The discrepancy between food plant preference and suitability in the moth *Dysauxes ancilla*

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Growth responses to and preference for different food plants were studied in larvae of the geographically isolated Swedish population of the moth *Dysauxes ancilla*. Laboratory rearing of *D. ancilla* larvae showed that, besides a mixed diet, four species from different plant families supported development to the adult moth. There was a significant suitability order among these species according to higher female adult weight and shorter development time; mixed diet and *Calluna vulgaris* > *Hieracium pilosella* > *Thymus serpyllum* > *Brachytecium* sp. However, these species were not top ranked in preference trials by the larvae. Instead larvae preferred *Rumex acetosella*, a plant that did not support development to adult moth as a single food source. This discrepancy between larval performance and preference may be explained by advantages from food mixing by the polyphagous larvae; an improved nutrient balance, a possibility of diluting toxic secondary substances and of switching foods to fit changing physiological needs. In Nature other factors such as microclimatic conditions, predators and parasitoids probably also influence the foraging behaviour of *D. ancilla* larvae.

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The moth *Dysauxes ancilla* (Lepidoptera: Ctenuchidae) is an endangered species in Sweden, restricted to a single population only. It is not known which food plants are used by the larvae, even though the larva is considered polyphagous. The diet width and the pattern of host use may differ among populations in a polyphagous species. Host preference and suitability may be determined by allelochemicals, nutritional chemistry, plant morphology, microclimatic conditions, natural enemies and larval feeding pattern (Fox and Morrow 1981, Thompson and Pellmyr 1991, Renwick and Chew 1994). A good correlation between larval performance and preference implies that plant characteristics are the most important factors influencing the performance (Nylin and Janz 1993), while a low correlation implies that predation, parasitism and microclimate conditions are acting in the field (Scriber and Slansky 1981, Wiklund 1982). Therefore knowledge of the diet width and pattern of host use is essential for the understanding of the ecology of this endangered population.

The objective of this study is to determine growth responses to, and preference for, different food plants by the larvae of the Swedish population of *D. ancilla*. I used laboratory rearings in this study since the scarceness of the larvae makes it impossible to study the foraging behaviour in the field (cf. Betzholtz 2003). I also discuss what the present findings suggest for the larval food plant use in nature.

Methods

Study organism

The Swedish population of the moth *Dysauxes ancilla* (Lepidoptera: Ctenuchidae) is restricted to a small area of 4 ha near Beijershamn, on the Baltic island of Öland (Betzholtz and Lindeborg 1996). This population is geographically isolated from the species' continuous breeding area in central and eastern Europe (Rougeot and Viette 1980). In Sweden *D. ancilla* flies in one generation in July and hibernates in the larval stage. Many taxa are listed as food sources in literature. These include lichens such as *Parmelia* (Gymnocarpeae), bryophytes such as *Jungermannia* (Jungermaniaceae), seed plants like *Plantago* (Plantaginaceae) and some Asteraceae such as *Lactuca*, *Taraxacum* and *Senecio*, and litter (Höfner 1905, Razowski 1971, Rougeot and Viette 1980, Koch 1984, Chinery 1989, Ebert et al. 1994).

The habitat consists of dry meadows with short vegetation and solitary junipers and oaks. Within the habitat females oviposit, by dropping their eggs to the ground, in warm microclimatic positions with a high abundance of potential food plants (Betzholtz 2002, 2003). Hence the final choices of food plants are made by the larvae.

Larval performance

Larval survival, weight gain and development time were measured on thirteen food plants in a laboratory rearing experiment. This procedure measures, in isolation, the effect of plant quality as food (Courtney 1981). The different species were chosen to represent taxa suggested as food plants (see above), and to reflect the flora in the habitat of *D. ancilla* on Öland. A mixed diet, composed of all the plant species used in the experiment, was also included in the experiment.

Eggs from 6 wild caught females were hatched in 14 different cohorts consisting of 30 larvae each. Each female contributed 5 of the 30 larvae in each cohort. Larvae were kept individually in small pots in semi-natural conditions, in a cold storage room with windows. They were moistened regularly and fed ad libidum, and fresh food plants from the breeding habitat were served every third day.

Larvae, pupae and imagines were weighed on an elec-

trobalance with 0.1 mg accuracy. Before hibernation larval weights were sampled as the weight of a cohort, after hibernation larvae were weighed individually. Pupae were weighed at day 2 after pupation and adults were weighed about 3 hours after eclosion.

Larval preference

Larval choice of food plants was studied in preference trials, using small petri dishes. In this experiment I used a second set of larvae, from eggs oviposited by the 6 wild caught females described above. To find out if the preference for certain food plants varied during larval development I repeated the trials on three different occasions (August, April and June). The larvae were randomly chosen for the different trials on each occasion, and were offered a mixed diet between the different occasions. In each trial, which was replicated 10 times with 10 different larvae, I presented the larvae of two plant species only. The different species combinations (cf. Table 4) were chosen to compare the larval preference between different taxa suggested as food plants. Several trials included *Rumex acetosella* (Polygonaceae) because the rearing experiment indicated a high suitability for this plant at the time the preference trials started.

Two equally sized pieces of each of the two plant species, evenly spaced out at 0° and 180°, 90° and 270° respectively, were offered in the trials. The dishes were turned 90° every twelfth hour. Moist filter paper covered the bottom of the dishes. During three days and three nights the dishes were checked for foraging larvae every fourth hour. When the larva was feeding I recorded the plant species. The feeding frequency between larvae in the replicates differed. In some replicates the larva was recorded feeding only on a few occasions, while other larvae fed almost on every occasion checked. Therefore, in the evaluation of the trials this variation in feeding frequency among larvae was excluded by scoring the plant species with the highest number of feeding records in each replicate as 1. If both plant species had equally feeding records, they were each given a score of 0.5. Hence every trial, containing ten replicates, had a total score of 10.

Statistics

Survival differences to adulthood, among larvae reared on different food plants, were tested with chi-square statistics. Tablewide significance level was adjusted to a = 0.05 with sequential Bonferroni correction (Rice 1989). Differences in weight and development time among larvae reared on different food plants were tested with ANOVA, with the statistical package SPSS (Norusis 1993). To see if food choice was consistent across development the preference trials were tested with a homogeneity test (Zar 1999).

Results

Larval performance

The larvae grew slowly until the onset of hibernation, in the third instar, in September–October. After hibernation larval growth started in April and further accelerated in May. The larvae pupated, after five instars, in the beginning of June (Fig. 1).

Calluna vulgaris (Ericaceae), *Thymus serpyllum* (Lamiaceae), *Hieracium pilosella* (Asteraceae), *Brachytecium* sp. (Brachyteciaceae) and the mixed diet supported a significantly higher survival to adulthood than the other nine food plants (Table 1). *Quercus robur* (Fagaceae), *Plantago lanceolata* (Plantaginaceae) and *R. acetosella* supported an equally high survival as these plants up to hibernation. However, after hibernation larvae reared on these plants subsequently died. Surviving larvae reared on *R. acetosella* had the highest weight when hibernation was completed (Table 2).

Among the cohorts that survived to adulthood the weight of pupae and adults was significantly higher for the mixed diet and *C. vulgaris* than for the other three plant species, and for female pupae and adults there were also a significant difference among the other three species (*H. pilosella* > *T. serpyllum* > *Brachytecium* sp.; Table 2).

The mean development time, from hatched egg to adult moth, varied between 317 and 325 d and lasted significantly longer when larvae were fed with *Brachytecium* sp. (Table 3). There was no difference in total development time between the sexes (p = 0.865, $F_{1,88}$ = 0.03, ANOVA). However, male larvae had a significantly shorter development time than female larvae (p < 0.01, $F_{1,88}$ = 10.39, ANOVA), and female pupae a significantly shorter development time than male pupae (p < 0.001, $F_{1,88}$ = 85.63, ANOVA).

I did not estimate the exact consumption of different food plants in the mixed diet by the larvae. However, observations revealed that all species in the mixed diet, except for *Sedum acre* (Crassulaceae), *Deschampsia flexuosa* (Gramineae), *Juniperus communis* (Cupressaceae), *Galium verum* (Rubiaceae) and *Hypogymnia physodes* (Gymnocarpeae), were consumed, and also that individual larvae consumed several different species. During hibernation, larvae were partly active at temperatures from +2–3°C. During such periods larvae mostly fed on *Q. robur* litter.

Larval preference

Six out of eleven preference trials showed a developmental variation in preference of food plant by the larvae (Table 4). There was also a clear difference between the suitability order of plants in the rearing experiment and the result from the preference trials. In four out of the five trials without developmental variation larvae had a significant preference of one of the two available food plants. However, it was only in one of these trials that the larvae preferred the highest ranked plant species according to the rearing experiment. Instead larvae significantly preferred *R. acetosella* in those trials where it was included, even though this plant did not support development to adulthood. Further, *C. vulgaris*, the most suitable plant in the rearing experiment, was significantly preferred in one trial and rejected in another.

In five out of the six trials with developmental variation larvae significantly preferred one of the two plant species available, at least at one sample occasion. However, only in one of these trials did larvae prefer the highest ranked plant species. *Rumex acetosella* was significantly preferred in two out of three trials where it was included.
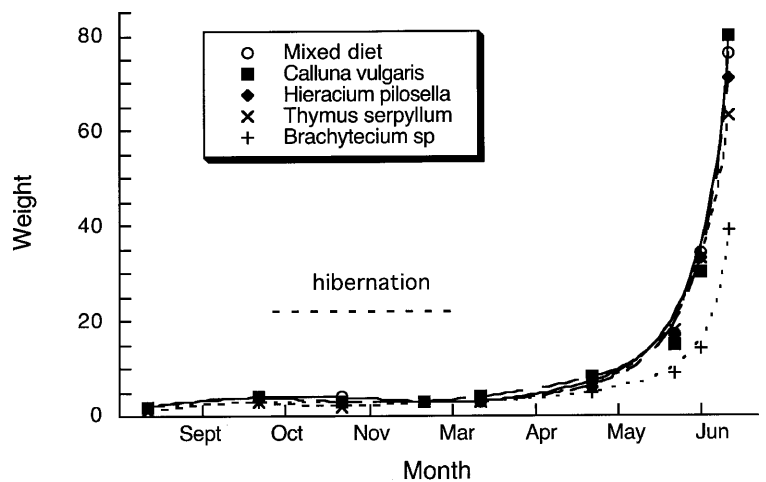
Fig. 1. Mean weight (mg) of *D. ancilla* larvae reared on different plant species that supported development to adult moth. The largest standard deviation in any cohort, at any time, is 18.6%.

Table 1. Survival of *D. ancilla* on different plant species from hatched eggs to adults in a rearing experiment. Each cohort initially consisted of 30 larvae. Survival was observed during four periods: I) from start of the experiment to onset of hibernation, II) hibernation, III) end of hibernation to pupation, and IV) the time spent as pupa to eclosion of the adult moth.

Plant species	No. individuals surviving Period			
	I	II	III	IV
Mixed diet[1]	26	26	23	23[a]
Calluna vulgaris	30	30	25	25[a]
Thymus serpyllum	30	30	24	16[a]
Hieracium pilosella	26	26	13	13[a,b]
Brachytecium sp.	25	25	18	13[a,b]
Sedum acre	10	9	5	4[b,c]
Quercus robur	30	30	2	2[b,c]
Plantago lanceolata	27	23	1	1[c]
Rumex acetosella	19	7	0	–
Hypericum perforatum	3	2	0	–
Deschampsia flexuosa	2	2	0	–
Juniperus communis	2	0	–	–
Galium verum	0	–	–	–
Hypogymnia physodes	0	–	–	–

[1] a mixture of all plant species used in the rearing experiment.
Survival differences to adulthood were tested with chi square statistics. Tablewide significance level (a=0.05) was adjusted with sequential Bonferroni correction. Plant species significantly different from each other are denoted by different letters.

Discussion

Nine plant species, representing taxa listed as food plants in the literature, did not support development to adulthood. However, *Q. robur*, *P. lancelota* and *R. acetosella* supported survival up to hibernation, but larvae reared on these plants subsequently died. This may be explained by nutritional deficiencies and by sensitivity to toxic secondary compounds. *Querqus robur* leaves contain tannins which, although not highly toxic, cause a complex binding of proteins and therefore reduce the nutritional intake of proteins for a herbivore. Thus, larvae of *D. ancilla* reared on this substrate may have died from nutritional deficiency. Larvae reared on *R. acetosella*, containing oxalic acid, and on *P. lanceolata* containing iridoid glycosides (Wahlberg 2001), may not tolerate large amounts of these compounds and died when the levels of these toxins became too high.

There was also a significant difference in weight gain and growth rate of larvae, among the four plant species that supported development to adulthood as single food

Table 2. Mean weight (mg) of *D. ancilla* larvae, pupae and adult moths on different plant species during development. Cohorts with less than five surviving larvae at any time during development have been excluded from the table. For pupae and adults, both male and female weights are given.

Plant species	Weight (mg)					
	Before hibern.	After hibern.	Pupae Males	Females	Adults Males	Females
Mixet diet	3.8	3.4[b]	38.7[a]	53.8[a]	19.3[a]	42.5[a]
Calluna vulgaris	3.8	3.5[b]	43.3[a]	56.5[a]	20.5[a]	45.0[a]
Hieracium pilosella	3.6	3.3[b]	32.5[b]	40.5[b]	15.0[b]	31.8[b]
Thymus serpyllum	3.0	2.6[b]	32.0[b]	35.6[c]	14.7[b]	25.5[c]
Brachytecium sp.	3.0	2.5[b]	26.6[b]	28.0[d]	13.8[b]	18.5[d]
Sedum acre	2.9	2.5[b]				
Quercus robur	3.2	2.8[b]				
Planatgo lanceolata	3.5	3.1[b]				
Rumex acetosella	5.5	5.2[a]				

Means followed by different letters (a–d) are significantly different (ANOVA, p<0.05, Tukey´s post hoc test). Before hibernation differences in weight between cohorts were not tested statistically, because larvae were not weighed individually until after hibernation.

Table 3. Mean development time (days) in preimaginal stages for *D. ancilla* on different plant species. Cohorts with less than five eclosed adults are excluded from the table.

Plant species	Development time (days)					
	Larvae		Pupae		Total	
	Males	Females	Males	Females	Males	Females
Mixed diet	301.0[a]	303.3[a]	16.4[a]	13.4[a]	317.4[a]	316.7[a]
Calluna vulgaris	300.8[a]	304.7[a]	16.8[a]	13.2[a]	317.6[a]	317.9[a]
Hieracium pilosella	301.4[a]	304.2[a]	16.9[a]	13.3[a]	318.3[a]	317.5[a]
Thymus serpyllum	302.7[a]	304.4[a]	16.1[a]	12.9[a]	318.8[a]	317.3[a]
Brachytecium sp.	312.8[b]	316.3[b]	12.2[b]	11.0[b]	325.0[b]	327.3[b]

Means followed by different letters (a and b) are significantly different (ANOVA, $p < 0.05$, Tukey's post hoc test).

sources. This suggests that these species have different food quality. Since the Swedish population of *D. ancilla* is a northern outpost population there may be selection for food-plant interactions with a rapid larval development since the vegetational period is shorter than it is within the species' continuous distribution area (Chew 1975). Rapid development can also shorten foraging time which may reduce predation and parasitation risks (Heinrich 1979, Butler 1985), and increase the larval survival (Thomas 1985). Among the four food plants that supported development to adulthood only *Brachytecium* sp. supported longer development time than the other species, and should therefore be considered less suitable for larval growth. The weight of female pupae and adults was higher and more variable than for male pupae and adults (Table 2). This suggests that females have different nutritional demands than males, which may be explained by a higher

relative contribution of larval nutrition to egg production (Scriber and Slansky 1981). There is also a general positive correlation between female adult weight and fitness in lepidopterans (Courtney 1981, Hesjedal 1983, Holliday 1985, Braby and Rhondda 1995). Therefore, the significant suitability order of food plants in the Swedish population of *D. ancilla*, judged by higher larval survival, higher female adult weight and shorter development time was mixed diet and *C. vulgaris* > *H. pilosella* > *T. serpyllum* > *Brachytecium* sp.

The four food plants supporting survival to adult moth belong to different plant families. This broad taxonomic range of food plants is uncommon in lepidopterans. However, polyphagous species may have a wide food plant range and many arctiid moths, taxonomically close relatives to *D. ancilla*, are considered as highly polyphagous (e.g. Singer and Stireman 2001). Observations in the

Table 4. Plant choice in larvae of *D. ancilla* at three different occasions during development; early August, early April and early June. Each trial had a total score of +10. The scoring procedure is described under methods. The first plant in each trial is the most suitable according to the rearing experiments.

Plant species	Sample occasion			Homogeneity test among sample occ.	Test of difference between species
	August	April	June		
Calluna vulgaris/ Thymys serpyllum	8/2	8.5/1.5	5/5	p = 0.058	21.5/8.5*
Calluna vulgaris/ Quercus robur	4.5/5.5	7.5/2.5	6/4	p = 0.165	18/12
Calluna vulgaris/ Rumex acetosella	3.5/6.5	1.5/8.5	2/8	p = 0.427	7/23*
Hieracium pilosella/ Rumex acetosella	0.5/9.5*	1.5/8.5*	5/5	p = 0.012	
Hieracium pilosella/ Plantago lanceolata	9.5/0.5*	5.5/4.5	7/3	p = 0.039	
Hieracium pilosella/ Brachytecium sp.	5/5	0/10*	6/4	p < 0.001	
Hieracium pilosella/ Quercus robur	4/6	0.5/9.5*	5.5/4.5	p = 0.005	
Brachytecium sp./ *Rumex acetosella*	3/7	7/3	3/7	p = 0.014	
Quercus robur/ Rumex acetosella	1.5/8.5*	5.5/4.5	3/7	p = 0.038	
Plantago lanceolata/ Rumex acetosella	2/8	2.5/7.5	5/5	p = 0.127	9.5/20.5*
Rumex acetosella/ Hypogymnia physodes	6.5/3.5	9.5/0.5	9/1	p = 0.129	25/5*

Homogeneity among the three occasions was tested for each trial. Data in homogeneous trials was pooled for the test of difference between species. In heterogeneous trials test of difference between species for each occasion was tested separately. Significant differences in preference between species (χ^2 contingency table, $p < 0.05$) are denoted by *.

mixed diet trials also showed that individual *D. ancilla* larvae consumed several different plant species. There are several advantages from such a food-mixing foraging behaviour. Larvae may mix different food plants to improve the nutritional balance (Bernays and Minkenberg 1997) or they may keep levels of secondary compounds low (Singer 2000), the latter discussed above for *D. ancilla*. Indeed several studies on grasshoppers, and a few studies on other insect taxa, demonstrated an increased survival and growth rate from food-mixing (MacFarlane and Thorsteinson 1980, Hesjedal 1983, Waldbauer et al. 1984, Nieminen 1996). Which of these factors that is most important for the food-mixing behaviour in *D. ancilla* larvae is not possible to tell from the results of this study. However, surviving larvae reared on *R. acetosella* had a significantly higher weight than larvae reared on any of the other species, and surviving larvae reared on *P. lanceolata* had equally high weights as larvae reared on the other plants in the rearing experiment (Table 2). Further, when active during hibernation, larvae in the mixed diet mostly fed on *Q. robur*. This suggests that plant species individually unsuitable for complete development are also included in the natural diet.

There are no indications that the most suitable plant for larval development in the rearings, *C. vulgaris*, is included in the natural diet. This plant was not consistently preferred in the preference trials, and it only grew in 8% of the plots where larvae were found (Betzholtz 2003). Larvae of *D. ancilla* have specific microclimatic demands of both warmth and humidity, and may not use a suitable food plant as *C. vulgaris* growing under the wrong microclimatic conditions. Another explanation is suggested by Bernays and Singer (2002), who pointed out the importance of avoidance of predation and parasitism for the foraging tactics of a polyphagous larvae. Larvae should avoid a host if it attracts parasitoids or invertebrate predators such as carabid beetles, ants and spiders. Further, Curl and Burbutis (1978) and García-Barros (1986) showed that ctenuchid moths are attacked by hymenopteran parasitoids. I have no evidence that there is a high predation or parasitoid pressure in or around plants of *C. vulgaris*, but no parasitism was detected in rearing of larvae of the Swedish population found in nature.

Larvae may also improve the fit for changing physiological needs during development by food-switching (Bernays and Minkenberg 1997), as shown in some species of Lepidoptera (Barbosa et al. 1986, Gaston et al. 1991). This is a possibility also in *D. ancilla*. The most suitable plant species in the rearings were not ranked highest in the preference trials. Instead there was an overall preference for *R. acetosella*, a plant not supporting development to adulthood. There was also a variation in preference for certain food plants during larval development indicating that food-switching may occur in the field. *Rumex acetosella*, *P. lanceolata* and *H. pilosella*, the latter also the second most suitable plant in the rearing experiment, were preferred in all trials in the end of larval development but not in all trials before and after hibernation. Even though all of these trials were not significantly different per se this suggests that these food sources play an important role at the end of development when most of the larval growth takes place. It is also interesting that *H. pilosella* and *P. lanceolata* occur more frequently where larvae are found, and that *R. acetosella* had an approximately equal occurrence as in the habitat as a whole, while the other suitable plants were less frequent (Betzholtz 2003). However, on the other hand the number of significant preference trials is lowest in June, in the end of larval development. This in turn suggests that there is a lower preference for certain food plants during this period. The possibility of food-switching in *D. ancilla* larvae should therefore be seen as more speculative. Performance advantages from food-mixing and food-switching may be tested by rearings of larvae with a mix of the above species, but also of other species combinations, performed in the same way as the rearings presented in this paper.

The overall understanding of host plant use and feeding patterns in polyphagous lepidopterans is poor. However, laboratory rearings of *Grammia geneura*, an arctiid moth with polyphagous larvae, demonstrated large performance differences among larvae reared on different food plants, but also that low quality food plant species were consumed in a mixed diet despite the presence of higher quality food plants (Singer 2000, 2001). A field study of the same species showed an opportunistic feeding behaviour determined partly by preference partly by food plant abundance (Singer and Stireman 2001). Such a feeding behaviour provides individual larvae to sample locally available food plants, which means they may adjust a nutritional imbalance, dilute toxic substances and respond rapidly to variations in resource quality.

Larvae of *D. ancilla* are ground-living, mobile and occur in the warmest parts of the habitat, where there is a high number of food plant species (Betzholtz 2003). Even though females oviposit in these positions larvae choose their microhabitats since the overall number of plant species is higher where larvae occur than where females oviposit. This suggests that larvae choose microhabitats with a high abundance of suitable food plants, as well as a high diversity of plant species. During extremely warm and dry years, plants in the microhabitats where larvae of *D. ancilla* occur may suffer from drought. This leaves a plant community that is more variable and unpredictable for the larvae. Larvae of *D. ancilla* therefore may have advantages from choosing microhabitats with a high diversity of plant species.

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