Habitat utilization by ovipositing females and larvae in an endangered population of the moth *Dysauxes ancilla* (Lepidoptera: Ctenuchidae)

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Abstract. Habitat utilization by ovipositing females and larvae was studied in the endangered Swedish population of the moth *Dysauxes ancilla*. Ovipositing females and larvae were found to have specific habitat requirements, being restricted to edge zones facing south and to an ancient shore line facing southwest. The dependence of these microhabitats can be ascribed to two factors. First, larvae occur where there are both a high abundance of food plants and well developed layers of *Quercus robur* litter. Second, being on the northern edge of the species' distribution the need for warm microclimatic conditions is strong. These conditions were only met in the preferred microhabitats. Among the larval food plants *Hieracium pilosella* was clearly indicated to be the most important species. The habitat preferred by larvae and ovipositing females constitutes a transient successional stage. This highlights the need of maintaining a continuity of the preferred microhabitats and prevent them from overgrowth.

Key words: conservation, food plant, larvae, microclimate, oviposition, Sweden

INTRODUCTION

Lepidopteran populations have declined in many parts of the world during the last century (Pollard & Eversham 1995). As a consequence, the interest in conservation work of Lepidopterans has increased. Several studies have shown that ovipositing females and preimaginal stages of Lepidoptera usually have a much narrower niche range than was formerly believed (Thomas 1984, New et al. 1995). This seems to be even more apparent in endangered species (e.g. Warren 1987), which require specific microclimatic conditions or host plants growing only at certain microsites (Thomas et al. 1986, Warren 1993, 1995). In early conservation attempts habitats were often set aside without identifying the needs of the endangered species in focus. This caused the extinction of several butterfly species in nature reserves in Great Britain (Thomas 1991). Thus, detailed knowledge of habitat requirements of ovipositing females and larvae is crucial for a successful conservation of endangered Lepidopterans.

The Swedish population of *Dysauxes ancilla* (Linné 1767) (Lepidoptera: Ctenuchidae) is currently restricted to a small area (4 ha) near Beijershamn on the Baltic island of Öland (Betzholtz & Lindeborg 1996). The population constitutes an isolated northern outpost, separated from the species' main distribution area in central and eastern Europe (Betzholtz 2000). The preferred habitat of the Swedish population consists of the edge zones of dry meadows with short vegetation and solitary junipers and oaks. An ancient shore line, 6000 years old, from the Litorina era is also part of the breeding habitat. This shore line is now 400 m from, and 5 m above, the sea level due to the postglacial landupheavel. It is 5 m wide and with a slope of 15° towards southwest. The vegetation of the shore line is an open short grass community.

During the last few decades overgrowth has led to a reduction of the species' habitat. As a result *D. ancilla* has disappeared from a large part of its former area and the population size was estimated

at approximately 2000 individuals in 1993 (Betzholtz & Lindeborg 1996). The species is listed as critically endangered in Sweden (Gärdenfors 2000).

In Sweden the species is univoltine. Adult moths fly between late June and middle July, and are active mainly during daytime and at dusk. The species hibernates in the larval stage. An experimental study of food plant suitability for larvae of *D. ancilla* (P-E Betzholtz, unpublished manuscript) showed that four plant species supported full development to the adult moth, as did a mixed diet composed of all plant species included in the experiment. According to survival, larval development time and female imago weight there was a significant suitability order between these plants. *Calluna vulgaris* (Ericaceae) and the mixed diet were equally suitable and preferred over *Hieracium pilosella* (Asteraceae) which was preferred over *Thymus serpyllum* (Lamiaceae) which was preferred over *Brachytecium* sp. (Brachytheciaceae).

The objective of this study is to determine the habitat and food plant preference by ovipositing females and larvae of *D. ancilla* in the field.

METHODS

Oviposition

Ovipositing females of *D. ancilla* sit low in the vegetation and drop their eggs to the ground, without attaching them to any substrate (P-E Betzholtz, unpublished manuscript). Females of some other species with polyphagous grazing larvae oviposit near but not on the preferred food plant (Thompson 1988, Bergman 1999). Therefore, I consider every oviposition as a choice of food plant or a choice of microclimatic condition.

I actively looked for ovipositing females in the habitat and immediately after oviposition the exact position of the oviposition site was recorded. I then measured the orientation to, and distance from, the nearest edge zone or the ancient shore line base for each oviposition. All plant species within 1 m² around the oviposition site were recorded.

Larvae

The edge zones and the ancient shore line, where females had been observed ovipositing, were searched for larvae along 15 randomly selected transects at three different occasions; late

September, early April and early June. The transects, 1 m wide and perpendicular to the edge zones, extended 5 m out on the open meadow and 5 m in under the tree canopy. Five transects were orientated towards south, five towards east and five towards west. In edge zones facing north I never observed any ovipositions. At the ancient shore line I had nine transects, perpendicular to the shore line and extending 5 m out from the base and top respectively. Larvae are partly active during night (P-E Betzholtz, personal observation). Therefore, one third of the transects were searched at night with a halogene spotlight.

Along the transects all larvae found were recorded and I noted orientation to, and distance from, the nearest edge zone or the ancient shore line base. All plant species within 1 m² around the larval finding were recorded.

All larvae found in the field were brought to the laboratory and reared. In this way information of the parasitoid pressure on *D. ancilla* was obtained.

Vegetation

To find out if there was a preference for certain plant species among ovipositing females or among larvae, I did a vegetational analysis. I randomly chose 50 1-m² plots in the dry meadows of the breeding habitat and recorded all occurring plant species including *Quercus robur* litter within the plots. I calculated the relative frequencies for each species by dividing the number of plots where the species occurred by the total number of plots analyzed. I used data from the oviposition and larval plots described above to calculate the relative frequency of all plants found in these plots. Then, I calculated the deviations between random plots, and oviposition and larval plots, for each plant species. The deviations were calculated as the relative frequency in oviposition or larval plots minus the relative frequency in the random plots. A positive deviation means a higher occurrence of the plant species at the oviposition or larval sites, a negative deviation a higher occurrence at the random sites.

C. vulgaris, *H. pilosella*, *T. serpyllum* and *Brachytecium* sp. supported full development to the adult moth in an experimental study (P-E Betzholtz, unpublished manuscript). These species are hereafter referred to as food plants. In order to compare their distribution across the edge zones, with the ovipositions and larval findings, I

determined their occurrence along the transects described above for the larvae. Along the transects I recorded the presence or absence of these four food plants, with all four treated as a group, in continuous 1 m² plots. I also recorded the presence or absence of *Q. robur* litter. The distribution of food plants and *Q. robur* litter was analyzed with a logistic model with distance from the canopy edge as regressor (Sokal & Rohlf 1995).

RESULTS

Thirty ovipositions were observed and 40 larvae were found in the field. Ovipositing females and larvae showed a strong affinity for the edge zones (ovipositions: *n*=23; larvae: *n*=26) and the ancient shore line (ovipositions: *n*=6; larvae: *n*=14), and only one female oviposited in a meadow far from any edge zone. 83% of the ovipositions and 70% of the larvae were found within 1 m from the canopy edge (Fig. 1). Edge zones facing south, that is orientated east-west, were preferred both by ovipositing females and larvae (ovipositions: X^2 =23.7, df=3, p<0.001; larvae: X^2 =29.8, df=2, p<0.001; Fig. 2). At the ancient shore line all six ovipositions were found within 2 m, and all larvae within 3 m, from the base.

All larvae were encountered during the survey in early June, and all except two were recorded during daytime. No parasitoids emerged from the larvae or pupae reared. All larvae were found on the ground and only where a layer of *Q. robur* litter was present. Furthermore six of the larvae were foraging, all on *Q. robur* litter, when encountered. To find out if the distribution of *Q. robur* litter was important to the larvae, I divided the 1 m² plots where larvae were found into three classes according to percentage cover of *Q. robur* litter; I: 0—25% coverage, II: 25—50% coverage, III: > 50% coverage. Since most larvae were found within 1 m from the canopy edge facing south, randomly chosen plots in this microhabitat were also analyzed for percentage cover of *Q. robur* litter. The distributions (larvae: I=4, II=11, III=25; random: I=12, II=14, III=14) differed significantly (X^2 =14.5, df=2, p<0.001), showing that larvae occurred in plots with well developed layers of *Q. robur* litter.

The frequencies of plant species at the oviposition, larvae and random sites are shown in Table 1. The plant frequency at the random sites differed significantly from those at the oviposition sites (X^2=36.4, df=21, p<0.05) and from those at the sites where larvae were found (X^2 =37.8, df=21, p<0.05). The difference was, in both cases, mainly due to the distribution of *Q. robur* litter (Fig. 3). Further, among the food plants of *D. ancilla* larvae only *H. pilosella* was frequent in the larval plots and in fact was more frequent there than in the habitat
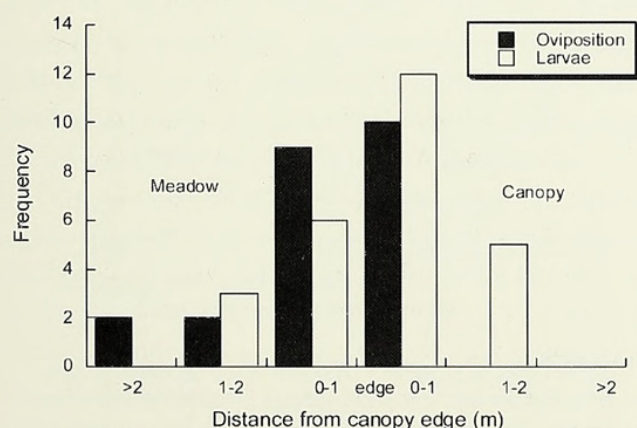

Fig. 1. Number of ovipositions (n=23) and findings of larvae (n=26) in *Dysauxes ancilla* at different distances from the nearest canopy edge.
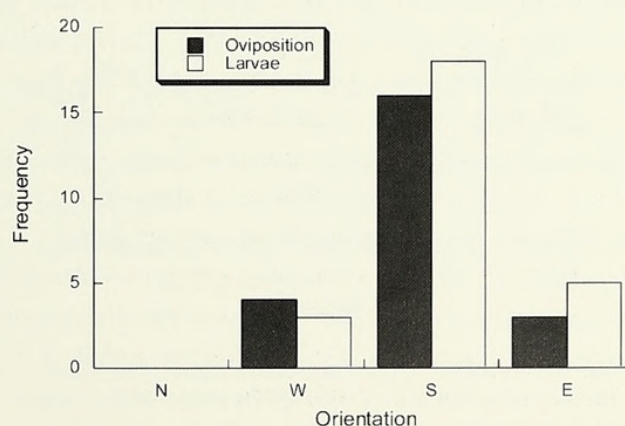

Fig. 2. Number of ovipositions (n=23) and findings of larvae (n=26) in *D. ancilla* in relation to the orientation of edge zones. Orientation denotes the direction that the edge zone is facing.

Table 1. Frequencies of plant species in 1 m² plots at the random sites (n=50), at the oviposition sites (n=30) and at the sites of larval findings (n=40) of *Dysauxes ancilla*. Plant species with five or less occurrencies at random sites are excluded from the table. The plant species are sorted after decreasing frequency at the random sites and the species number refers to Fig. 3.

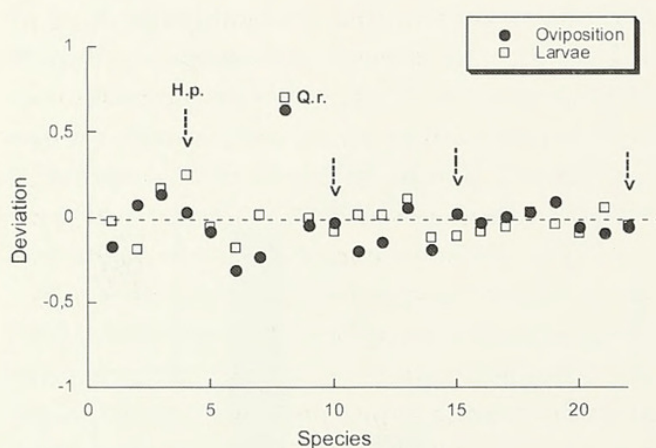|	Plant	Random	Oviposition	Larvae
1.	*Achillea millefolium*	35	16	27
2.	*Galium verum*	33	22	19
3.	*Deschampsia flexuosa*	25	19	27
4.	*Hieracium pilosella*	20	13	26
5.	*Festuca ovina*	19	9	13
6.	*Veronica officinalis*	19	2	8
7.	*Plantago lanceolata*	18	4	15
8.	*Quercus robur*, litter	15	28	40
9.	*Arrhenaterum elatius*	14	7	11
10.	*Brachytecium* sp.	13	7	7
11.	*Hypericum perforatum*	13	2	11
12.	*Lychnis viscaria*	12	3	10
13.	*Melampyrum pratense*	12	9	14
14.	*Rumex acetosa*	11	1	4
15.	*Calluna vulgaris*	9	6	3
16.	*Allium oleraceum*	8	4	3
17.	*Phleum pratense*	8	5	4
18.	*Potentilla argentea*	7	5	7
19.	*Rumex acetosella*	7	7	4
20.	*Sedum acre*	6	2	1
21.	*Sedum telephium*	6	1	7
22.	*Thymus serpyllum*	6	2	3

Fig. 3. Deviations in plant species frequency between random sites and sites of ovipositions and larval findings of *D. ancilla*. A positive deviation means that a plant has a higher relative frequency in the oviposition or larvae sites than in the random ones. It is clear that *Quercus robur* litter (Q.r.) has a much higher occurrence in oviposition and larvae sites than in random ones. Among the food plants of *D. ancilla*, denoted by arrows, *H. pilosella* (H.p.) is clearly indicated to be the most important species to the larvae. The species number refers to Table 1.
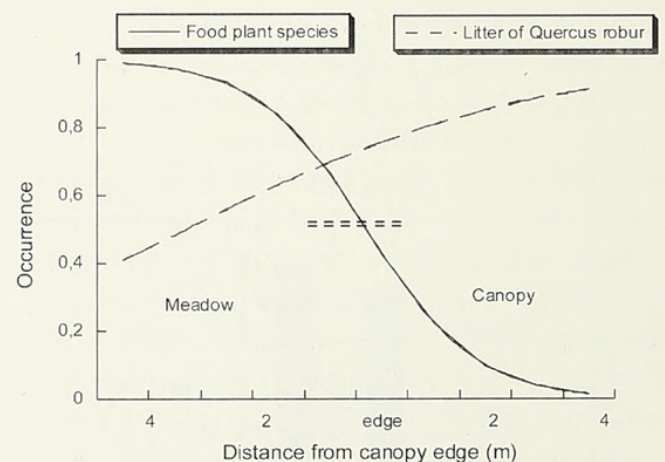

Fig. 4. Logistic regression models of the occurrences of *Q. robur* litter and food plant species for larvae of *D. ancilla* along 15 transects perpendicular to the edge zones. A high frequency of both *Q. robur* litter and food plants is only found in a narrow zone close to the canopy edge, where also larvae of *D. ancilla* were found (denoted by = = = =).

as a whole.

The plant frequency at the oviposition sites did not differ significantly from the one where larvae were found (X^2=25.3, df=21, p=0.236). However, the mean number ($\pm$ SD) of plant species was significantly higher at the sites where larvae were found (9.3 $\pm$ 2.7) than at the oviposition sites (7.8 $\pm$ 2.8) (t=25.9, df=69, p<0.001).

The occurrence of food plants was significantly higher out on the open meadow than under the canopy (Wald´s X^2=42.4, df=1, p<0.001, logistic regression; Fig. 4), while Q. robur litter was significantly more abundant under the canopy than out on the open meadow (Wald´s X^2=17.2, df=1, p<0.001, logistic regression).

DISCUSSION

The null hypotheses were rejected, showing that ovipositing females and larvae in the Swedish population of D. ancilla have specific habitat requirements. Both stages were restricted to edge zones facing south and to the base of an ancient shore line facing southwest. Several recent studies of endangered Lepidoptera also showed a very high specificity in niche range by the ovipositing females and the preimaginal stages (Thomas 1984, New et al. 1995). Two important factors determining niche range are food plant suitability and microclimatic conditions (Chew & Robbins 1984). Food plants of D. ancilla grew in all parts of the studied habitat but all ovipositions except one, and all the larvae, were found in the microhabitats described above. These microhabitats probably provide temperatures high enough since their orientation ensure a high solar insolation. This is consistent with the findings of Bourn and Thomas (1993) who pointed out that the abundance of food plants growing under the right microclimate conditions is more important to the preimaginal stages than the total abundance of food plants.

The oviposition behavior of D. ancilla differs from the majority of Lepidoptera (Chew & Robbins 1984) in that eggs are dropped to the ground and not attached to a plant substrate. Thompson and Pellmyr (1991) stated that such a behavior was associated with polyphagy in the larvae. Further, Porter (1992) pointed out that an apparent non-selectivity in female food plant choice can be related to a stronger dependency on microclimate conditions. The oviposition behaviour of D. ancilla could therefore be a strategy for occasions when high insolation and extreme drought only provide high humidity near the ground. High humidity has been shown an important factor in egg hatchability, especially in species which drop their eggs to the ground (Karlsson & Wiklund 1985, Bergman 1999).

In a univoltine species as D. ancilla, with hibernation in the larval stage, high ground temperatures in spring provide an early start of larval activity (Dugdale 1996) with an increased development rate and survival in larvae (Thomas 1985). Larvae of D. ancilla could also gain an extra advantage if they use the canopy edge in a flexible manner under extreme conditions. When weather is warm and dry the larvae may crawl into shady areas under the canopy, while remaining in the warmer edge zones during colder conditions.

All larvae were found in well developed layers of Q. robur litter. However, in a rearing experiment this substrate as a single food source did not support development to imago (P-E Betzholtz, unpublished manuscript). This indicates that Q. robur litter is not primarily used as a food substrate. Instead, I suggest that larvae of D. ancilla are dependent on a certain amount of humidity, as shown in other larvae of Lepidoptera living in the litter layer (Dugdale 1996).

The dependence on specific microclimatic conditions is pronounced in Lepidoptera living in the northern part of their distribution area (Warren 1989, Thomas 1993). The Swedish population of D. ancilla constitutes an isolated northern edge population. Thus, my results indicate that ovipositing females and larvae have a strong dependence of warm microhabitats with sufficient humidity, conditions only met in sun-exposed edges and slopes with Q. robur litter.

Among the food plants, according to the laboratory rearing experiment of D. ancilla, only H. pilosella had a higher relative frequency in larval plots than in random ones indicating it as the most important larval food plant. In addition, larvae of D. ancilla are mobile and starvation tolerant, surviving more than a week without food (P-E Betzholtz, unpublished data). Therefore, larvae should have no difficulty searching for foodplants growing in the proximity of the litter while spending most of the other time hiding in the litter. Dethier

(1987) observed the same pattern for *Diacrisia virinica* (Arctiidae), a polyphagous species taxonomically related to *D. ancilla*. High abundance of both food plants and *Q. robur* litter was only found in the narrow zone along the canopy edge and along the shore line base providing a likely explanation for occurrence of the larvae in these microhabitats.

There were no indication that *C. vulgaris*, the most suitable plant in the laboratory rearing experiment, was included in the larval diet. *C. vulgaris* had a lower relative frequency in the larval plots than in the random ones, and indeed only occurred in 8% of the larval plots. Other things being equal, it seems that the most suitable food plant should be included in the diet. Hesjedal (1983) showed that polyphagous species have a faster development, a higher weight gain and a higher reproductive capacity when feeding on the most suitable food plant. Furthermore, low correlation of larval preference and performance indicates that factors other than food plant characteristics influence larval performance (Wiklund 1982, Thompson 1988), especially in species where larvae feed as grazers and move among several plants during development (Thompson & Pellmyr 1991). One explanation for the poor correspondence in *D. ancilla* could be selection for enemy-free space (Gilbert & Singer 1975). If the selection pressure on larvae feeding on the suitable food plant species is very high due to parasitism (Bernays & Graham 1988), predation (Rausher 1979, Warrington 1985) or competition, then species lower in suitability rank may be used. In this respect it is of interest to note that there was no parasitism on larvae of *D. ancilla* found in the litter layer, and that *H. pilosella*, clearly the most utilized plant, was the second most suitable species in the laboratory rearing experiment (P-E Betzholtz, unpublished data). Ctenuchid species are attacked by ichneumonids (Curl & Burbutis 1978), and the taxonomically related *Paidia murina* (Arctiidae), is attacked by at least four different parasitoids (García-Barros 1984).

Another explanation for the poor correspondence is that *C. vulgaris* is rare in, or grows in unfavorable parts of, the breeding habitat of *D. ancilla*. However, the frequency of the perennial *C. vulgaris* is stable and grows along the preferred edge zones and on the ancient shoreline. Given the results of this study it is not possible to distinguish among the above explanations for avoidance of *C. vulgaris*.

I conclude that the habitat utilization of *D. ancilla* depends on choices made both by ovipositing females and in dispersing larvae. First, ovipositing females choose warm microclimatic sites with a high abundance of food plants and well developed layers of *Q. robur* litter. These conditions are only met along the edge zones facing south and at the base of the shore line facing southwest. Second, the free-living larvae search for, and stay on, suitable individual plants when foraging and spend most of their time concealed from predators and parasitoids in the litter. The ability of larvae to endure starvation permit them to disperse and find suitable microhabitats. Finally, *H. pilosella* is the most important food plant species for larvae of *D. ancilla* in this edge-of-range population.

CONSERVATION IMPLICATIONS

Ovipositing females and larvae of *D. ancilla* were found to have specific habitat requirements both with respect to warm microhabitats and vegetation composition. The preferred micro-habitats, edge zones of the dry meadows facing south and the ancient shore line, constitutes a successional stage that in the long run will be overgrown rendering the habitat unsuitable to *D. ancilla*.

During the last decades the area of the breeding habitat in Beijershamn has decreased by overgrowth (Betzholtz & Lindeborg 1996). Currently there are no other suitable habitats in the surrounding matrix. Hence, a key factor for short-term management to provide future survival of *D. ancilla* is to maintain these specific microhabitats. This could be achieved either by manual clearings at regular intervals or by selective grazing to prevent overgrowth. It is important to maintain both the warm edge zones and the plant community of the dry meadows containing *H. pilosella*. If the vegetation height of the dry meadows is allowed to increase, this will be harmful to the larval food plants of *D. ancilla*. However, some recently overgrown areas situated adjacent to the current breeding habitat still have a suitable flora. I suggest that these areas be improved by clearing of trees and shrubs. Several old oak trees remain in this area. If some of the oaks are spared,

there will also be suitable edge zones in the cleared area. The long-term survival of *D. ancilla* is dependent on the maintenance of suitable edge zones and openness which enhances the plant community of the dry meadows. Therefore, it is important to include the vegetation dynamics of the habitat, and the regeneration of future edge zones, into any management plan. The possibilities for creation of new suitable habitats in the surrounding matrix should also be considered. The Swedish population of *D. ancilla* thus far remains genetically intact (Betzholtz 2000), hence the population could be used for an expansion in the adjacent area.

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