

The life history and ecology of *Melitaea diamina* (Nymphalidae) in Finland

Niklas WAHLBERG

Department of Ecology and Systematics, Division of Population Biology, P. O. Box 17 (Arka-diankatu 7), FIN-00014 University of Helsinki, Finland

Summary

The previously unknown life history, ecology and early life stages of the endangered false heath fritillary *Melitaea diamina* (Lang, 1789) are described. The larval host plant in Finland is recorded definitely for the first time. Females lay eggs only on non-flowering *Valeriana sambucifolia* Mikan fil. plants. Larvae also feed exclusively on *V. sambucifolia*. Larvae go through six instars and diapause in the 4th instar. Males search for females using only the patrolling tactic. Females are more sedentary than males. The study contributes to the knowledge of other Melitaeini in Europe and North America.

Zusammenfassung

Es werden die bisher unbekannte Biologie, Ökologie und die ersten Stände der gefährdeten *Melitaea diamina* (Lang, 1789) beschrieben. Die Futterpflanze der Art wird für Finnland erstmals genannt. Die Weibchen legen ihre Eier nur an die noch nicht geöffneten Blüten von *Valeriana sambucifolia* Mikan fil. Die Larven fressen ausschliesslich an dieser Pflanze. Die Männchen finden die Weibchen, indem sie in den Habitaten auf- und ab patrouillieren. Die Weibchen zeigen ein eher träges Verhalten und sitzen in der Vegetation. Die vorliegende Untersuchung erweitert unsere Kenntnisse auch anderer die Melitaeini in Europa und in Nordamerika.

Résumé

La biologie, l'écologie et les stades pré-imaginaux, précédemment inconnus, de l'espèce menacée qu'est le Damier noir *Melitaea diamina* (Lang, 1789), sont décrits. La plante nourricière de la chenille en Finlande est indiquée avec certitude pour la première fois. Les femelles ne pondent que sur les plantes non en fleurs de *Valeriana sambucifolia* Mikan fil. Ces chenilles se nourrissent également exclusivement de *V. sambucifolia*. Les chenilles traversent six stades larvaires et entrent en diapause au quatrième stade. Les mâles adultes recherchent les femelles en utilisant la tactique du 'patrolling'. Les femelles sont plus sédentaires que les mâles. L'étude contribue à la connaissance d'autres Melitaeini étudiés en Europe et en Amérique du Nord.



Fig. 1. A mating pair of *Melitaea diamina*.

Introduction

The false heath fritillary *Melitaea diamina* (Lang, 1789) (Fig. 1) is a rare butterfly within much of its range in Europe (Heath, 1981). While some other Melitaeini species in Europe have been studied extensively (Porter, 1981 ; Warren, 1987a, 1987b, 1987c, 1994 ; Hanski *et al.*, 1994, 1995a, 1995b, 1996), very little has been published about the ecology and life history of *M. diamina* (see Ebert, 1991). In Finland, it is classified as endangered species and is protected (Rassi *et al.*, 1992). It occurs presently in two widely separated regions in south-western Finland (Marttila *et al.*, 1990) (Fig. 2). Prior to 1995, there were no records of the larval host plant in Finland and the ecology of adults was poorly known.

I studied the only well-known Finnish metapopulation of *M. diamina* in the Tampere region (Fig. 2) during spring and summer 1995. The main objective of this study was to survey an area of 20×30 km² for all suitable habitat patches and determine which patches were occupied by the species. The results of the survey are presented else-

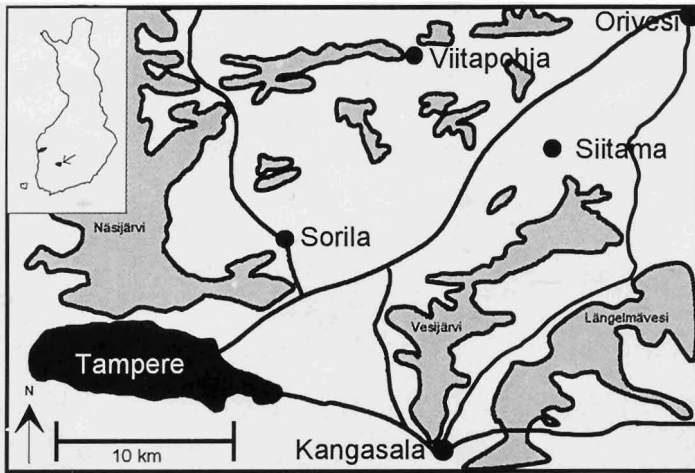


Fig. 2. A map of the study area in the Tampere region. Black areas are cities or towns, grey areas denote lakes and the lines are major roads. There were 35 populations of *M. diamina* spread throughout the study area in 1995. Most observations were made in the area of Siitama. The smaller map (insert) gives the current distribution of *M. diamina* in Finland with the study area indicated by an arrow.

where (Wahlberg *et al.*, 1996). I also made detailed observations on the ecology of the larvae and adults and report these observations in this article.

Study sites

I made most observations in the Siitama area within the $20 \times 30 \text{ km}^2$ study area and close to the city of Tampere (Fig. 2). The Siitama area contains 18 meadows suitable for *M. diamina*, of which 14 were occupied by the butterfly in 1995. *M. diamina* has a classical metapopulation structure (Harrison, 1991 ; Hanski, 1994), in which local populations are connected to each other through infrequent migration and there is no large “mainland” population. The metapopulation of *M. diamina* exists in a stochastic equilibrium between extinction of local populations and colonisation of empty habitat patches (Wahlberg *et al.*, 1996).

In the Tampere region, *M. diamina* inhabits moist meadows with relatively low vegetation. The meadows are surrounded mainly by fields or spruce *Picea abies* (Karsten) forests. The plant community of the meadows is species rich, containing many flowering plants that are

potential nectar sources for the adult butterflies. The meadows have been kept open largely as natural pastures for cattle. The amount of cattle in Finland has decreased in the last few decades (Raatikainen, 1986), which has led to the overgrowth of *M. diamina* habitat. This is probably the main reason for its decline in Finland.

Description of premature stages

EGG (Fig. 3a). Nearly spherical with flattened top and base. Approximately 22 longitudinal ridges extending from top to base. Sides and top with irregular pitting. Colour yellow-green when freshly laid.

1ST INSTAR LARVA (Fig. 3b). Head dark brown with some colourless setae. Body clear yellow with gut giving green colour to fore body. Body with colourless setae arising from papillae that are darker than body. Prolegs concolorous with body, true legs are brown. Body has 13 segments, 1st segment has a saddle-like pattern. Larvae about 2 mm long.

2ND INSTAR LARVA (Fig. 3c). Head black with light brown setae. Body developing characteristic colour pattern of later instars : being brown with light grey spiracles. Ventrolateral band dull grey. Saddle-like pattern on 1st segment with black setae. Prolegs light grey, true legs dark brown. Branching spines develop from papillae and simple setae of 1st instar ; shafts of spines light grey with black setae. Seven longitudinal rows of spines except in thoracic segment, where only 1st and 3rd ventral rows on both sides are present. Larvae about 4 mm long.

3RD INSTAR LARVA (Fig. 3d). Head capsule black with black setae. Body dark brown with grey spiracles. Ventrolateral band no longer distinct, but lighter brown in colour than rest of body. Prolegs grey and true legs dark brown. Spine shafts almost black with grey tips and black setae. Base of spine shafts have a grey ring around them. Larvae about 6 mm long.

4TH INSTAR LARVA. Head capsule black with black setae. Body dark brown with grey dots on upperside and a dark dorsal stripe, light brown on underside. True legs dark brown. Prolegs white with light brown bases. Spines black with yellow ring around base of spine shafts. Fringing spine shafts dark yellow. Dorsal spine shafts black with grey tips. Larvae about 7 mm long.

5TH INSTAR LARVA. Overall pattern as in previous instar, but body black and all spine shafts dark yellow with grey tips. Dots on body clearer and lighter grey in colour. Larvae about 11 mm long.

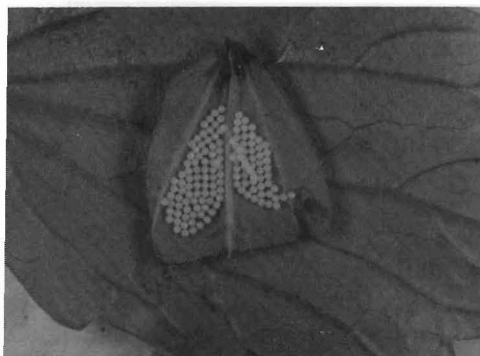


Fig. 3. Early life stages of *M. diamina* : a — egg cluster, b — 1st instar larvae, c — 2nd

6TH INSTAR LARVA (Fig. 3e). Continued development of previous patterns. Dorsal spine shafts bright yellow with grey tips, fringing spine shafts entirely grey. Bases of spine shafts black along with rest of body. Larvae about 18 mm long.

PUPA (Fig. 3f). Ground colour ivory white with black markings. Abdominal segments have 3-5 bright orange warts on dorsal side. Pupae length about 11 mm.

Ecology

OVIPOSITION. The larval host plant has never been reported for Finland. My observations of both larvae and ovipositing adult females showed that *M. diamina* larvae feed exclusively on *Valeriana sambucifolia* Mikan fil. (Valerianaceae) in the Tampere region. *V. sambucifolia* is a large herb, growing up to 1 m tall, common in south-western Finland. The leaves are bipinnate with 3 to 7 leaflet pairs and a terminal leaflet. In central Europe other host plants have been recorded, e.g., *Valeriana officinalis* L., *V. dioica* L., *Plantago lanceolata* L. (Plantaginaceae) and *Veronica chamaedrys* L. (Scrophulariaceae) (Lepidopterologen-Arbeitsgruppe, 1987 ; Ebert, 1991). Of these species only *V. chamaedrys* occurs in the present study area, but I never observed larvae feeding on it.

I observed 13 ovipositing females by following them from a distance of a few meters. Ovipositing females were identified by their distinctive prealighting or postalighting behaviour (Mackay, 1985). For five females I recorded all the plant species on which they alighted before ovipositing. The other eight females were found immediately prior to the beginning of oviposition.

Females mainly oviposited during mid afternoon. They spent long periods of time searching for larval host plants (range 8-108 min, observed mean 51 min, n = 5). Females often landed on *Aegopodium podagraria* L. (Apiaceae) which has a similar leaf structure to *V. sambucifolia*. *A. podagraria* is a very common species on meadows suitable for *M. diamina*. According to Wiklund's (1984) terminology, this gives *V. sambucifolia* a low apparency to visually searching butterflies. The effect is compounded by an observation that females laid eggs only on non-flowering *V. sambucifolia* plants. I searched both flowering and non-flowering host plants intensively and found a total of 46 egg clusters (including those laid by the females that had been followed). All egg clusters were on non-flowering plants, even though females fed regularly on *V. sambucifolia* flowers (Table 1).

Table 1

The use of food sources by adult *Melitaea diamina* butterflies.

Food source	Number of observations
<i>Ranunculus repens</i>	289
<i>Valeriana sambucifolia</i>	137
<i>Geranium sylvaticum</i>	22
Moist soil	11
<i>Aegopodium podagraria</i>	7
<i>Lathyrus pratensis</i>	2
<i>Leucanthemum vulgare</i>	2
<i>Pilosella praealta</i>	1
<i>Achillea millefolium</i>	1
<i>Filipendula ulmaria</i>	1
<i>Campanula patula</i>	1

Once a female found a host plant, it investigated the plant thoroughly, tapping the leaves with its fore legs and curling its abdomen underneath the leaves. The eggs were laid in clusters of about 100 eggs (range 30-200, mean 97, $n = 46$) on the underside of a host plant's leaflet. The eggs were usually placed in a single layer without regard to the position of the leaflet (Fig. 3a). Oviposition lasted 30 ± 1.6 min (mean \pm SE, $n = 11$). The postalighting behaviour of *M. diamina* is similar to that in the congeneric *M. cinxia* (Linnaeus, 1758) (Wahlberg, 1995). Several *M. diamina* egg clusters can be found on a single *V. sambucifolia* plant, though usually on separate leaflets. In an extreme case, one plant had 17 egg clusters on it. I also observed two females ovipositing simultaneously a few centimetres apart on another plant.

EGG DEVELOPMENT AND PREDIAPAUSE LARVAE. In 1995, the egg clusters hatched from the middle of July to the beginning of August. Egg mortality appeared to be low, and most eggs in all the observed egg clusters hatched. The summer of 1995 was very sunny, but because the meadows have a dense cover of vegetation, humidity probably remained relatively constant around the egg clusters.

I observed the behaviour of prediapause larvae in the field and in indoor rearing. Newly emerged larvae fed partially on their egg shells and then began feeding on the underside of *V. sambucifolia* leaves. The larvae remain as a group and spin a thin silken web, under which they feed. The web becomes conspicuous when larvae reach the 3rd instar. 1st and 2nd instar larvae feed only on the lower epidermis and parenchyma of the leaves, leaving the upper epidermis and veins intact (Fig. 4). 3rd instar larvae feed also on the upper epidermis, but leave the thicker veins intact.



Fig. 4. A *Valeriana sambucifolia* plant that has been fed on by a group of 2nd instar *M. diamina* larvae. The silk spun by the larvae is fairly inconspicuous, but the upper epidermis left uneaten by the larvae becomes conspicuous when it dries.

I collected four groups of 2nd and 3rd instar larvae (613 individuals) and reared them to investigate the incidence of parasitoids in *M. diamina*. No parasitoids emerged from the larvae. It seems likely that specialist parasitoids are absent from the Tampere region, though in Sweden *M. diamina* is attacked by a braconid, *Cotesia melitaeorum* (Wilkinson, 1937) (C. Eliasson, pers. comm.). The size of the *M. diamina* metapopulation in the Tampere region may be too small for a specialist parasitoid to persist, as has been suggested for some *M. cinxia* metapopulations (Lei & Hanski, 1997).

4th instar larvae enter diapause towards the end of August. The larvae diapause in dead, curled leaves beneath the plant that they fed on. Usually a larval group splits into smaller groups of 20 to 30 individuals that diapause within adjacent leaves. 4th instar larvae no longer feed even if conditions are favourable.

POSTDIAPAUSE LARVAE. Larvae terminate diapause soon after the snow melts, which usually happens around the beginning of May in

the Tampere region. 4th and 5th instar larvae feed on newly sprouting *V. sambucifolia* either alone or in small groups of 2-16 individuals. They bask actively in small groups on cool but sunny days, as do the larvae of the congeneric *M. cinxia* (Kuussaari *et al.*, 1995). Larvae were difficult to find on warm sunny days. Presumably they were hidden in leaf litter. 6th instar larvae fed usually alone. *M. diamina* larvae spin only very thin webs during spring.

The incidence of parasitism was checked by rearing 24 larvae collected from 19 groups during May. All three spring instars were collected. Once again, no parasitoids emerged and all larvae pupated successfully.

PUPAE. Pupation takes place at the end of May. The pupal stage lasts about three weeks. I did not find pupae in the field. Presumably *M. diamina* pupates within the dense meadow vegetation, probably on or close to the ground, as has been observed in *M. cinxia* (Kuussaari *et al.*, 1995).

ADULTS. The adult flight season extends from the middle of June to about the middle of July (Marttila *et al.*, 1990). *M. diamina* is protandrous, as most butterflies are (Wiklund & Fagerström, 1977). In a mark-recapture performed in the Siitama area (Fig. 2), males predominated the captures for the first five days of the flight season. Conversely, females predominated the captures of the last five days of the mark-recapture study.

Males search actively for newly emerged females throughout the day, i.e. they use the patrolling tactic for mate location (Scott, 1974). Once a male finds a basking female, it lands next to it and initiates copulation immediately. There is no courtship ritual. Females probably mate only once, as the females in 14 observed mating pairs were all fresh. Mated females refused to remate by lifting their abdomen and spreading their wings out. I observed this in old females (which I inferred had mated earlier) and in females I had observed in copula earlier. One mating is enough for a *M. cinxia* female to fertilise all her eggs (Wahlberg, 1995). Freshly mated *M. diamina* females had a distinctive brown mass on the opening of the bursa copulatrix, which indicates that males place a mating plug in the female to prevent further matings. This has been recorded in several related species (Labine, 1964; Porter, 1981; Dickinson & Rutowski, 1989), but not in *M. cinxia* (Wahlberg, 1995).

Both sexes feed actively throughout the day. Of 474 recorded feeding bouts, 61% were on flowers of *Ranunculus repens* L. (Ranunculaceae) and 29% were on flowers of *V. sambucifolia*. The use of these flowers was separated temporally as *R. repens* flowers were used mainly in

June and *V. sambucifolia* flowers in July. A further eight species of flower were used occasionally (Table 1), but the majority of flower species on the meadows were unused. I observed males feeding on moist soil occasionally.

M. diamina is a fairly sedentary species, especially females. Of all females captured and marked ($n = 285$), only 6% were recaptured in a different meadow. Several females were recaptured repeatedly in the same small area of one meadow. Males are relatively more mobile, possibly as a consequence of their mate-searching tactic (see above). Of the 557 males captured and marked, 18% were recaptured in another meadow during their lifetime.

Discussion

Females actively feeding on *V. sambucifolia* flowers did not exhibit any interest in ovipositing on the same plants. The observation that females lay eggs on non-flowering host plants appears to be connected to the phenology of the larval host plants. *V. sambucifolia* is a perennial plant (Aalto, 1980), but I observed that flowering host plants senesced already at the beginning of August, when most larvae were in their 2nd instar. Thus there is strong selection on females to lay eggs on non-flowering host plants. The mechanism that females use to differentiate between flowering and non-flowering plants is probably visual, though this has not been studied.

Knowledge of the ecology and life histories of endangered species is necessary for their successful conservation. This study shows that only meadows containing *V. sambucifolia* are suitable habitat for *M. diamina* in Finland. I found that the butterfly is relatively sedentary and thus needs a dense network of habitat patches, which are usually small, for its metapopulation to persist. The decline in the number of populations in Finland during the last few decades can largely be attributed to meadows becoming unsuitable and the suitable meadows becoming more isolated from each other. This is apparent in the Tampere region, where I found six isolated populations (Wahlberg *et al.*, 1996). These populations are probably remnants of a network of meadows, in which the other meadows have already become overgrown. The overgrowth of the meadows by willows is the most important threat to *M. diamina* at present.

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