local abundance often reflects the relative abundances of their preferred hosts (Strong *et al.*, 1984). Periodically, species may undergo expansions or shifts in their geographic ranges. Recent range expansions have been reported in a number of herbivorous insects, and attributed mainly

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to climate change (Thomas *et al.*, 2001; Root *et al.*, 2003; Battisti *et al.*, 2005) and human-caused habitat expansion (Gutiérrez & Thomas, 2000). As insect herbivores colonise new areas, they may encounter novel host plants, and, except in the case of strict specialists, will often accept those that are closely related to their original host(s) (Scriber & Ordling, 2005). Oligophagous species, in particular, may find potential hosts even in areas where their original or preferred hosts are absent or much less abundant. The availability of the new hosts can thus facilitate further expansion into regions beyond the geographic range of the original hosts (Gutiérrez & Thomas, 2000).

At least in theory, ovipositing females are expected to prefer hosts that are the most suitable for larval development, and accept less suitable plant species only when the optimal (preferred) host is either absent or not found (Jaenike, 1978; Thompson, 1988; Awmack & Leather, 2002; but see Courtney & Kibota, 1989; Scheirs & De Bruyn, 2002). Host recognition and preferential oviposition should then lead to hierarchies of host use, and these hierarchies should be reflected in the frequency of host acceptance and measures of larval performance, such as larval mortality or relative growth rate (e.g. Jaenike, 1990; Thompson & Pellmyr, 1991). However, a novel host encountered during range expansion may fall anywhere within the preference–performance hierarchy because of the lack of common evolutionary history (Thompson, 1996).

As the range of an insect herbivore expands, habitats with multiple hosts may be replaced with single-host habitats in which the preferred host is missing and only the less preferred (or novel) host is present. Consequently, females may only encounter hosts perceived as less attractive in a multi-host setting. If discrimination among hosts is behaviourally relatively fixed, one might expect that the preference hierarchy will still hold. Accordingly, the relative frequencies of females that accept each host for oviposition in a single-host (no-choice) setting should reflect the degree to which that host is accepted in a multi-host (choice) setting. On the other hand, a number of models of parasite–host systems predict that certain life-history traits, such as egg load or longevity, may cause females to adaptively modify their host (or habitat) preference hierarchy (Levins & MacArthur, 1969; Ward, 1987; Mangel, 1989; Jaenike, 1990; Carriere, 1998), and to accept hosts more indiscriminately if not presented with a choice (e.g. Díaz-Fleischer & Aluja, 2003). For instance, species in which females are extremely short-lived as adults are under a strong time limitation to oviposit (Courtney, 1982; Leather & Burnand, 1987; Wiggins, 1997; Scheirs & De Bruyn, 2002; Jervis *et al.*, 2005). Persistent rejection of less attractive hosts may then severely compromise their realised fecundity, because strongly discriminating females may never encounter a more attractive host, or even another less attractive host, and may be exposed to other risks, such as predation and inclement weather. In such time-limited species, the original hierarchy of female preference in a multi-host setting may therefore break down in a single-host setting, and the differences in acceptance of each host may disappear.

In the context of this theoretical framework, the present study investigated the patterns of host use of the winter pine processionary moth (*Thaumetopoea pityocampa* Denis & Schiffermüller), an economically important defoliator of pines (*Pinus* spp.) in

southern Europe. This insect has been expanding its latitudinal and altitudinal range in the Italian Alps over recent decades (Benigni & Battisti, 1999; Battisti *et al.*, 2005). In this region, *T. pityocampa* is typically associated with Austrian black pine, *Pinus nigra* Arnold (Masutti & Battisti, 1990). However, in the course of the recent expansion, it has been increasingly encountering and colonising two other pine species: *P. sylvestris* L. (Scots pine), which historically represented a secondary host utilised less frequently and mostly at the margins of the past range of *T. pityocampa*, and a novel host *P. mugo* Turra (mountain pine), which was only rarely colonised in the past and probably did not support any viable populations. While population densities and outbreak frequencies vary among the host species (Masutti & Battisti, 1990), it is unclear whether these differences are driven by oviposition preference, larval performance, a combination of both, or by other factors. Importantly, females typically live only one night, and therefore are under strong time limitation to locate and accept a host on which to lay their single batch of eggs.

To evaluate the relative role of host attractiveness and suitability in the patterns of host use by *T. pityocampa* in the Italian Alps, and to provide a basis for predictions on future expansion, the following series of tests were designed. First, the utilisation of the three hosts in mixed stands at two sites in the expansion range were assessed. Subsequently, it was tested whether the hierarchy of host use at these sites was consistent with female *T. pityocampa* discrimination among the three hosts in controlled experiments. If the natural densities of the insect on the three hosts were driven primarily by differential female preference, the highest frequency of oviposition would be expected on the preferred host (*P. nigra*), relative to the secondary host (*P. sylvestris*) or the novel host (*P. mugo*). Second, oviposition rates were compared on each of the three hosts when females were not presented with a choice. Specifically, the following hypothesis was tested: due to limited female longevity, the original preference hierarchy in *T. pityocampa* would break down in a single-host (expansion) situation and frequency of oviposition would be similar on all three hosts. Finally, to check whether the observed preference patterns reflect the relative suitability of the hosts, larval performance on the three hosts were compared, both in laboratory and field experiments. If female oviposition patterns consistently showed little differentiation (hierarchy) in the controlled experiments, the natural colonisation pattern could be driven largely by differential larval survival on the three hosts. However, if clear hierarchies in female preference were detected, larval performance could either counteract or amplify oviposition preference in the overall patterns of host use. The findings are discussed in the context of *T. pityocampa*'s ecology, and a synthetic perspective on its future expansion on the secondary and novel hosts in the Alps are presented.

## Methods

### Study system

*Thaumetopoea pityocampa* is a univoltine Lepidopteran oligophage on coniferous trees. Its main hosts in the study areas

are *Pinus* spp., but it can also attack *Cedrus* spp. and the introduced *Pseudotsuga menziesii* (Roques *et al.*, 2002). Emergence of adults occurs after dusk, and females typically live only one night (Démolin, 1969). After mating, females disperse by flight to search for a suitable host on which they lay their single batch of 210–280 eggs (Masutti & Battisti, 1990). The larvae feed gregariously during autumn and winter, and construct a conspicuous silk nest, typically near the tip of a branch or treetop. *Thaumetopoea pityocampa* frequently reaches outbreak densities throughout the Mediterranean basin, and now extends its range well into the southern Alps and central France. Defoliation by the late larval instars can reduce tree growth (Laurent-Hervouet, 1986), and the larvae produce urticating hairs that can cause an allergic reaction (contact dermatitis) and pose a public health risk (Lamy, 1990). Because of its economic and medical importance, *T. pityocampa* populations have been monitored for many years, by means of winter nest censuses and pheromone trapping, as part of pest management programmes throughout the Mediterranean region.

*Pinus nigra* is considered the primary native host of *T. pityocampa* in the study area, and the planting of *P. nigra* outside its native range in the eastern Alps into many reforested regions of northern Italy has promoted population growth and outbreaks of *T. pityocampa* (Masutti & Battisti, 1990). Especially in mixed stands, it has also led to increased colonisation and defoliation of the native *P. sylvestris*, which is at the southern edge of its distribution in Italy, and has historically been a secondary host for *T. pityocampa*, generally colonised at lower densities and in only certain parts of the insect's former range (Démolin, 1969). In contrast, oviposition has been reported only infrequently on *P. mugo*. This pine is primarily a subalpine species with a restricted distribution largely outside the original range of *T. pityocampa*. Until recently, it was considered unsuitable for larval development due to climatic factors (especially snow cover) (Masutti & Battisti, 1990; A. Battisti, pers. obs.).

#### Nest census

Colonisation of trees by *T. pityocampa* under mixed-stand conditions was surveyed in two censuses of winter nests (Table 1). Winter nests can be detected easily even at low population densities (Geri & Millier, 1985); in contrast, egg batches are inconspicuous and difficult to detect except on small trees. While a nest census likely underestimates the initial number of egg batches laid, due to early larval mortality, a previous study (Benigni & Battisti, 1999) did not detect any differences in overall larval mortality among the three pine species.

The first census was conducted in October 2004 at a site near Rovereto, Italy, at the edge of the historical range of the insect. Here, all three hosts grew intermixed at a low density (mean distance between trees  $4.7 \pm 0.27$  m), with *P. nigra* and *P. sylvestris* reaching 1.5–5 m in height, and the shrub-like *P. mugo* reaching 1–2 m. The number of nests present was assessed on all trees inside a randomly chosen area of about 0.4 ha, comprising 35 *P. mugo*, 58 *P. nigra*, and 55 *P. sylvestris* trees. The height of each tree was also measured to account for likely differences in apparency among the hosts; visual cues

guide female host search before alighting (Démolin, 1969; A. Battisti, unpublished).

The second census was carried out in November 2004 at a site in Venosta Valley, Italy, within the new range of the insect following a recent range expansion. Only *P. nigra* and *P. sylvestris* grew in this region. A 3-ha site with natural regeneration was chosen, with isolated trees 3–8 m in height, growing in a transition between a meadow and a continuous pine stand. Nests on 58 *P. nigra* and 58 *P. sylvestris* trees selected at random within the site were counted.

#### Choice and no-choice experiments

To compare the results of nest surveys (natural colonisation patterns) with female oviposition preference, choice and no-choice experiments were designed in outdoor enclosures, in which confounding effects and standardised host parameters were minimised. The experiments were carried out on the campus of the University of Padova, Agripolis Legnaro, in four large, tunnel-shaped cages. A  $1 \times 1$  mm mesh net (Artes Politecnica, Santorso Vicenza, Italy) allowed near-ambient light and temperature conditions, and a black landscaping tarp (Artes Politecnica) covered the floor of the cages. Each cage was divided into two sections of  $6 \times 4 \times 2.7$  m, providing a total of eight rooms in which experiments could be carried out simultaneously.

#### Insect material

Thirty winter nests (about 5000 larvae) were collected in December 2003 from each of eight populations from core (historical) and expansion (recent) parts of the insect's range (cf. Battisti *et al.*, 2005), chosen to include a wide geographic area and all the available hosts (Table 1). The larvae of each population were reared until pupation in the eight separate rooms, on pine branches from the host species from which they were collected. In late winter, the larvae were allowed to pupate in a 40-cm wide ditch running along the perimeter of each room, which was filled with sand (45%), peat (45%), and leaf mould (10%) to a depth of 15 cm. To facilitate adult emergence and wing extension, wooden sticks (20 cm in length, 1.5 mm in diameter) were inserted in the ditch in vertical position. Emergence and oviposition were checked daily by counting and removing dead insects and egg batches.

#### Plant material

Pine trees used in the experiments were obtained from a forestry nursery situated in north-eastern Italy (Tolmezzo UD). To obtain individuals of the normally shrub-like *P. mugo* that would be of comparable size to those of *P. nigra* and *P. sylvestris*, the upright *P. mugo* var. *uncinata* Miller was used, from a nursery in Aosta (north-western Italy). The plants were raised from local seed sources and were 5–6 years old, with an average height of about 120 cm.

**Table 1.** Populations of *Thaumetopoea pityocampa* and sites used in the experiments, with an indication of which hosts were native and which were introduced in the sampling area.

Population	Type	Geographic coordinates	Altitude (m)	Host species: original (introduced)	Nest census: no. of nests	Preference experiments: no. of females		Performance experiments: no. of egg batches		
						Choice	No-choice	First instar, Petri dish	Third instar, potted tree	Field test
Fumane	Core	45°32'N 10°52'E	630	<i>sylvestris</i> ( <i>nigra</i> )		36		11		
Rivoli Bianchi	Core	46°16'N 13°06'E	240	<i>nigra</i>		74		17		60
Rovereto	Core	45°50'N 10°06'E	650	<i>sylvestris</i> ( <i>mugo</i> , <i>nigra</i> )	74					
Cimolais	Expansion	46°22'N 12°21'E	760	<i>mugo</i> , <i>nigra</i> , <i>sylvestris</i>		174			20	
Friuli extreme*	Expansion	46°22'N 13°18'E	860–1200	<i>nigra</i>			407		20	
Moggio	Expansion	46°28'N 13°12'E	760	<i>mugo</i> , <i>nigra</i>		141	248	23		
Venosta N	Expansion	46°37'N 10°46'E	1090	<i>sylvestris</i>		132		20		
Venosta S	Expansion	46°38'N 10°46'E	1210	<i>sylvestris</i> ( <i>nigra</i> )	44	68		12		60

\*Friuli extreme nests were collected at the expansion edge in the south-eastern Alps within a radius of about 10 km from the location specified by the coordinates.

To standardise tree appearance among hosts of varying architecture, an arbitrary measure of visual similarity to the insect, correlated with tree height, was used (A. Battisti, unpublished). The side-view total leaf area ( $A$ ; hereafter, silhouette) was calculated using the formula

$$A = L_{TB} \times N \times L_N \times W,$$

where  $L_{TB}$  is the total length of branches bearing needles,  $N$  is the mean number of needles per cm branch length,  $L_N$  is the mean length of the needles, and  $W$  is the maximum width of the needle section, measured at the midpoint of needle length. In order to reduce variation among individual trees and reach comparable values of silhouette per host species,  $A$  was calculated for each plant and then plants were selected and grouped together such that collectively they would give a target silhouette of 9000–12 000 cm<sup>2</sup>. Characteristics of the trees used in the experiments are given in Table 2.

#### Experimental set-up

In the choice experiment, one pot each of the three pine species (*P. mugo*, *P. nigra*, *P. sylvestris*) was offered simultane-

ously in each room. Every morning, eggs and emerged females were counted, and then removed. After the collection of egg masses, the pots were rotated clockwise among room corners. In the no-choice experiment only one potted pine species per room was offered to the insects. The experiments started on 25 June 2004, at the beginning of the emergence period, which collectively lasted 36 days. For both types of experiment, each insect population was tested for several nights in a row, depending on the availability of emerged insects and on the number of egg batches obtained. At least two choice and two no-choice experiments were running simultaneously on the same night with different populations. A complete randomisation of the experiments among the populations was not possible because of the unpredictability of adult emergence. While the cage experiments faced the usual challenges of obtaining mated females and egg batches under captivity, the present study achieved the highest rate of oviposition described in the literature for this species (up to 50%; Démolin, 1969). In both experiments, the collected egg batches were kept in the laboratory at 24 °C until they were used for larval performance experiments. Female realised fecundity was estimated by counting the total number of eggs per egg batch.

**Table 2.** Mean height and needle traits ( $\pm$  SE) of the trees used in the experiments. Different letters indicate significant differences in pairwise comparison of means (Tukey's test,  $P < 0.05$ ).

Host	Tree height (cm)	Needle length (cm)	Needle perimeter (mm)	Leaf area (cm <sup>2</sup> )
<i>Pinus mugo</i>	108 $\pm$ 10 b	3.9 $\pm$ 0.4 a	3.1 $\pm$ 0.2 b	10 179 $\pm$ 811 a
<i>Pinus nigra</i>	132 $\pm$ 17 a	6.6 $\pm$ 0.9 c	3.2 $\pm$ 0.2 b	9010 $\pm$ 1148 a
<i>Pinus sylvestris</i>	132 $\pm$ 23 a	3.9 $\pm$ 0.6 a	3.5 $\pm$ 0.5 c	9381 $\pm$ 890 a

### Larval performance experiments

To test for differences in host quality under a variety of conditions and for larvae of different ages, three separate experiments were conducted, measuring larval performance on the three host species.

In the first experiment, first-instar larvae from two core and three expansion populations were reared under laboratory conditions (Table 1). The larvae were obtained from egg batches laid during the preference experiments (see above). Larvae were fed 1-year-old needles of the three host species (*P. mugo*, *P. nigra*, *P. sylvestris*) that were collected either from potted trees or from naturally growing trees (hereafter, 'needle origin'; potted or wild respectively). In both cases, needles came from 10 to 15 trees and were randomised. In the bioassay, 15 full-sibling neonate larvae were placed inside each Petri dish (9 cm  $\phi$ ), and provided with 750 mg of fresh needles of either potted or wild origin, replicated for each host species. One brood (egg batch) allowed to cover all six treatments, with the total number of replicates for each treatment corresponding to the number of broods used (Table 1). The needles were changed after 3 days (in all treatments before being consumed completely). After 5 days, all surviving larvae were weighed, and relative growth rate (RGR,  $\text{mg mg}^{-1} \text{day}^{-1}$ ) was calculated using their initial and final weight (Bauce *et al.*, 2002). Per cent mortality was also noted. Nitrogen content of the needles used in the experiments was assessed by the Kjeldahl method from samples taken before the bioassay started (Huhn & Schulz, 1996). Needle toughness was measured by determining the force needed to penetrate the needles using a calibrated penetrometer. The leaf was fixed between two metal plates, and the penetrometer needle was inserted through the central part of the upper, rounded surface. Five needles were measured per tree, and three readings were taken per needle, avoiding the distal parts.

In the second experiment, larvae from two expansion populations were reared until the third instar on potted trees (Table 1) under outdoor conditions on the university campus. On each of 13 *P. mugo*, 13 *P. nigra*, and 13 *P. sylvestris* trees enclosed inside a 1  $\times$  1 mm mesh net sleeve, we placed a single egg batch obtained from the preference experiments. As soon as the larvae moulted to the third instar, the total number of living larvae and weight of the survivors were determined. The original egg batches were collected to determine the number of hatched eggs (initial colony size).

In the third experiment, larval performance from a core and an expansion population on each host species under field conditions across the 2004–2005 season were compared. The experiment was conducted at a site near Cimolais (expansion area), where a sufficient number of trees of the three host species grew intermixed in an area of about 1 ha. Natural egg batches, collected at Venosta, northern Italy (expansion population) in mid-July 2004, and at Rivoli Bianchi, north-eastern Italy (core population) in mid-August 2004, were used. From each population, 20 egg batches were selected at random and assigned singly to 20 trees of each host species (a total of 120 batches). The egg batches were fixed to a branch and enclosed inside a 1  $\times$  1 mm mesh net sleeve of 50  $\times$  120 cm. After hatching, egg batches were collected to determine the number of hatched eggs

(initial colony size). The sleeves were inspected periodically, and the colonies were transferred to another branch of the same tree when needles started to be in short supply. In mid-November 2004, half of the colonies from each population and host were collected, and larval survival, instar, and weight were recorded. The remaining colonies were left on the trees until early April 2005, when they were collected, analysed as above, and reared for another 4–5 weeks until pupation.

### Statistical analyses

The distribution of nests among the pine species in the field (host colonisation pattern) was tested against the null hypothesis by the  $\chi^2$  test, and the number of nests per tree by Kruskal–Wallis ANOVA by ranks (Sokal & Rohlf, 1995). To test for preference differences in the choice experiment, we used a log–linear analysis with three factors: host species, population type (core vs. expansion), and the original host (*P. nigra*, *P. sylvestris*), and included interaction terms between the three factors (Sokal & Rohlf, 1995). Log–linear analysis differs from the analysis of variance in that the latter tests for significance of main effects while log–linear analysis tests for significant interactions. Significance of an interaction term was assessed from the  $\chi^2$  value obtained by the difference of  $\chi^2$  values of models including or not including that interaction term. Since the experiments involved a diffuse source of multiple emerging insects (rather than individual releases of single females), host trees could be treated as independent from one another. Before analyses, the numbers of egg batches laid on different hosts were first converted to relative frequency of egg batches (% egg batches), then corrected to account for the differences in the total number of females that had emerged in each population. The same correction, and the log–linear analysis, were also employed to test for oviposition frequency in the no-choice test. ANOVA was employed to compare the realised fecundity of females between core and expansion areas and among populations, again using the relative frequency of egg batches as the dependent variable. Tukey's test was used for pairwise comparison of means. Differences in the performance of first-instar larvae among core and expansion populations, and host species, were tested using factorial ANOVA with RGR and per cent mortality of each population as variables. For the potted tree experiment and the field experiment with third-instar larvae, the same variables were analysed using ANOVA and a log-likelihood *G*-test (Sokal & Rohlf, 1995) respectively. In all cases in which ANOVA was employed, the basic assumption of homogeneity of variance was met, and variables were tested without any transformation.

## Results

### Host selection patterns – nest census

In the mixed stand at Rovereto, nests were more abundant on *P. nigra* (65.5% of trees attacked) than on *P. mugo* (42.8%) and *P. sylvestris* (29.1%), with significant differences on the whole

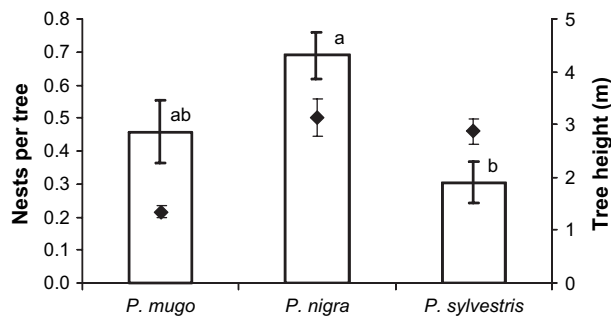
( $\chi^2 = 8.17$ , d.f. = 2,  $P = 0.016$ ) and in any pairwise comparison with the exception of *mugo-sylvestris*. The mean number of nests per tree differed significantly among hosts (Fig. 1; Kruskal–Wallis rank ANOVA  $H_{2,149} = 14.8$ ,  $P < 0.01$ ). However, *P. mugo* trees were significantly shorter than those of the other two species (ANOVA  $F_{2,149} = 10.3$ ,  $P < 0.01$ ), and hence less prominent in appearance. At Venosta, where *P. mugo* was absent, *P. nigra* tended to have more nests than *P. sylvestris* (34.5% and 17.2% of trees attacked respectively;  $\chi^2 = 3.3$ , d.f. = 1,  $P = 0.067$ ), and nests were more than twice as abundant per tree on *P. nigra* ( $0.58 \pm 0.12$ , mean and SE respectively) than on *P. sylvestris* ( $0.23 \pm 0.07$ ) (Kruskal–Wallis rank ANOVA  $H_{1,111} = 4.7$ ,  $P = 0.03$ ).

#### Female preference – cage oviposition experiments

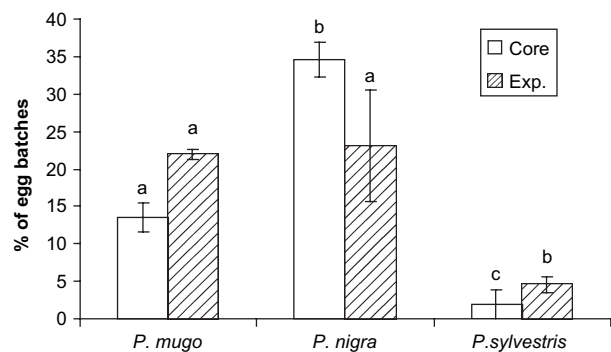
In the choice experiment, *P. sylvestris* was clearly less preferred than either *P. nigra* or *P. mugo* ( $\chi^2 = 90.1$ , d.f. = 2,  $P < 0.01$ , log–linear), whereas we could not document any consistent preference for *P. nigra* over *P. mugo* ( $\chi^2 = 1.26$ , d.f. = 1,  $P = 0.25$ ) (Fig. 2). Overall, core and expansion populations did not show any significant differences in their oviposition preferences ( $\chi^2 = 0.02$ , d.f. = 1,  $P = 0.90$  for *P. mugo* vs. *P. nigra*). However, there was a significant interaction between population type and host species ( $\chi^2 = 10.6$ , d.f. = 2,  $P < 0.01$ ). For instance, *P. mugo* received more oviposition from the expansion than the core populations, whereas the trend was reversed for *P. nigra*. Also, the core populations largely preferred *P. nigra* over the other two hosts, while the expansion populations seemed to be less selective (Fig. 2). Other interaction terms were not significant.

In the no-choice experiment, a higher proportion of egg batches was laid on *P. mugo* and *P. nigra* than on *P. sylvestris* ( $\chi^2 = 12.5$ , d.f. = 2,  $P < 0.01$ ) (Fig. 3), consistent with what was found in the choice experiment.

Oviposition was more frequent amongst females of some populations than of others ( $\chi^2 = 31.9$ , d.f. = 6,  $P < 0.01$ ), but the populations did not differ in the mean number of eggs per



**Fig. 1.** Mean number ( $\pm$  SE) of winter nests of *Thaumetopoea pityocampa* per tree (columns) and mean tree height ( $\pm$  SE) (black diamonds) on three different *Pinus* species in a mixed stand at Rovereto, Italian Alps ( $n = 35, 58, 55$ , respectively). Different letters indicate significant differences in pairwise comparisons of means of nests per tree (Kruskal–Wallis rank ANOVA,  $P < 0.05$ ).

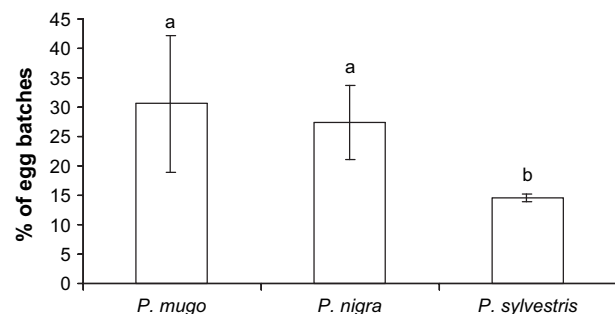


**Fig. 2.** Rate of host acceptance in the choice experiment: mean percentage ( $\pm$  SE) of egg batches laid on each host out of the total number of egg batches laid by females from two core populations (Fumane, Rivoli Bianchi) and four expansion (Exp.) populations (Cimolais, Moggio, Venosta N, Venosta S) of *Thaumetopoea pityocampa*. The total numbers of egg batches laid were 26 and 141, respectively. Different letters indicate significant differences in pairwise comparisons of means within population types ( $\chi^2$  test, d.f. = 1,  $P < 0.05$ ).

egg batch ( $F_{6,262} = 1.29$ ,  $P = 0.27$ ) (Table 3). Realised fecundity (mean number of eggs per batch) was similar in both choice and no-choice experiments, and among the host species (Table 3;  $F_{2,230} = 2.01$ ,  $P = 0.14$ ).

#### Larval performance – laboratory and field experiments

In the Petri dish bioassay with neonate larvae, no significant differences in RGR between core and expansion populations, among host species, or between needle origin (potted vs. wild trees) were found. Neither were any of the interactions significant. Larval mortality, however, was slightly higher on wild plants ( $F_{1,6} = 6.3$ ,  $P = 0.04$ ). Nitrogen content differed significantly among hosts ( $F_{2,6} = 16.6$ ,  $P < 0.01$ ) but not between needle origin. Interestingly, *P. nigra* had a lower nitrogen content [ $0.81 \pm 0.01\%$  dry weight (DW)] than *P. mugo*



**Fig. 3.** Rate of host acceptance in the no-choice experiment: mean percentage ( $\pm$  SE) of egg batches laid on each host out of the total number of egg batches laid by females from two expansion populations (Moggio, Friuli) of the *Thaumetopoea pityocampa*. The total numbers of egg batches laid were 54 and 55, respectively. Different letters indicate significant differences in pairwise comparisons of means within population types ( $\chi^2$  test, d.f. = 1,  $P < 0.05$ ).

**Table 3.** Percentage of female *Thaumetopoea pityocampa* that laid eggs in the choice and no-choice experiments (pooled), and mean number of eggs per egg batch ( $\pm$  SE) for the populations used in the study.

Population	Type	% ovipositing females	Eggs/batch
Fumane	Core	30.6	200 $\pm$ 8
Rivoli Bianchi	Core	18.9	181 $\pm$ 11
Cimolais	Expansion	19.0	189 $\pm$ 12
Friuli extreme	Expansion	19.4	175 $\pm$ 13
Moggio	Expansion	25.2	180 $\pm$ 12
Venosta N	Expansion	18.2	202 $\pm$ 13
Venosta S	Expansion	52.9	182 $\pm$ 10

(0.97  $\pm$  0.03% DW) and *P. sylvestris* (1.2  $\pm$  0.06% DW). Needle toughness did not differ significantly among hosts ( $F_{2,15} = 2.16$ ,  $P = 0.15$ ), with a mean value of 72.5  $\pm$  8.3 g for *P. mugo*, 93.2  $\pm$  3.1 g for *P. nigra*, and 82.7  $\pm$  8.4 g for *P. sylvestris*.

In the outdoor experiment on potted trees, both larval mortality and RGR were similar among host species ( $F_{2,35} = 0.07$ ,  $P = 0.93$  and  $F_{2,35} = 2.56$ ,  $P = 0.12$  respectively), with moderately low mean values of per cent mortality (22.1  $\pm$  7.3; 21.1  $\pm$  8.6; 25.6  $\pm$  10.8) and low mean values of RGR (0.058  $\pm$  0.002; 0.053  $\pm$  0.002; 0.061  $\pm$  0.003 mg mg<sup>-1</sup> day<sup>-1</sup>) for *P. mugo*, *P. nigra*, and *P. sylvestris* respectively.

In the field experiment, no differences were found in mortality and RGR among host species (Table 4), in spite of the fact that the few colonies alive at the end of the winter were only observed on *P. nigra* and *P. mugo*, and never on *P. sylvestris*. The effect of the host species was marginal in a log-likelihood test of per cent mortality ( $G = 5.52$ , d.f. = 2,  $P = 0.10$ ). Both the core and the expansion population contained colonies that survived until the end of the experiment; thus, the earlier hatching of the expansion population relative to the core population did not appear to enhance winter survival.

## Discussion

Host utilisation is of central interest in range expansions of phytophagous insects, as novel hosts may provide means for col-

onisation of areas where the original or primary hosts do not occur. The present study explored the relative roles of female preference and performance, and larval performance to assess recruitment potential of *T. pityocampa* within and beyond its expansion areas in the Italian Alps. Below we discuss the observed discrepancy between female preference and larval performance, evaluate recruitment potential on the secondary and novel hosts in the light of limited longevity of females, and provide a synthesis of host utilisation and future range expansion of *T. pityocampa*.

### Host acceptance: preference and performance of females

In the nest survey of the stand where all three pine species grew intermixed, *T. pityocampa* larval nests occurred more frequently on the primary host, *Pinus nigra*, than on the smaller-statured *P. mugo*, while *P. sylvestris* was the least attacked host even though its height was comparable to that of *P. nigra*. To test whether this pattern reflected a preference hierarchy in oviposition, a controlled experiment was conducted with the three hosts of comparable appearance (silhouette) presented to emerging females inside a cage. The basic hierarchy observed in the field was confirmed: the primary host (*P. nigra*) was preferred consistently, the secondary host (*P. sylvestris*) was accepted the least frequently, and the novel host (*P. mugo*) showed intermediate, or even equal, attractiveness relative to the primary host. Interestingly, in a study of *T. pityocampa* in a mixed stand in southern Spain, Hodar *et al.* (2002) found that field oviposition rates, measured as egg mass density, were similar between the indigenous subspecies of *P. nigra* and *P. sylvestris*, and lower on co-occurring *P. pinaster* (but see Calas, 1900). While Hodar *et al.* (2002) did not explicitly test female preference, the discrepancy between their and the present field observations is not unexpected, as it could be attributed to region-specific characteristics of hosts and/or oviposition behaviour of the insect. In any case, the results presented here provide additional evidence that the distribution of larval colonies among the three hosts in multi-host stands is less likely to be generated by differential post-oviposition mortality (cf. Benigni & Battisti, 1999), and that female preference alone could drive the patterns.

**Table 4.** Summary of results from the field experiment on larval performance of *Thaumetopoea pityocampa*, carried out at Cimolais in 2004–2005, with the initial number of 20 egg batches for each host species of *Pinus*.

Population type	Host	Number of colonies alive in		Condition of colonies in November				
		November	May*	Total no. larvae alive $\pm$ SE	% larvae in third instar	% larvae in fourth instar	Third instar RGR†	Fourth instar RGR†
Core	<i>P. mugo</i>	18	0	80.6 $\pm$ 18.5	51	49	0.058 $\pm$ 0.003	0.071 $\pm$ 0.001
	<i>P. nigra</i>	14	2 (43, 1)	96.1 $\pm$ 19.9	100	0	0.060 $\pm$ 0.003	–
	<i>P. sylvestris</i>	16	0	79.6 $\pm$ 7.8	89	11	0.061 $\pm$ 0.001	0.067 $\pm$ 0
Expansion	<i>P. mugo</i>	12	1 (47)	74.4 $\pm$ 11.0	57	43	0.046 $\pm$ 0.001	0.052 $\pm$ 0.003
	<i>P. nigra</i>	13	1 (4)	69.1 $\pm$ 10.0	12	88	0.045 $\pm$ 0	0.054 $\pm$ 0.001
	<i>P. sylvestris</i>	10	0	58.1 $\pm$ 17.2	4	96	0.047 $\pm$ 0	0.055 $\pm$ 0.002

\*Number of larvae found in each of the remaining colonies included in parentheses.

†Mean  $\pm$  SE of relative growth rate (mg mg<sup>-1</sup> day<sup>-1</sup>).

Multiple-host stands with the primary and alternative hosts do not represent the typical situation in expansion areas of *T. pityocampa*, where the insect is increasingly faced with no-choice situations in single-host stands (pure *P. sylvestris*, or pure *P. mugo*). Under such conditions, the preference hierarchy may break down because of a conflict with female performance (Scheirs *et al.*, 2000; Scheirs & De Bruyn, 2002), since, after emergence, females only have one night to locate a suitable host for laying a single batch of eggs. Time limitation may then effectively make their oviposition behaviour less conservative by increasing acceptance of normally less preferred hosts (Jaenike, 1978; Courtney, 1982; Mayhew, 1997; Rosenheim, 1999; Díaz-Fleischer & Aluja, 2003; but see Stamp *et al.*, 2005). *Thaumetopoea pityocampa* females behaving conservatively may risk not ovipositing at all, because (1) the most attractive host may be rare or absent; (2) host-searching dispersal may lead them to areas with only non-hosts; and (3) the probability of pre-oviposition mortality due to predation, weather, or ageing will increase over time. This system also lacks other components of female performance that could confound or obscure the effect of time limitation, such as feeding by adults (e.g. Scheirs *et al.*, 2000).

Contrary to expectations, the present study did not provide support for the hypothesis that all hosts would be accepted equally in the absence of alternative choices. Rather, when each of the hosts was offered singly in the controlled no-choice cage experiment, the females showed near equal rates of host acceptance for *P. nigra* and *P. mugo*, but 50% lower oviposition rates on *P. sylvestris* than on either of the other hosts. Therefore, females behaved conservatively, following a similar pattern of host acceptance as in a multi-host setting. On the other hand, such conservative behaviour might be expected from an alternative perspective: because each female lays only a single batch of eggs, but hedging through repeated oviposition on a number of hosts is not possible in *T. pityocampa*, and continued search for another host may be a more adaptive strategy (but see Díaz-Fleischer & Aluja, 2003; also see next section). Finally, conclusions can only be made about the relative (not absolute) rates of differential host acceptance; oviposition would likely be higher under natural conditions than in the experimental setting. These results imply that the innate host recognition behaviour can override time limitation trade-offs with female performance, ultimately leading to a failure to reproduce in individuals that died before accepting a less attractive host.

#### *Larval performance vs. female host acceptance*

The three hosts did not differ in larval growth and mortality: the larvae fared equally well on *P. nigra*, *P. sylvestris*, and *P. mugo*, and the three hosts appeared equally suitable even after considering a full range of larval stages, duration of feeding, and both controlled and field conditions. These results are in partial contrast with the findings of Hodar *et al.* (2002) in southern Spain, in which first-instar larvae performed much better on the local subspecies of *P. sylvestris* than on *P. nigra*, but agree with the observations by Devkota and Schmidt (1990) in Greece. Possible differences in needle secondary chemistry were not in-

vestigated (but none were found by Hodar *et al.*, 2002), but no link was found between performance and the observed differences in nitrogen content, often invoked as a key determinant of insect performance (e.g. Underwood, 1994). Oligophagous insects can be expected to possess considerable physiological plasticity in dealing with hosts of different nutritional or chemical composition, and may maintain similar performance on related hosts (Roininen & Tahvanainen, 1989; Bernays & Chapman, 1994; Leyva *et al.*, 2000). Still, the lack of differences in suitability among the three hosts underlines a partial discrepancy between female preference and larval performance. *Pinus sylvestris* was accepted relatively infrequently for oviposition even though the larvae developed well on this host. Conversely, the offspring that developed on *P. nigra* or *P. mugo* did not derive any added benefit from the preferred choice of the mother.

It is not uncommon to find a mismatch between oviposition preferences and hierarchies of host suitability for larval performance, with examples from a variety of insect systems (Dethier, 1954; Wiklund, 1975; Jaenike, 1990; Mayhew, 1997; Leyva *et al.*, 2000). A substantial body of theory exists to account for these discrepancies, invoking either oviposition mistakes by females (e.g. Larsson & Ekblom, 1995), or additional factors, such as adult performance (e.g. Scheirs *et al.*, 2000), host plant abundance (e.g. Kuussaari *et al.*, 2000), habitat suitability (e.g. Rausher, 1979), sequestration of secondary metabolites (e.g. Björkman *et al.*, 1997), and enemy-free space (e.g. Denno *et al.*, 1990). The relatively high attractiveness of *P. mugo* in the present study, especially in the no-choice situation, was somewhat unexpected. A variety of intrinsic factors influence host recognition in Lepidoptera, including needle chemistry (Schopf & Avtzis, 1987) and needle morphology (Renwick & Chew, 1994), and, possibly, females responded to phenotypic similarity between needle traits of the closely related *P. nigra* and the novel host. Equivocality in the patterns of preference and performance on novel hosts is the norm (Jaenike, 1990; Thompson, 1996; Barre *et al.*, 2002). In some cases, performance is lower on a novel host; for instance, *Panolis flammea* does not perform as well on *Pinus contorta* as on the native *P. sylvestris*, in spite of the occurrence of outbreaks on the novel host (Vanbergen *et al.*, 2003). In other cases, novel hosts appear perfectly suitable (e.g. *Papilio* butterflies; Scriber & Ording, 2005). The paradox of *T. pityocampa* females ovipositing infrequently on the otherwise suitable, historical, *P. sylvestris* presents a question to which ultimate rather than proximate answers are difficult to find without further study.

#### *Implications on future range expansion*

The ability of an insect herbivore to complete its development on alternative hosts is one of the prerequisites for continuing range expansion beyond the extent of the distribution of its original hosts (Gutierrez & Thomas, 2000). On the one hand, larvae of *T. pityocampa* achieve comparable performance on all three hosts that occur at the range boundary in the southern Italian Alps; hence, the insect is not limited in its spread by the lack of hosts of sufficient quality. On the other hand, females show

conservatism in host acceptance, frequently rejecting a suitable host despite compromising their own performance. Thus, female oviposition behaviour may limit recruitment potential, particularly in stands of pure *P. sylvestris*, compared with *P. nigra* stands. An intriguing scenario in areas dominated by *P. sylvestris* is the potential for future adaptation of populations in the expansion range (e.g. Thomas *et al.*, 2001; Vanbergen *et al.*, 2003), leading to a relaxation of the behavioural conservatism of *T. pityocampa*, particularly if gene flow is limited (e.g. Via, 1986). Although only suggestive evidence was found of this already occurring in the expansion populations used in the present study (a significant population type  $\times$  host interaction; Fig. 2), strong directional selection can be expected for increased acceptance of the less attractive host. The situation is likely to be different at sites dominated by *P. mugo*. While the results indicate that this novel host species is accepted as frequently as *P. nigra* in single-host settings, recruitment of *T. pityocampa* on *P. mugo* is likely to be limited by another, habitat-related, factor. Specifically, the smaller size and prostrate architecture of this predominantly subalpine shrub creates a risk of colony mortality when nests become buried under a heavy snowpack for extended periods of time (A. Battisti, pers. obs.). Similarly, habitat suitability is the most important factor affecting host choice and survival in the related species, the acacia processionary moth *Ochrogaster lunifer* (Floater & Zalucki, 2000). Finally, both *P. sylvestris* and *P. mugo* occur extensively in areas beyond the current altitudinal and latitudinal range boundary of *T. pityocampa*, beyond which climatic conditions become suboptimal or even prohibitive for larval survival, mostly due to thermal requirements for larval feeding (Battisti *et al.*, 2005). The future expansion rates will therefore depend on the combination of host use patterns and climatic suitability of the habitat.

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