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Suboptimal patch and plant choice by an ovipositing monophagous moth – an insurance against bad weather?

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The egg distribution of the monophagous noctuid moth *Abrostola asclepiadis* was related to the characteristics of host plant patches and individual plant shoots. Both the density and size of egg batches were greater in small, shaded host plant patches than in large, sun-exposed ones, and egg batches were larger on short host plants than on tall ones. We examined the consequences of this egglaying 'preference' on offspring performance.

In the field, there was no difference in either egg or larval mortality between patches differing in degree of sun exposure or size. Nor did mortality differ between batches on small plants and those on taller plants. Furthermore, neither larval growth rate nor pupal size showed any relation to egg-laying 'preferences'. Larvae fed foliage from small, shaded plants ended up smaller than larvae fed foliage from large, sun-exposed plants, but the development rates of the two groups were similar. There was no difference in weight or rate of development between larvae fed foliage from large, sun-exposed plants and those fed foliage from large, shaded plants. Hence, neither the 'preference' for certain patches nor that for certain host plant individuals seemed to be related to larval performance.

Reasons for the tendency to deposit large egg batches on small plants remain obscure. However, there is an alternative explanation as to why more eggs were laid in shaded patches, namely that these patches are less subjected to drought, and host plant wilting is therefore less common. An 18-yr record shows that droughts intermittently cause severe drying out of plants in sun-exposed, rocky positions.

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In many species of insect herbivores, the female choice of an oviposition site is of great importance to her offspring. Larvae, which usually have a limited dispersal ability, can only survive if eggs are deposited close to suitable host plants. However, it is not always clear what makes a plant suitable, and the linkage between preference and suitability may be weak or absent (Wiklund 1981, Thompson 1988, Courtney and Kibota 1990, Price et al. 1990). Thus, in addition to choosing the host plants that provide the best quality food for their offspring, the female may also prefer plants that are more abundant (Root 1973), support more offspring (Jones and Ives 1979), provide a better microclimate (Forsberg 1987), provide protection from enemies or diseases (Damman 1987, Courtney 1988, Denno et al. 1990, Schultz and Keating 1991, Ohsaki and Sato 1994, Hacker and Bertness 1995) or have a lower chance of drying out (Singer 1972).

Oviposition patterns may also be constrained by factors that do not relate directly to host-plant or habitat suitability. Many host plants have a patchy distribution, necessitating longer flights between egg-laying opportunities. Female motivation to oviposit may vary with the time elapsed since start of flight

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(Jaenike 1978), age, nutritional status or eggload, as well as with weather conditions (Gossard and Jones 1977). Hence, patterns that are often interpreted as the result of 'preferences' may actually have been governed by a sequence of situations that left few options. In general, females cannot afford to 'comparison-shop' but instead must decide whether or not to accept each potential oviposition site in a series of 'take-it-or-leave-it' offers (Jones 1991).

Furthermore, some types of oviposition behaviours suggest that females may spread out risks of predation or parasitization (e.g. Root and Kareiva 1984). Thus, some female butterflies follow more or less linear routes, along which they make intermittent stops and oviposit without considering resource abundance (Jones 1977, Root and Kareiva 1984), whereas other butterflies turn to the nearest plant from a random point (the female position, Mackay and Singer 1982). Both behaviours lead to an aggregation of eggs on isolated plants or plant clusters. Root and Kareiva (1984) modelled this behaviour for the cabbage butterfly and found that the variability in offspring mortality was averaged out.

This study describes egg distribution patterns in the field and analyses their consequences in the monophagous noctuid moth *Abrostola asclepiadis* Schiff. (Lepidoptera: Noctuidae), which lives on a patchily distributed herbaceous host plant, *Vincetoxicum hirundinaria* Med. (Asclepiadaceae). The aims were to 1) examine how egg batches were distributed on plants of different sizes and in patches differing in size and degree of sun exposure, 2) determine how these 'choices' with regard to plant and patch characteristics affect the survival and development rate of offspring. Consequences for the population dynamics of the species are discussed.

Material and methods

Organisms and study areas

The noctuid moth *Abrostola asclepiadis* feeds exclusively on the perennial asclepiadaceous plant *Vincetoxicum hirundinaria*. Adults usually hatch in the beginning of June and oviposition starts shortly thereafter. Eggs are laid in small batches (median batch size was 3 eggs) on host plant leaves. Development of eggs and the five larval instars is completed in about six weeks. The first two larval instars usually remain feeding on the leaves of the native plant, whereas larvae in later instars may move around between plant shoots, concentrating their feeding to the upper parts of the host plant. Younger larvae feed during all parts of the day and night, whereas larvae in the two final instars stay concealed in the vegetation close to the ground during daytime and feed at night. Pupation takes place in leaf litter and moss during August. A detailed account of the biology of the moth is given in Förare (1995a).

The host plant grows in tufts, often comprising more than fifty shoots, that originate from rhizomes. Several tufts make up a patch. Studies were conducted in host plant patches around the town of Uppsala (north of Stockholm, Sweden at 59° 49′N, 17° 39′E) and at Tullgarn (south of Stockholm, at 58° 58′N, 17° 35′E, cf. Solbreck and Sillén-Tullberg 1986).

Eggs and larvae were monitored in plots. Plots were sections, usually quadratic, of plant resource within the patches. One to three plots of sizes from 0.5 to 5 m^2 of plant resource (representing about 50 to 1500 plant shoots) were selected in most patches (which ranged from 2.5 to 200 m^2 of host plant resource). For the two smallest patches all shoots were monitored. There was a total of ten plots in five patches sampled around Uppsala and eight plots in six patches at Tullgarn. The plots were designated as being either shaded (by dense forest or the canopy of large trees) or sun-exposed (growing on exposed, bare cliffs or at field margins) and as belonging to a large (>11 m^2) or a small (<11 m^2) patch (the breakpoint being chosen as the median size of the Uppsala set). Thus, in large patches there was often one shaded and one exposed plot, while in small patches there was only one category of exposure. The plots were considered as independent samples in the analysis, since within the same patch they were separated from each other by distances of more than 20 m. This design was chosen to ensure that several plant clones would be represented, as well as to eliminate the risk of encountering the same larvae in more than one of the plots in the same patch. Furthermore, all patches in the investigation were situated less than 2 km away from several large patches. At this scale, isolation is not considered important for *A. asclepiadis* (Förare 1995b).

To investigate the role of plant size in oviposition, shoot lengths of randomly chosen individual shoots (see next section) were classified into short (<15 cm), medium (15–50 cm) and tall (>50 cm) groups. A tall shoot has more leaf area than is normally needed for a single larva to complete development (a 50-cm plant usually carries the necessary 170–200 cm^2, Förare 1995a).

To compare larval mortality between small and large plants in the field, only two size categories were used. This was because field notes only discriminated between plants shorter or taller than approximately 15 cm.

Field and laboratory studies

For five summers, all eggs and larvae were monitored weekly in all plots, from the onset of oviposition until no more final instar larvae were encountered (Förare 1995b). There was rarely more than one egg batch on each shoot. In total, more than 2000 egg batches were encountered and shoot length was recorded for a total of over 600 randomly chosen shoots.

Since eggs were sought only once a week, a correction had to be made for the number of new eggs after each visit. The observed number was multiplied by a factor corresponding to eggs that might have disappeared before the visit, yielding an adjusted egg number. The correction factor was obtained from the disappearance rate of undeveloped eggs, and the number of batches was increased according to the adjusted number, dividing it by 3, the median batch size (Förare 1995b). The estimate of egg mortality included all eggs that had been parasitized, preyed upon (sucked out or disappeared) or died from unknown causes (including some probably unfertilized eggs).

There was no consistent pattern of change in mean batch size with time from the onset of oviposition, except for two different years in two plots, where there was a significant negative relationship. These two cases were interpreted as resulting from mass significance, since altogether about 80 relationships were tested (Spearman rank correlation test).

An experiment was set up to determine if larval performance depended on plant phenotype. Earlier observations suggested that high densities of eggs often occurred in shady patches, and that large egg batches were often deposited on small plants (usually newly established from seeds), both in shaded and sun-exposed patches. Eggs from more than 100 batches were collected around Uppsala in the summer of 1994 and brought to rearing cabinets. Using a split brood technique, eggs were placed in plastic Petri dishes, kept in plastic bags, with moist filter paper on leaves from one of three plant categories: 1) large exposed plants, 2) large shaded plants and 3) small shaded plants. All plants were taken from different parts of the same, large (>80 m^2) patch. This procedure probably yielded a random mixture of several plant genotypes. Leaves from intermediate nodes were picked in the laboratory and given as larval food. Fresh leaves were provided three times a week and the filter paper kept moist by watering. Eggs and larvae were kept at one of four temperatures: 14, 18, 22 and 26°C under a long-day light regime of L:D 22:2. These settings encompassed the mean summer temperature (around 16°C), and the daylength corresponded to natural light conditions at the onset of the experiments (around midsummer). As measures of larval performance, developmental rate (the inverse of development time from egg hatch to pupation in days) and pupal weight were used. Fresh weight was measured 1–2 d after pupal formation.

The egg batches used in the experiments had all been found on medium and tall plants (see previous section) and mostly in sun-exposed positions. Furthermore, batches usually consist of only a few eggs (Förare 1995a), and many eggs were parasitized or failed to hatch. Therefore it was not possible to get enough data to analyse within-batch differences in offspring performance among foliage categories in relation to the original plant category chosen by the female.

Statistical procedures

Some field data were transformed to allow analyses using parametric methods (factorial ANOVAs and regression analyses). The egg batch density for each plot was calculated as a logarithmic ratio: log(no. of batches + 1)/log(amount of leaf area in plot). The egg mortality ratio was arcsine-transformed according to the Freeman and Tukey procedure described by Zar (1984).

Larval mortality was estimated as a k-value in the ANOVA, i.e. the difference between the logarithms of hatched eggs and number of last-instar larvae, replacing zeroes in the latter term by 0.1, where they occurred.

Plots were regarded as independent units. All ANOVAs were performed in two steps: the first on plot means from all five years, with plot size and sun exposure as independent factors, and the second investigated differences between years for the whole dataset. Data for both study areas were pooled after testing means for equality with a t-test ($P>0.05$ in all mean comparisons). Field data that did not approach normality upon transformation were tested using non-parametric methods (Mann-Whitney U-tests, Kruskal-Wallis test). Data from the laboratory experiments were treated with standard linear regression and ANOVA.

Results

Distribution of eggs in relation to patch and plant characteristics

The density of *A. asclepiadis* egg batches in host plant patches seemed to be affected by a combination of patch size and degree of sun exposure. Egg batch density did not differ with degree of sun exposure (Fig. 1, Table 1), but was significantly higher in small patches than in large ones (Fig. 1, Table 1). Although there was no significant effect of exposure, there was a significant interaction between patch size and exposure (Table 1). Thus, small, shaded patches had higher batch densities compared with other patch types. There was also a significant difference between years, but there were no interactions between year and patch size or sun exposure (Table 1). Egg batch size was larger in shaded patches than in exposed ones (Fig. 2A) and was also larger in small patches than in large ones (Fig. 2B).

Plant characteristics also seemed to affect egg distribution, with shorter plants within a patch tending to receive more eggs. A comparison of all shoots with

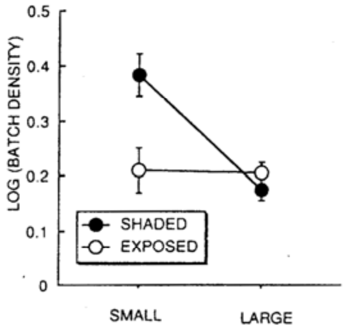

Fig. 1. Egg batch density of *Abrostola asclepiadis* in relation to degree of sun exposure and size of host plant patches. Batch density was log transformed (see text). Means ± s.e. are shown. For statistical tests, see Table 1.

batches showed that shorter shoots received the largest number of eggs (Fig. 3). Note that small plants not only received more eggs per plant, but also ended up with more eggs per unit leaf area.

Egg and larval mortality in the field

Patch type

Egg mortality did not differ significantly between exposed and shaded patches or between small and large patches (Table 2). There was a significant difference among years, but no interactions between year and patch variables (Table 2). Patch size and degree of sun exposure did not affect larval mortality (Table 3). There were, however, differences in larval mortality between years and an interaction between year and degree of sun exposure (Table 3).

Plant height

Egg mortality did not differ between batches on plants in different height categories ($P = 0.10$, Kruskal-Wallis test). Larval mortality with regard to plant height is harder to investigate, since larvae move around. In a small patch, where all shoots were monitored during a summer, no larvae from small plants (< 15 cm) were ever observed to reach the final instar. However, survival rates of the larvae from the two categories of plants did not differ significantly from each other (Table 4).

Table 1. ANOVA table for the density of egg batches (1990–1994) in plots in two study areas with year, patch size and degree of exposure as independent variables. In the upper part, the effects of size and sun exposure are tested on plot means for all years, while in the lower part the differences between yearly means are assessed.

Factor	df	Mean square	*F*	*P*
Size	1	0.040	8.089	<0.05
Sun exposure	1	0.018	3.642	0.077
Size × Sun exposure	1	0.037	7.436	<0.05
Residual 1	14	0.0050		
Year	4	0.142	17.863	<0.001
Size × Year	4	0.010	1.278	0.287
Sun exposure × Year	4	0.0043	0.543	0.705
Size × Sun exposure × Year	4	0.0027	0.340	0.850
Residual 2	70	0.0080		

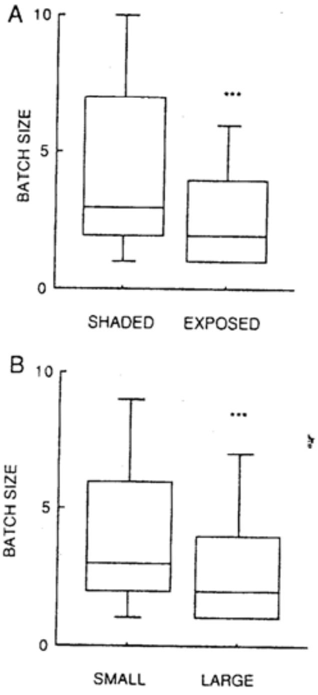

Fig. 2. Egg batch size of *Abrostola asclepiadis* in relation to (A) degree of sun exposure and (B) size of host plant patches. Medians, 10th, 25th, 75th and 90th percentiles are shown. *** denotes a significant difference between the medians at the 0.001-level (Mann-Whitney U-test).

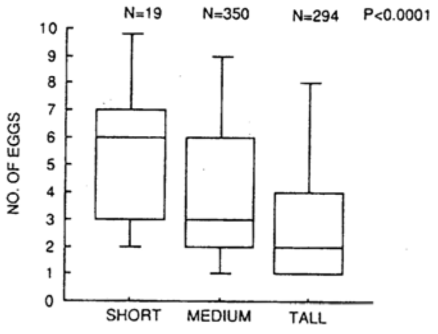

Fig. 3. Numbers of *Abrostola asclepiadis* eggs on *Vincetoxicum hirundinaria* plants in different height categories at Uppsala and Tullgarn 1990–1994. Data are represented as in Fig. 2. *P*-value refers to a Kruskal-Wallis test.

Table 2. ANOVA table for egg mortality (1990–1994) in plots in two study areas with year, patch size and degree of exposure as independent variables. In the upper part, the effects of size and sun exposure are tested on plot means for all years, while in the lower part the differences between yearly means are assessed.

Factor	df	Mean square	F	P
Size	1	0.125	3.228	0.094
Sun exposure	1	0.020	0.518	0.484
Size × Sun exposure	1	0.005	0.126	0.728
Residual 1	14	0.039		
Year	4	0.376	3.725	<0.01
Size × Year	4	0.171	1.688	0.165
Sun exposure × Year	4	0.144	1.422	0.238
Size × Sun exposure × Year	4	0.037	0.368	0.830
Residual 2	59	0.101		

Performance on different plant phenotypes in the laboratory

One reason for depositing larger egg batches on small plants could be to provide young larvae with the small and tender leaves, which are characteristic of (mostly newly established) small plants both in the sun and in the shade. These leaves are presumably easier to chew and digest. But young larvae (first two instars) of *A. asclepiadis* fed three different extreme plant phenotypes, viz. large, sun-exposed (toughest leaves), large shaded and small shaded (most tender leaves), did not show any significant differences in development rates (Fig. 4A, Table 5A). Nor could any differences be found when the entire larval period was considered (Fig. 4B, Table 5B). Hence, no effect of plant phenotype on developmental rates could be detected.

However, pupal weight was affected by plant phenotype. Larvae fed foliage from small, shaded plants ended up significantly smaller than larvae fed foliage from exposed plants (Fig. 5, Table 6). Furthermore, pupae from all treatments were significantly smaller at the highest temperature compared with those at lower temperatures ($P < 0.01$ in all comparisons within treatments).

Table 3. ANOVA table for larval mortality (1990–1994) in plots in two study areas with year, patch size and degree of exposure as independent variables. In the upper part, the effects of size and sun exposure are tested on plot means for all years, while in the lower part the differences between yearly means are assessed.

Factor	df	Mean square	F	P
Size		0.175	1.418	0.254
Sun exposure	1	0.007	0.057	0.814
Size × Sun exposure	1	0.030	0.246	0.627
Residual 1	14	0.123		
Year	4	1.234	6.149	<0.001
Size × Year	4	0.047	0.237	0.917
Sun exposure × Year	4	0.555	2.767	< 0.05
Size × Sun exposure × Year	4	0.215	1.073	0.378
Residual 2	56	0.201		

Table 4. Number of *Abrostola asclepiadis* offspring that died as eggs or young larvae or successfully reached the last instar in a patch outside Uppsala in 1992. Fisher's exact test: $P =$ 0.238, NS.

Plant size	No. surviving to the last instar	No. dying
Tall	15	248
Short	0	42

Discussion

Abrostola asclepiadis ovipositing on *Vincetoxicum hirundinaria* showed egg-laying 'preferences' at both the patch and the plant levels. Females laid more and larger batches in small and shaded patches and larger batches on small plants. Furthermore, the relationships were consistent over years with different egg densities. However, there seemed to be little correspondence between these 'preferences' and any aspect of offspring performance.

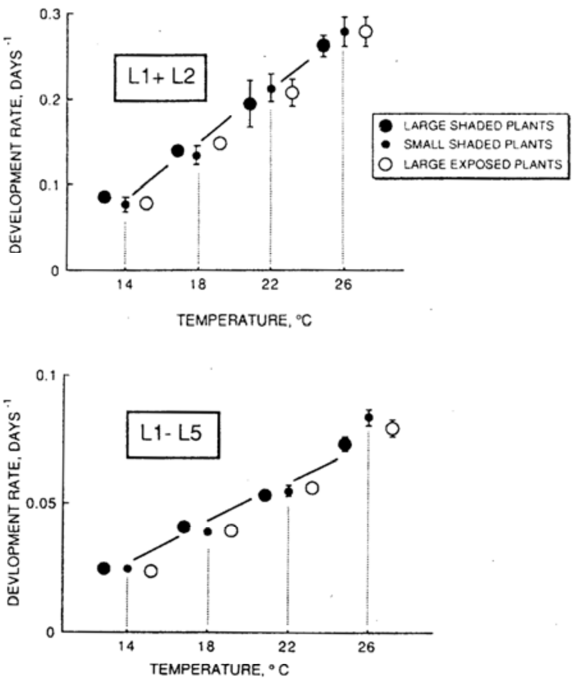

Fig. 4. The relationships between temperature and (Top panel) development rate for the first two larval instars. (Bottom panel) development rate for the whole larval period, from egg hatch to pupal formation, for larvae of *Abrostola asclepiadis*. Means ± s.e. is shown together with a common regression line for all treatments.

Table 5. ANOVA table for the development rate of the first two larval instars with temperature and leaf type as independent variables. B. ANOVA table for the development rate of all five larval instars with temperature and leaf type as independent variables.

A. Variable/interaction	df	Mean square	*F*	*P*
Temperature	3	0.107	121.7	<0.001
Leaf type	2	0.00028	0.323	0.725
Temperature × Leaf type	6	0.00031	0.348	0.908
Residual	58	0.00088		

B. Variable/interaction	df	Mean square	*F*	*P*
Temperature	3	0.00874	380.6	<0.001
Leaf type	2	0.00004	1.603	0.210
Temperature × Leaf type	6	0.00005	2.193	0.056
Residual	58	0.00003		

At the patch level, neither egg nor larval mortality varied significantly between patches differing in size or degree of sun exposure. At the plant level, the mortality of eggs laid on small plants was about equal to that of eggs placed on tall ones. Mortality of larvae on short plants seemed not to differ from that of larvae on larger plants. Furthermore, in the laboratory, larvae reared on foliage from the 'preferred' short, shaded plants did not grow faster or become larger than larvae reared on other kinds of foliage; rather the opposite at the highest temperature. But this could be due to a higher water loss from small leaves at that temperature, despite the countermeasures taken (fitting the Petri dishes with moist filter paper and keeping them in plastic bags). How then can this discrepancy between preference and performance be explained in terms of host suitability, oviposition strategies and constraints?

First, females appeared to have laid a single, small egg batch on each selected plant. In addition, small host plant patches ended up with higher densities than large ones. Both these observations suggest that females were using a risk-spreading strategy similar to the one described for pierid butterflies (Jones 1977, Root and Kareiva 1984), in which butterflies fly along straight paths laying a single egg or batch in each patch encountered, regardless of patch size. As well, in *A. asclepiadis* also eggbatch size was larger in small and shaded patches. That small host plant patches tend to end up with higher egg and larval densities has also been shown when a larger number of patches around the Tullgarn area have been surveyed (Förare 1995b). Adult densities of *A. asclepiadis* are very low (Förare 1995b); thus it is unlikely that interference among egg-laying females could explain the observed distribution of eggs.

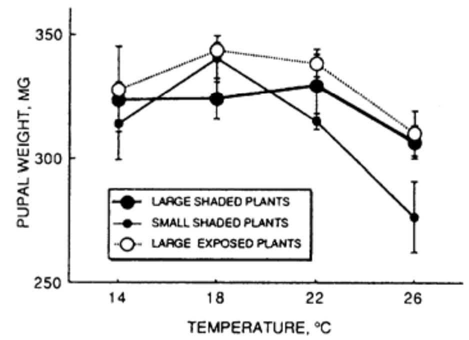

Fig. 5. The relationship between pupal weight and temperature for *Abrostola asclepiadis* larvae fed foliage from different categories of plants. Means ± s.e. is shown together with a common regression line for all treatments.

Table 6. ANOVA table for pupal weight with temperature and leaf type as independent variables.

Variable/interaction	df	Mean square	*F*	*P*
Temperature	3	5393.8	10.71	<0.001
Leaf type	2	1888.9	3.749	<0.05
Temperature × Leaf type	6	692.1	1.374	0.240
Residual	59	503.8		

Second, the seemingly maladaptive laying of large batches on small plants is difficult to explain. The foliage on these plants cannot support the growth of even a single larva to pupation and often gets entirely consumed by young larvae. Possibly, there is some shortcoming in the female's ability to assess plant suitability, or she may somehow find it easier to adopt a good egglaying posture on a shorter plant for physical reasons. Large batches on small plants could also be expected if females rest close to the ground on small plants during daytime. Unfortunately, direct observations of females, their preferences for flight in different habitats or egglaying behaviour (as in e.g. Rausher 1979) have not been possible. Nor have attempts at keeping adult moths in the laboratory to observe their behaviour been successful. Studies have only provided insight into the egglaying process at a larger scale. Females seem to have good means of dispersal, and did not seem to have any problems moving between the patches in the study areas (Förare 1995b). The high larval mortality found among the offspring from batches on small plants was probably associated with a dispersal forced by the small amount of food resources available at the oviposition site. Short plants are also likely to provide less physical protection for larvae. For example, Harcourt (1966) showed that *Pieris* larvae on small plants succumbed more easily to rainfall than larvae on larger plants. Many other examples of apparently maladaptive host plant choices, resulting in increased mortality, have been reported among butterflies (e.g. Dethier 1959, Courtney 1981, Singer 1984, Karban and Courtney 1987).

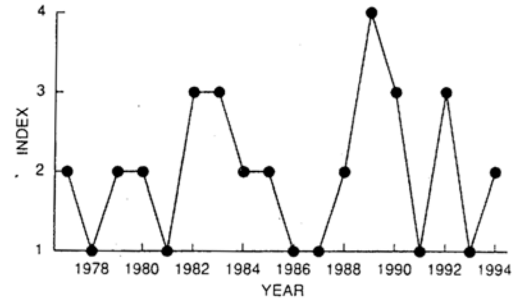

Fig. 6. An 18-yr drought index record for sun-exposed *Vincetoxicum hirundinaria* patches at Tullgarn. Index values denote increasing effects of drought: 1 = all plants show good vigour, 2 = some plants with wilted leaves, 3 = most plants with wilted leaves, some plants completely dried out (leaves fracture when squeezed), 4 = most plants completely dried out.

Third, it is possible that egglaying behaviour is related to some component of plant or patch quality not considered here. The present study dealt mostly with degree of plant exposure and patch or plant size, and less with other potentially important factors as nutritional composition and levels of secondary compounds. These factors could strongly influence the host suitability for a poisonous plant like *V. hirundinaria*, inhabiting habitats with a thin and possibly nutrient-poor soil layer (Coley 1993). However, our results show that the suitability of foliage as food does not seem to differ much between the phenotypic extremes chosen in this study. Furthermore, the difference observed was in the direction favouring the less 'preferred' sun-exposed plants. It is also interesting to note that the pattern of suitability is consistent over years. The experiments reported in this study were performed during a warm summer, but very similar results were obtained during the previous, unusually cold and wet summer (Engqvist 1995).

Available data (Solbreck and Sillén-Tullberg 1986, Solbreck unpubl.) instead suggest that the suitability of the host plant as food is determined more by its water status than by its nutrient status (cf. Scriber 1978). The results of several years of monitoring have showed that the degree of sun exposure may interact with weather in determining host plant suitability. For instance, under summer conditions with recurrent precipitation and moderate temperatures, exposed patches are likely to provide good conditions for egg and larval development. These patches provide a warmer microclimate, which speeds up development, thereby reducing egg and larval mortality, the predominant causes of population decline in this species (Förare 1995b). During such years, last-instar larvae are found earlier in exposed patches than in shaded ones. Nevertheless, overall egg and larval mortality did not differ between patch types.

However, conditions influencing development and survival may change dramatically in hot summers, when differences between plants growing in shaded and exposed areas can be pronounced. Drought occurs intermittently in sun-exposed portions of patches, leaving plants with wilted or totally dried up leaves, totally unsuitable as larval food. An 18-yr record from Tullgarn shows that this situation is not uncommon (Fig. 6). We believe that the high risk for drought in exposed areas can best explain the preference for shaded environments (cf. also Ehrlich et al. 1980, Murphy and White 1984). In the last year of the study (1994), a summer with dry conditions during the larval period, no larvae survived to the last instar in the exposed plots in the Tullgarn area (whereas nine completed development in shaded patches, Förare 1995b). Around Uppsala, where some additional plots were monitored that year, only one larva reached the last instar in an exposed patch, whereas about ten succeeded in shaded plots. Other possible explanations include a high enemy pressure in some of the large exposed patches, but there are no observations supporting such a habitat-related difference in predation pressure (Förare 1995b).

Thus, it seems likely that the recurrent droughts have shaped the pattern in egg distribution found in *A. asclepiadis*. Ehrlich et al. (1980) similarily demonstrated that drought had some dramatic and unexpected effects on checkerspot butterfly populations in California. Differences in survival due to variation in local climate have also been demonstrated in other studies (Singer 1972, Rodriguez et al. 1994). The present study highlights the importance of studying insect herbivores in a range of habitats and over a longer time period than is commonplace (cf. Rodriguez et al. 1994). Otherwise important selective forces in the environment that can strongly affect the spatial distribution may be overlooked. These forces may play an important role in the understanding of the larger scale dynamics of insect herbivore populations (cf. Solbreck 1995).

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