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Host plant relationships of an endangered butterfly, *Lopinga achine* (Lepidoptera: Nymphalidae) in northern Europe

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Abstract The aim of the present study was to evaluate—in a geographic perspective—the role of host plant as a determinant of habitat quality for *Lopinga achine*, a satyrine butterfly endangered over much of its European range. Laboratory trials were performed to record host choices made by the ovipositing females as well as by neonate larvae. In rearing experiments, growth performance and mortality on different host plants was determined. Oviposition was found to be indiscriminate but larvae were shown to be able to choose between host plants, with the choices made broadly consistent with growth performance of the larvae on particular hosts. Nevertheless, most grasses and sedges offered were found to support larval development reasonably well. No clear superiority of the previously suggested primary host plant *Carex montana* could be shown. Importantly, no differences in host plant relationships were found between the populations of Sweden, western Estonia and eastern Estonia. In particular, the larvae originating from eastern Estonian populations developed on *C. montana* equally well even if the plant is absent from their native habitat. In the context of species conservation, one should conclude that *L. achine* is polyphagous enough on various grasses and sedges so that the presence of any particular host species cannot be a critical component of habitat quality. Nevertheless, some preference to broad- and soft-leaved hosts, as well as sensitivity to host wilting, may partly explain the butterfly's preference to moist forest habitats, further emphasizing the central role of habitat management in the conservation practice of this species. In turn, the absence of ecological differences between geographic populations should enable conservationists to successful transfer their experience across national boundaries.

Keywords *Lopinga achine* · Lepidoptera · Host plant preference · Conservation

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Introduction

Populations of numerous butterfly species have recently dramatically declined, with habitat deterioration clearly being the primary cause of the negative trend (Van Swaay et al. 2005; Van Dyck et al. 2009; Nakamura 2011). Nevertheless, proximate factors determining habitat suitability have often remained unclear. In the typical case, there is insufficient information about the relative role of host plant abundance in determining the quality of the habitat. The role of the host is not necessarily straightforward: for example, Bergman (1999) showed that the occurrence of a butterfly in the field depends more on the co-occurrence of the plant and suitable microclimatic conditions rather than on the absolute abundance of the plant.

Another frequent complication for evaluating the importance of the host plant in the species conservation context is the often substantial geographic differences in host plant use. Perhaps the best known examples are provided by various checkerspot butterflies

(e.g. *Euphydryas editha*, *Melitaea cinxia*) in which host plant preference may vary even at a limited geographic scale (e.g. Singer 1971; Hanski and Singer 2001). Furthermore, also for *Polygonia c-album* it was recently confirmed that host use of this species varies considerably throughout Europe (Braschler and Hill 2007), and numerous examples from herbivorous insects other than butterflies exist (e.g. Zovi et al. 2008; Logarzo et al. 2011). Consequently, one should preferably rely on locally derived data on host plant use when deciding about conservation actions.

Naturally, the more restricted a species is in its host plant use, the higher the potential importance of host abundance is for the welfare of its populations. The "browns" (Nymphalidae: Satyrinae) are frequently considered to be polyphagous on grasses but, with the exception of a few extensively studied species (e.g. Gotthard 2004), there is little reliable, experimentally confirmed data on host use in these butterflies. Despite the ubiquity of grasses, there is still a high number of endangered species in this butterfly subfamily (see Eales 1999, Dierks 2006, van Halder et al. 2008, for particular examples). Indeed, satyrine butterflies are frequently known to be habitat specialists and relatively poor dispersers which may at least partly explain the vulnerability of populations. Nevertheless, the role of the host plant related parameters in habitat specificity remains largely unknown. For example, *Coenonympha arcania* was found to use 11 different host plants in mainland Europe, in contrast to only using one in Sweden (Nylin and Bergström 2009). Revealing the role of the host plant in the habitat specificity of the brown butterflies is therefore of clear applied significance.

Lopinga achine is an example of an endangered satyrine, with its distribution having drastically declined in western Europe as well as in Japan (Bergman 2001; Bergman and Landin 2001). Indeed, this species preferring half-open woodlands has already disappeared from many of its previous habitats (Bergman 1999, 2005; Bergman and Landin 2002; Bergman and Kindvall 2004; Konvička et al. 2008). Following the general pattern, the main reason for this situation has been seen as habitat deterioration (Bergman and Landin 2002). Nevertheless, causal connections between proximate parameters of the habitat and its suitability for *L. achine* have remained unclear, and the role of the host plant in this is poorly known especially in the context of potential geographic variability in host use.

Lopinga achine has been generally known to feed on sedges and grasses but the reliable empirical information comes from just a limited number of studies, and geographic locations. For example, in the Czech Republic, it has been observed to oviposit on *Carex fritschii* and *C. michelii* (Konvička et al. 2008). In Sweden, the calciphilous *Carex montana* is considered the main host plant of *L. achine*; partly because the distribution of the

butterfly follows that of the plant (Bergman 1999, 2000), but there are also direct field observations of larvae feeding on *C. montana* (Bergman 2000). However, even within its Swedish range, *L. achine* is not present at every site with *C. montana* abundantly growing (Bergman 2000). Moreover, the broader range of the host plant than that of the butterfly suggests that other factors than host plant should affect the distribution of the insect. In turn, the wide distribution of *L. achine* in the geographically close eastern Estonia (Kesküla 1992) suggests that alternative host plants must be used also within northern Europe: *C. montana* is absent over most of that region (Kukk and Kull 2005).

A recent phylogeographic study of *L. achine* showed that European populations are genetically differentiated which suggests that gene flow between different regions is limited (Kodandaramaiah et al. 2012). This is also true for northern Europe: the two Swedish populations of *L. achine* form a distinct genetic group in comparison to Estonian populations, which harbor a higher genetic diversity (Kodandaramaiah et al. 2012). Limited gene flow allows one to expect local adaptations. One might therefore speculate that the Swedish and, potentially western Estonian populations, may be specialized on *C. montana* while eastern Estonian populations use a wider range of plants. A considerable, and geographically variable, role of the host plant as a determinant of habitat quality is therefore possible, but has so far remained unclear.

The aim of the present study was to experimentally determine host plant preference, as well as larval performance on different host plants for three North-European populations of *L. achine*. This was done to empirically evaluate the degree of host specificity of the species in general and, more specifically, to reveal potential differences in host plant use between different geographical populations. Multiple choice oviposition experiments were performed to determine if female butterflies show any preference to different hosts. In parallel, host choice and growth performance experiments were performed with larvae representing Swedish, western Estonian and eastern Estonian populations of the species. The results are discussed from the perspective of conservation management of this regionally endangered species.

Methods

Oviposition preference

The oviposition preferences of adult females were tested in a laboratory setting. In respective trials, *C. montana*—a candidate to be the primary host plant—was compared to two grasses: *Brachypodium pinnatum* and *Deschampsia flexuosa*. In Sweden, *B. pinnatum* is known to be used by

other satyrines and is also common in the *L. achine* habitat on Gotland (B. Johansson & K. Gotthard, personal observations). In turn, *D. flexuosa* is the second most common species (after *C. montana)* from the families Cyperaceae and Poaceae in another Swedish *L. achine* habitat, in Linköping (Bergman 2000).

Females from two Swedish populations—Gotland (57º30′N, 18º30′E) and Linköping (58º25′N, 15º37′E)—were collected in the field during the last days of June and the first days of July 2007. Forty-five females were let to oviposit in the laboratory, 19 from Gotland and 26 from Linköping. Each female was tested in two different trials: a choice between *C. montana* and *D. flexuosa* (A) and a choice between *C. montana* and *B. pinnatum* (B). Half of the females were tested first in trial A, and in B thereafter, while the other half of the sample was subjected to the opposite order of trials. The females were kept individually in cages (0.5 × 0.5 × 0.5 m), under approximately 25 °C being exposed to artificial daylight from 9.00 to 17.00. Females of *L. achine* do not attach their eggs to the host plant, but drop them close to potential hosts (Karlsson and Wiklund 1985). To explore potential host preferences of the females we therefore measured how close to potential host females dropped their eggs. Potted plants representing the two alternative oviposition substrates were placed in opposite corners of a quadrangular cage. The placement of plants was randomized between trials and a lamp just above the transparent top of the cage provided an independent light source for each cage. The diagonal line was marked so that the "*C. montana* half" and "the alternative plant half" was formed. Throughout the trials the butterflies had access to food and water. After 48 h, the eggs the female had laid in each plant half were counted.

Larval preference and performance trials

The host plant preference of neonate larvae was tested, and growth performance experiments were conducted on seven species of grasses and sedges, all of them representing potential host plants of *L. achine*: *C. montana* and *C. sylvatica* (Cyperaceae), *Melica nutans*, *Festuca ovina*, *Calamagrostis canescens*, *Deschampsia flexuosa* and *B. pinnatum* (Poaceae). *M. nutans* was selected for the experiments (along with *C. montana*) as a plant being highly abundant in the Gotland habitat and *F. ovina* because of being a common grass that is used by a range of satyrines. *C. sylvatica* and *C. canescens* were chosen as potential hosts abundant in the habitat of *L. achine* in eastern Estonia. *B. pinnatum* is used by various other satyrines and is also common in the habitat of *L. achine* in Gotland (B. Johansson & K. Gotthard, personal observations) whereas *D. flexuosa* is a common plant at the Swedish sites (Bergman 2000). The experiments were performed at the University of Tartu in 2009.

In the host preference trials, sections of two plant species were offered simultaneously to neonate larvae. A Petri dish was prepared with damp filter paper and one leaf from each plant was placed on opposite sides of the dish, with the distance of about 6 cm from each other. All the plant sections were of approximately equal size (ca 3 cm) and the relative position of different species was alternated with respect to the light source. The preference trials were performed in three series, with *C. montana*, *F. ovina* and *M. nutans* respectively as reference species. The reference plants were tested against the other species from the sample in pairwise trials. A newly hatched caterpillar was placed in the center of the dish and after 24 h it was determined which of the two plants the caterpillar had been eating. Usually, the caterpillar was found resting on the host plant it had preferred; only rarely it was necessary to determine the preference by inspecting feeding marks. In total, host preference was recorded for 1,125 larvae.

Two series of experiments were conducted to study the performance of the larvae: on growing host plants and on fragments of host plants. These two settings are complementary to each other. Measuring performance of the larva on a living host plant is certainly the most natural way to assess plant quality in the laboratory. Conversely, the advantage of rearing the larvae on detached fragments of host plants is more feasible logistically, which allowed us to considerably increase sample sizes.

Larval performance of the two Swedish populations on living host plants was tested in 2007 at the University of Stockholm. The larvae were reared individually in plastic jars on a tuft of a host plant cultured in water of five grass species: *C. montana*, *B. pinnatum*, *D. flexuosa*, *F. ovina* and *M. nutans*. The representatives of different broods (i.e. offspring of a particular female) were divided equally between host plants. The host plants were replaced when significantly consumed or when showing signs of deterioration. The larvae (150 in total) were weighed 6 weeks after hatching. The experiment was carried out in the laboratory in a climate cabinet with a constant temperature of 17 °C and 17:7 h photoperiodic regime.

Performance of larvae from both Swedish and Estonian populations when reared on fragments of host plants was studied in 2009 at the University of Tartu. The larvae which had earlier been used in the preference tests (see above) were individually housed in plastic jars and fed with fragments of one of the five grass species: *C. montana*, *F. ovina*, *M. nutans*, *C. sylvatica* and *C. canescens*. The representatives of different broods were divided equally between the host plants: every third day the host plants of the larvae were renewed and moisture was provided on a piece of damp cotton wool. To obtain a measure of growth performance, the larvae were weighed 3 weeks after hatching (820 of 1,125 larvae reached that age). The

experiment was performed in the laboratory with the temperature 19 °C and 18:6 h photoperiodic regime.

The 2007 rearing experiment with living plants was based on larvae belonging to 45 broods of Swedish origin: 19 from Gotland and 26 from Linköping. The experiments of 2009 (both host preference trials, and rearing on plant fragments) used insects representing two localities within the eastern Estonian population: 11 females were collected at Karilatsi (58º08′N, 26º55′E) and four females at Laeva (58º29′N, 26º23′E); the 10 western Estonian butterflies originated from Tagamõisa (58º27′N, 22º0′E) on Saaremaa island. In 2009, the Swedish populations were represented by eight females from Linköping and nine from Gotland. To obtain rearing material for the experiments, the females were allowed to oviposit individually in plastic boxes equipped with some grass as oviposition stimulus, and cotton wool moistened with sugar water.

Data analysis

To determine oviposition preference, the number of eggs laid on a particular host plant (i.e. found in the respective half of the cage) was analyzed as dependent on plant species and population in a mixed ANOVA model. The identity of the female was the random variable.

To explore host plant preference, survival and performance of the larvae, mixed generalized linear models for binary response variables were constructed. When analyzing host plant preference, the results of the experiment were coded as '1' for the cases when the reference species was preferred, and as '0' when the alternative host species was chosen. The analyses were performed separately for the three reference plant species (see above). The model included population (Sweden, western and eastern Estonia), alternative plant, and the interaction between alternative plant and population.

The performance of the larvae on different host plants was expressed as weight attained at six (the 2007 experiment with living host plants), or 3 weeks (the 2009 experiment on fragments of host plants). These response variables were analyzed by mixed ANOVA as dependent on food plant and population (Sweden, eastern and western Estonia). Additionally, for the 2009 experiment, the date of hatching was included as a covariate to account for changes in the experimental environment (in the course of the experiment: we noticed problems with some plant fragments drying; the subsequently increased humidity led to better larval performance on later dates). Survival of the larvae throughout the growth experiments was analyzed as a binary variable with the same set of independent variables. When analyzing the survival and the weight of caterpillars, the data relating to those caterpillars that were

reared on (1) *D. flexuosa* (experiment with living plants) and (2) *F. ovina* (plant sections) were excluded from analysis, because (1) no or (2) only a few individuals survived on these plants. In the analyses described, the model included random effects of brood (i.e. offspring of a particular female), and for the preference test, also the brood*alternative plant interaction. Data analysis was carried out using SAS software (SAS Institute Inc. 2008).

Results

Oviposition preference

The females laid on average 58 (SD = 26) eggs during an oviposition trial. The females of *L. achine* did not show preference when allowed to choose between *C. montana* and *B. pinnatum* (Table 1; Fig. 1a) or when *C. montana* and *D. flexuosa* were simultaneously exposed (Table 1; Fig. 1b).

Host plant preference of larvae

The pairwise host choice experiments with neonate larvae showed that *C. montana* as the reference plant was preferred over *C. canescens* and *F. ovina*, but not over *M. nutans* and *C. sylvatica* (Fig. 2). Nevertheless, no plant species was totally rejected: the least preferred host was *F. ovina* and the most preferred ones were *C. sylvatica* and *C. montana*. The trials with *M. nutans* as the reference species similarly indicated a low rank of *F. ovina* with all other species being nearly equal. Importantly, we did not find any differences between the populations in the food plant preference (Table 2). This is indicated by the non-significant main effect of population (that is, the populations did not differ in preferring *C. montana* over the other

Table 1 The results of the pairwise oviposition preference trials: *C. montana* (CM) compared to *B. pinnatum* (BP); and *C. montana* compared to *D. flexuosa* (DF)

Effect	Num *df*	Den *df*	F	*p*
CM versus BP				
Population (P)	1	85	5.57	0.02
Host plant (H)	1	85	0.73	0.39
P * H	1	84	0.06	0.8
CM versus DF				
Population (P)	1	44	6.8	0.01
Host plant (H)	1	44	1.66	0.2
P * H	1	44	0.42	0.52

The exclusion of the non-significant H * P interaction terms did not qualitatively change other results of the analyses. The model included the identity of the female as a random variable, to account for two measurements on each individual
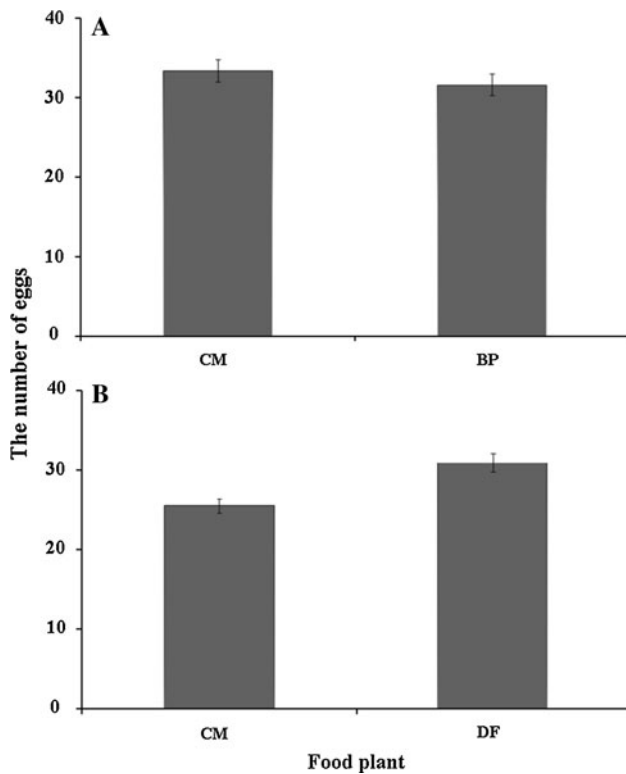
Fig. 1 Oviposition experiments: the number of eggs laid on *C. montana* (CM) in pairwise choice trial with *B. pinnatum* (BP) (ẋ ± SE) (**a**) and *D. flexuosa* (DF) (ẋ ± SE) (**b**)

plants), and the non-significant population*alternative plant interactions (i.e. the acceptance of the different alternative host plants did not vary among populations).

Growth performance of the larvae

The 2007 performance experiment on living host plants indicated that four of the plant species tested—*B. pinnatum*, *C. montana*, *F. ovina* and *M. nutans*—are all suitable hosts of *L. achine* (Fig. 3a) though the larvae were not able to develop on *D. flexuosa*. The weights attained on different plants did not differ when *D. flexuosa* was excluded from the data set ($F_{3,139} = 1.01$, $p = 0.4$).

The weights of the larvae reared on fragments of plants differed between the host species in a similar manner (Fig. 3b). The weight of the larvae growing on *C. montana*, *C. sylvatica*, *M. nutans* and *C. canescens* was broadly equal with *F. ovina* being a clear outlier. Nevertheless, when the outlier was excluded, the among-plant differences retained statistical significance (Table 3). There was some overall difference in growth performance among the populations: on average, the larvae from Sweden attained highest weights, those from East Estonia remaining the smallest (Fig. 3b). Importantly, no interaction between population and host plant species was found.
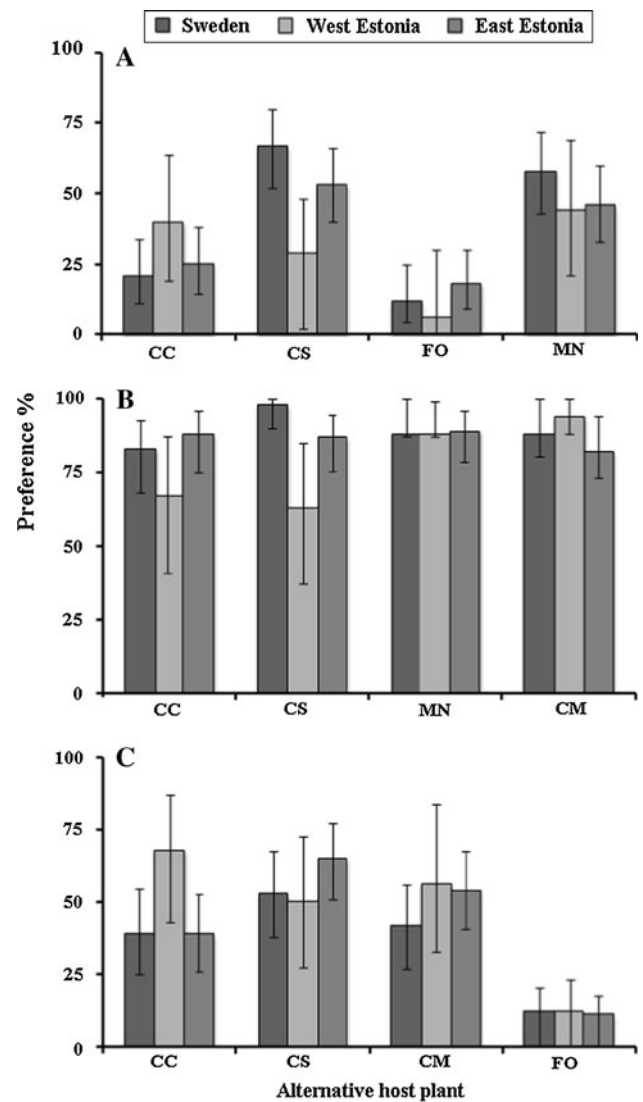

Fig. 2 Host plant preference (ẋ ± exact confidence limits of the binomial proportion, SAS User Inc. 2008) of the newly hatched larvae of *L. achine*. Pair wise choice experiments with *C. montana* (**a**), *Festuca ovina* (**b**) and *M. nutans* (**c**) as the reference plant. *C. canescens* (CC), *Carex sylvatica* (CS), *F. ovina* (FO), *M. nutans* (MN) and *C. montana* (CM). The *heights* of the *bars* indicate the proportion of larvae which preferred the alternative host plant over the reference species

Survival of the larvae

Survival was recorded at the time of weighing the larvae in the performance experiments (i.e. at 6 weeks of age in the 2007 experiment, and at 3 weeks in 2009). In the experiment with living host plants (2007), the overall survival was close to 50 %, and differed significantly between the host plants (Table 4). Larvae form Gotland survived better than the larvae from Linköping (Fig. 4A). When the larvae were fed with plant fragments (2009), survival on *C. montana*, *C. sylvatica*, *M. nutans* and *C. canescens* remained between 75 and 100 %. On the fifth food plant,

Table 2 The results of the pairwise host plant preference trials with neonate larvae, and with *C. montana* (CM), *F. ovina* (FO) and *M. nutans* (MN) as the reference plants

Effect	Num *df*	Den *df*	F	*p*
CM as reference				
Population (P)	2	33	0.75	0.48
Alternative plant (A)	3	92	10.2	<0.0001
P * A	6	92	2.03	0.07
FO as reference				
Population (P)	2	30	2.7	0.08
Alternative plant (A)	2	57	1.5	0.23
P * A	4	57	1.4	0.25
MN as reference				
Population (P)	2	30	0.88	0.42
Alternative plant (A)	1	30	0.99	0.32
P * A	2	30	2.41	0.10

The exclusion of the non-significant P * A interaction terms did not qualitatively change other results of the analyses

F. ovina the survival was—in contrast to the 2007 experiment—remarkably low (<10 %). There were statistically significant but still relatively minor differences between the populations in the chances of the larvae to survive on other host plants (Table 4). The larvae from the population of western Estonia survived best, with the highest mortality being among those from eastern Estonia (Fig. 4b).

Discussion

Our results did not provide support for the view that the females of the endangered butterfly *Lopinga achine* have a preference to oviposit on certain host plants (Bergman 2000), and confirm the idea about indiscriminatory oviposition behaviour in these butterflies (Settele et al. 1999; Bergman and Kindvall 2004). Nevertheless, our results should be treated with appropriate caution as the size of cages we used was limited due to logistic reasons. To what degree ovipositing *L. achine* females may sample host plant related information at a spatial scale that is larger than the cages used in this study is not known. However, using just a 15 cm radius from the oviposition site in the field allowed Bergman (2000) to detect oviposition that was non-random with respect to host plants. Moreover, all females observed to oviposit in the field were siting on the vegetation (Bergman 2000). Given these observations we find it likely that our laboratory experiments would at least be able to detect any strong host preferences of the females. Still we could not find an effect of host species on the number of eggs laid even in the case when a totally unsuitable host—*D. flexuosa*—was offered as a substrate (Bergman 2000, this study). This indicates that direct
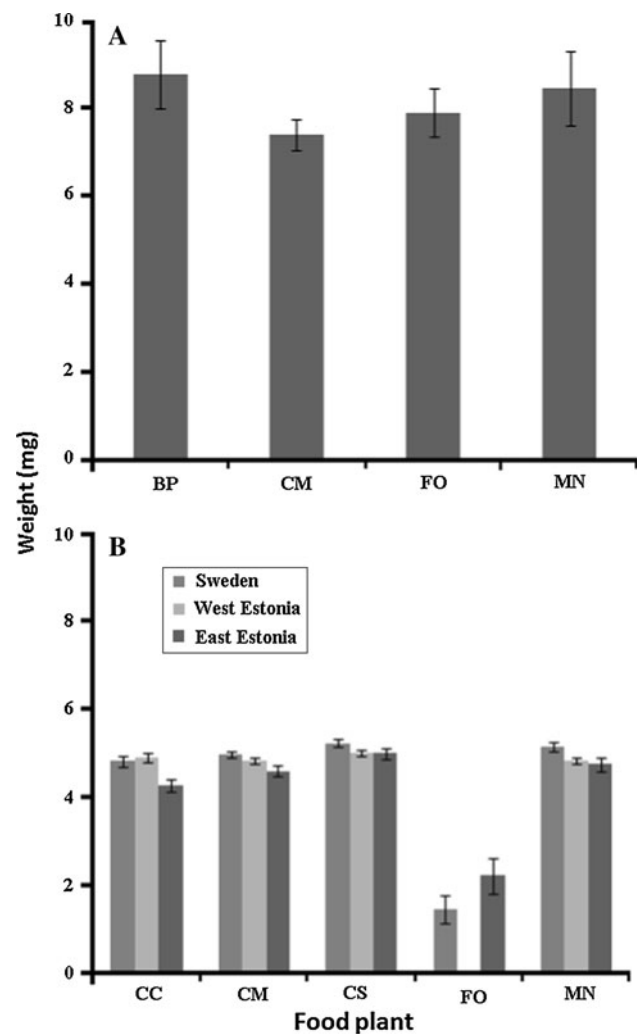

Fig. 3 Average weights (x̄ ± SE) of larvae from the Swedish populations on living host plants (**a**) and of larvae from three populations reared on fragments of plants (**b**). *C. canescens* (CC), *C. sylvatica* (CS), *F. ovina* (FO), *M. nutans* (MN), *C. montana* (CM) and *B. pinnatum* (BP)

Table 3 The results of larval performance trials with the weight attained at the age of 3 weeks as the dependent variable

Effect	Num *df*	Den *df*	F	*p*
Population (P)	2	25.2	7.76	0.0024
Host plant (H)	3	68.3	5.4	0.0022
Start	1	165	65.7	<0.0001
P * H	6	71.1	1.34	0.25

The mixed model included random effects of the brood, and the brood * host plant interaction. The date of hatching ("start") was also included in the model as a covariate to account for the changing rearing conditions. The exclusion of the interaction of population * host plant did not qualitatively affect the statistics associated with the main effects. *F. ovina* was excluded from analysis because only few larvae could survive on that plant

Table 4 Determinants of the survival of the larvae from the two Swedish populations on living host plants (experiment of 2007) and of larvae from Swedish and Estonian populations on fragments of host plants (2009)

Effect	Num df	Den df	F	p
Living host plants				
Population (P)	1	42	4.13	0.05
Host plant (H)	4	82	23	< 0.0001
P * H	4	82	0.28	0.9
Fragments of host plants				
Population (P)	2	32	5.06	0.01
Host plant (H)	3	92	0.6	0.61
P * H	6	92	25934	0.13

In the 2007 experiment, *D. flexuosa* is excluded from the analysis: none of the larvae could survive on that plant. *F. ovina* was excluded from analysis of the 2009 experiment. The exclusion of the interaction of host plant*population from the models did not qualitatively affect the statistics associated with the main effects. The mixed model included random effects of the brood, and the brood * host plant interaction
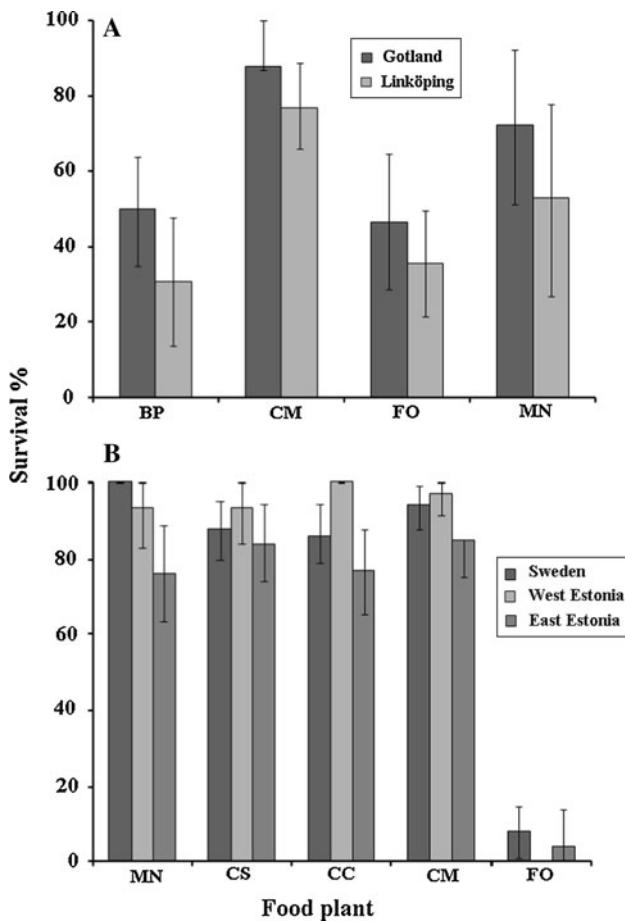

Fig. 4 The survival ($\dot{x}$ ± binomial error bars indicated) of the larvae representing the two Swedish populations from Gotland and Linköping (**a**) and the populations of Sweden, eastern and western Estonia (**b**) on potted live plants (**a**), or pieces of food plants (**b**). Figs 2 and 3 for abbreviations

information on host plant identity can only play a minor role in oviposition decisions of *L. achine*. Our results are thus in some conflict with field observations by Bergman (2000) who found the tendency of *L. achine* females to oviposit in the vicinity of *C. montana* plants. Nevertheless, the study design by Bergman (2000) did not exclude the possibility that microhabitat parameters rather than plant species itself constituted the proximate cue for oviposition. Further experiments where microclimatic conditions and host plant availability is varied independently at a larger spatial scale are necessary to definitively resolve this issue.

Oviposition behaviour indiscriminate to host plant species is in accordance with the female habit not to oviposit directly onto the plant but just to drop them on the soil. However, insensitivity to host plant is no way a trivial consequence of such a behavior. For example, females of the geometrid moth *Scotopteryx chenopodiata* do not attach their eggs to the plant either but oviposition behavior is nevertheless, strongly affected by the presence of a suitable host plant (Tammaru and Javoiš 2000; Javoiš and Tammaru 2004). Similarly, a study by Konvička and Kuras (1999) found that females of the butterfly *Parnassius mnemosyne* chose to lay their eggs freely on soil but still in the vicinity of the bulbs of the host plant, *Corydalis spp*.

Indiscriminatory oviposition in *L. achine* implies that it is the task of the newly hatched larvae to find a suitable host plant. Indeed, our experiments confirmed the observation by Bergman (2000) that the larvae are capable of host selection: the least suitable host, *F. ovina*, was largely (though not invariably) rejected. The differences in the acceptability of other potential host plants did not, however, differ markedly. Nevertheless, the preference of neonate larvae was in reasonable concert with growth performance: the two host species best supporting the growth of the larvae (*M. nutans* and *C. sylvata*) were also among the most frequently preferred ones (Figs. 2 and 3). In any case, however, host choices made by the larvae cannot have a major ecological significance due to the limited mobility of the newborns in this species. In practice, host selection must be limited to plant individuals growing next to each other (Zalucki et al. 2002).

We found that almost all sedges and grasses offered to *L. achine* larvae were close to be equally suitable for *L. achine* larvae; only one grass species, *D. flexuosa* was proven to fail to support larval development. We confirmed that *C. montana* is a favorable host for this species but could not repeat the results by Bergman (2000) who showed its' clear superiority over alternative hosts. The results of our two rearing experiments differed with respect to *F. ovina* but we suspect a technical reason here: in the experiments on pieces of host plant, the larvae were fed with plant fragments. Fragments of *F. ovina*, a particularly thin-leaved species, somewhat wilted in experimental

conditions during the three days, apparently turning to a low-quality food for the larvae. This result should not be interpreted as a failed element of the experimental design but rather as providing relevant ecological information: the larvae of *L. achine* are highly sensitive to wilting host plants which should contribute to the species' preference to forests rather than open meadows. This is also in line with results showing that dry conditions reduce egg survival in *L. achine* to a much higher degree than in other closely related species (Karlsson and Wiklund 1985).

Importantly, we were unable to show the existence of any among-population differences in the preference of, or performance on different host plants. Larvae from all the studied populations least preferred *F. ovina*; all populations showed no major differences in acceptance of, or performance on other plants. If anything, the differences in host plant relationships of different populations of *L. achine* appear to be limited enough to have only a marginal ecological significance. In any case, there was no indication of a difference in the expected direction, i.e. no evidence of the specialization of Swedish and western Estonian but not eastern Estonian populations on *C. montana*.

In summary, our results suggest that *L. achine* is broadly polyphagous on grasses and sedges. For this reason, we have to conclude that host species composition per se is of low importance regarding habitat quality for *L. achine*. There may only be some weak preference for soft- and broad-leaved grasses and sedges (*C. montana, C. sylvata, M. nutans* in our sample), which may partially explain the tendency of the species to prefer moist forests. For quite obvious ecophysiological reasons, in dry locations, most grasses tend to have narrow and tough leaves to resist desiccation (Gurevitch et al. 2006). In fact, at the predominantly drier locations on calcareous soils typical of the islands of Gotland and Saaremaa, *C. montana* may frequently be the only soft- and broad-leaved grass or sedge available for *L. achine*. This may well explain why exactly this plant may be the primarily used one in such situations.

From the conservationist point of view, the results of the present study are consistent with the habitat-oriented conservation practice of the species (Bergman 2001, 2005). Primarily, the species appears to require moderately moist forest landscapes with half-open elements (Bergman 2001; Bergman and Landin 2002; Bergman 2005), which is the vegetation creating suitable conditions for mesophytic grasses and sedges, i.e. the conditions which are shady and humid enough to prevent the host plants from drying before the larvae reach the developmental stage suitable for hibernation. Of practical importance for species conservation is also the conclusion that despite the genetic divergence of populations in northern Europe (Kodandaramaiah et al. 2012) there were no significant differences in adaptations underlying host plant use between populations,

which suggest that we are able to transfer ecological knowledge from country to country, at least across northern Europe.

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