The life history and ecology of *Euphydryas maturna* (Nymphalidae: Melitaeini) in Finland

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Summary. The life history and ecology of the scarce fritillary *Euphydryas maturna* (Linnaeus, 1758) in Finland are described. The main larval host plant of this endangered species is *Melampyrum pratense* in Finland, which is an annual herb. This differs from trees (e.g. *Fraxinus excelsior*) or bushes (e. g. *Viburnum opulus*) recorded as host plants elsewhere in Europe. Northern populations of *E. maturna* apparently have a facultative two-year life cycle. Larvae growing in a warm place can develop to adults in one year, whereas larvae growing in a cooler place return to diapause at the end of spring and develop to adults after a second winter diapause. In Finland, larvae are parasitized by two braconid wasp species, *Cotesia acuminata* (Reinhard, 1880) and *C. melitaearum* (Wilkinson, 1937), and by a tachinid fly, *Erycia fatua* (Meigen, 1824). Adult *E. maturna* males use only the perching tactic when searching for females.

Zusammenfassung. Die Biologie und Ökologie von *Euphydryas maturna* (Linnaeus, 1758) in Finnland werden beschrieben. Die wichtigste Raupenfutterpflanze dieser bedrohten Art in Finnland ist *Melampyrum pratense*, eine annuelle krautige Pflanze. Dies stellt einen wesentlichen Unterschied zu den Futterpflanzen im restlichen Europa dar, wo Bäume (z.B. *Fraxinus excelsior*) oder Sträucher (z.B. *Viburnum opulus*) nachgewiesen sind. Nördliche Populationen von *E. maturna* besitzen offensichtlich einen fakultativ zweijährigen Entwicklungszyklus. Raupen, die sich an warmen Lokalitäten entwickeln, ergeben den Falter in einem Jahr, Raupen, die an kälteren Orten leben, kehren nach Ende des Frühlings in Diapause zurück und entwickeln sich erst nach einer zweiten Überwinterung. Die Raupen werden in Finnland von zwei Braconiden-Arten, *Cotesia acuminata* (Reinhard, 1880) und *C. melitaearum* (Wilkinson, 1937), und einer Tachinen-Art, *Erycia fatua* (Meigen, 1824) parasitiert. Männliche Falter benutzen ausschließlich die Ansitz-Taktik (perching) bei der Suche nach Weibchen.

Résumé. La biologie et l'écologie du Damier du frène *Euphydryas maturna* (Linnaeus, 1758) est décrite en Finlande. La principale plante-hôte de cette espèce menacée est *Melampyrum pratense*, herbe annuelle dans ce pays. Elle diffère donc des autres plantes-hôtes connues en Europe, qui sont soit des arbres (p. ex. *Fraxinus excelsior*), soit des arbustes (p. ex. *Viburnum opulus*). Les populations nordiques d'*Euphydryas*

maturna ont apparemment un cycle facultatif sur deux ans. Les chenilles croissant dans une zone chaude se développent en une année, alors que celles dans une aire froide entrent en diapause à la fin du printemps et donnent des adultes après un second hivernage. En Finlande, les chenilles sont parasitées par deux espèces d'Hyménoptères Braconides, *Cotesia acuminata* (Reinhard, 1880) et *C. melitaearum* (Wilkinson, 1937), ainsi que par un Diptère Tachinide, *Erycia fatua* (Meigen, 1824). Les mâles adultes de *E. maturna* pratiquent seulement la stratégie du "perching" pour rechercher les femelles.

Introduction

The scarce fritillary *Euphydryas maturna* (Linnaeus, 1758) is an endangered species across almost all of its range in Europe (Heath, 1981). The species is protected in all EU countries under the 1992 European Community Council Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (EU directive 92/43/EEC). Information on the host plants and the life cycle of *E. maturna* is at best sketchy in all European countries. This dearth of information is a major obstacle when planning the conservation of the species.

E. maturna is still relatively common in SE Finland (fig. 1), where it is found on forest edges of a southern exposure (Marttila *et al.*, 1991). The forest edges are formed by clearcuts and overgrown meadows. The host plants reported for *E. maturna* vary widely, giving an impression that the species is polyphagous. Two species most closely related to *E. maturna, E. intermedia* (Ménétriés, 1859) and *E. gillettii* (Barnes, 1897) are however monophagous. *E. intermedia* is found on *Lonicera caerulea* (cf. Luckens, 1985) and *E. gillettii* feeds mainly on *L. involucrata* (cf. Williams *et al.*, 1984). Indeed, all well-studied Melitaeini species are mostly oligophagous, usually with one host plant species being preferred locally over the others. For instance, *E. phaeton* (Drury, 1767) feeds mainly on *Chelone glabra* (cf. Stamp, 1982), *E. aurinia* (Rottemburg, 1775) on *Succisa pratensis* (cf. Porter, 1981), *Melitaea cinxia* (Linnaeus, 1758) on *Plantago lanceolata* and *Veronica spicata* (cf. Thomas & Simcox, 1982; Hanski *et al.*, 1994) and *M. diamina* (Lang, 1789) on *Valeriana sambucifolia* (cf. Wahlberg, 1997). *E. editha* (Boisduval, 1852) has been recorded on many different host plants, but local populations tend to use one or two host plant species only (Singer,

1994). All of the plant species mentioned above contain iridoid glycosides (Jensen *et al.*, 1975), and it has been suggested that Melitaeini butterflies specialise on plants containing these chemicals (Bowers, 1983).

For *E. maturna*, the literature lists *Populus tremula, Fagus sylvatica, Betula* sp., *Salix caprea, Vaccinium myrtillus, Fraxinus excelsior, Lonicera xylosteum, Viburnum opulus, Veronica longifolia, Melampyrum sylvaticum* and *Plantago lanceolata* as host plants (Higgins & Riley, 1970; Marttila *et al.*, 1991; Ebert & Rennwald, 1991; Eliasson, 1991; Somerma, 1997; Tolman & Lewington, 1997). The first four plant species belong to groups that do not contain iridoid glycosides (Jensen *et al.*, 1975), and therefore are unlikely to be true host plants. There are confirmed observations of larvae feeding on *F. excelsior, V. opulus* and *Melampyrum* sp. in Sweden (Eliasson, 1991; C. Wiklund, pers. comm.), *Ligustrum vulgare, F. excelsior* and *F. angustifolia* in Hungary (Z. Varga, pers. comm.), and *L. xylosteum* (L. Kaila & G. Nordenswan, pers. comm.) and *V. opulus* (M. Kuussaari, pers. comm.) in Finland.

Eliasson (1991) reports a study on *E. maturna*, in which he suggests a perennial life cycle for the species in Sweden. His evidence is however rather circumstantial. In Hungary, *E. maturna* larvae develop in one year to the adult stage as in most Melitaeini species (Z. Varga, pers. comm.). On the other hand, closely related species have been observed to go through a two-year life cycle. Luckens (1985) reared a group of *E. intermedia* larvae collected as 2nd instar during the autumn. Most died during winter, but those survived developed to the 5th instar in spring and became inactive towards the end of spring. The larvae remained inactive throughout the summer and autumn. Two larvae survived till the next spring when they completed development to the adult stage. *E. gillettii* has a facultative biennial life cycle (Williams *et al.*, 1984). The species occurs in mountainous regions of western North America. At lower elevations, *E. gillettii* goes through a one-year life cycle, but at higher elevations the larvae have to go through a second winter diapause to complete development.

The purpose of this paper is to clarify the life history and ecology of *E. maturna* in Finland. I have made detailed observations on the ecology of larvae and adults in 1996 and 1997.

156

Fig. 1. The distribution of *E. maturna* in Finland (the study site indicated by a dot).

Study area

The study area is located in south-eastern Finland close to the Russian border in the commune of Joutseno (fig. 1). I have observed larval and adult behaviour in the Joutseno region in spring, summer and autumn 1996 and spring 1997. The study area is forested with many small clearcuts of varying ages and old overgrown meadows (Selonen, 1997). The main aim of the study in 1996 was to investigate the population structure of *E. maturna* through a capture-mark-recapture study in an area of about 2 × 3 km. The results of the capture-mark-recapture study are to be presented elsewhere (Wahlberg *et al.*, in prep.).

Ecology

Oviposition. I explored the oviposition preferences of *E. maturna* by following females showing prealighting oviposition behaviour. I was able to follow 9 females in 1996, of which 3 oviposited at the end of the observation period. The other six

157

were interrupted by bad weather or lost. Two females oviposited on *Melampyrum pratense* and one female oviposited on *Veronica longifolia*. I followed the females for an average of 32 minutes. The females showed prealighting and postalighting behaviour typical for Melitaeini butterflies (see Rausher *et al.*, 1981; Mackay, 1985; Wahlberg, 1997), i.e. they flew slowly over the vegetation, alighting frequently. I observed that the females alighted on average 9 times per minute ($\pm$ 7.29 S.D., $n = 71$ — this includes only periods when the females searched actively for the host plants) on a wide range of plant species. The females displayed postalighting behaviour only on three plant species, *M. pratense, V. longifolia* and *V. chamaedrys. Melampyrum sylvaticum* was ignored, even though it was relatively common at the study site.

Female butterflies are known to search visually for host plants during the prealighting period (Rausher, 1978; Rausher *et al.*, 1981). They are usually attracted to plants with a leaf shape similar to the host plants (Parmesan *et al.*, 1995). I recorded every species of plant on which the females alighted for seven females. The females alighted on a total of 36 taxa of plant (grasses and ferns were not identified to species). The most common plants on which females alighted were *Epilobium angustifolium, Anthriscus sylvaticus, Filipendula ulmaria, Rubus idaeus, Melampyrum sylvaticum* and grasses (table 1). *Populus tremula* and *Betula* sp. saplings were very common at the study site, but were virtually ignored by the females.

Females that alighted on *M. pratense* appeared to investigate the surroundings as if to ascertain that there were enough host plants to support a group of larvae. The females would make very short flights (ca. 5 cm) and alight on plants close by. The two females that eventually oviposited on *M. pratense* had alighted on nearby plants 7 and 8 times in succession before commencing oviposition. In contrast, the female that oviposited on *V. longifolia* did not leave the plant once it was found, until oviposition was over.

In a preliminary experiment, I tested the host plant preferences of four females in 1997 using Singer's (1982) method. Two females were reared from larvae collected from the Joutseno region and mated in cages and two females were caught in the Joutseno

158

Table 1. Plants most commonly visited by *Euphydryas maturna* females during the prealighting phase of host plant searching. The values refer to the mean proportion of all alightings each plant received.

Plant taxa	Proportion of alightings (mean ± S.E., $n = 7$ females)	Plant physiognomy
Epilobium angustifolium	0.254 ± 0.076	Large erect, leaves lanceolate
Anthriscus sylvestris	0.151 ± 0.068	Large erect, leaves tripinnate
Grasses	0.107 ± 0.033	Small rosette, leaves long and narrow
Rubus idaeus	0.081 ± 0.028	Large erect, leaves cordate
Filipendula ulmaria	0.077 ± 0.037	Large erect, leaves pinnate, elliptic
Melampyrum sylvaticum	0.041 ± 0.026	Small erect, leaves lanceolate
Geranium sylvaticum	0.029 ± 0.005	Large erect, leaves pinnate, elliptic
Veronica chamaedrys	0.027 ± 0.012	Small erect, leaves cordate
Ferns	0.024 ± 0.009	Large erect, leaves tripinnate
Sorbus aucuparius	0.024 ± 0.016	Large erect, leaves pinnate
Convalaria majalis	0.023 ± 0.023	Small rosette, leaves ovate
Populus tremula	0.019 ± 0.007	Large erect, leaves cordate
Melampyrum pratense	0.018 ± 0.017	Small erect, leaves lanceolate
Galium sp.	0.013 ± 0.005	Small vine, leaves trifoliate
Rubus saxatilis	0.012 ± 0.008	Small vine, leaves narrow
Cirsium helenioides	0.011 ± 0.007	Large rosette, leaves lanceolate

region. The reared females were tested on *V. longifolia* and *Fraxinus excelsior*, while the wild-caught females were tested on *M. pratense* and *Lonicera xylosteum*. The females were tested for between 10 and 45 min. and they were highly motivated to oviposit. During this time, they accepted only *V. longifolia* and *M. pratense*, and showed no interest in the other two plant species.

When a female finds a suitable host plant, it places itself underneath a leaf and begins ovipositing. The female is usually orientated away from the stem of the plant and thus the eggs are laid at the base of the leaf. The eggs are laid in batches of about 200 eggs (range 119–321, mean 205, n = 5) in a rough cluster. The eggs are strongly glued to each other by some substance that makes breaking the eggs apart very difficult.

Prediapause larvae. The larvae hatch from the eggs from late July to mid August. The larvae keep in swarms throughout autumn. I found 19 larval groups in the Joutseno region during August 1996. Of these 18 were on *M. pratense* and one was on *V. longifolia*. All larvae were at the same development stage, i. e. 2nd instar on 20 August 1996. In addition to this, I have

159

found *E. maturna* groups on *M. pratense* in the western part of its range in Finland, 5 groups in autumn 1997 and 10 groups in autumn 1998.

Newly emerged larvae feed partially on their egg shells and then begin feeding on the underside of the host plant leaves. The larvae spin a conspicuous silken web, within which they feed. The larvae consume the entire leaf leaving only the thickest veins intact. 2nd instar larvae enlarge the web to enclose most of the host plant (fig. 2).

Fig. 2. A group of *E. maturna* 2nd instar larvae feeding on a *Melampyrum pratense* plant. The silken web spun by the larvae is conspicuous in autumn.

Larvae enter diapause towards the end of August. I was unable to find any larvae after the onset of diapause and presume that they diapause singly or in small groups in the leaf litter. *E. maturna* larvae do not spin a winter web, unlike related *M. cinxia* (Hanski *et al.*, 1995) and *E. aurinia* (Porter, 1981). Larvae are

able to enter diapause as 3rd instar, but continue development to the 4th instar under favourable conditions. This is based on my observations of larvae in spring (see below) and of larvae reared in the laboratory.

Postdiapause larvae. Larvae terminate diapause as soon as the snow melts at the end of April — beginning of May. Soon after termination of diapause, larvae of one group can be found feeding and basking singly within an area of approx. 1 m². They feed on the newly emerging seedlings of *M. pratense* (on cotyledons) and bask on dry leaves and other dark substrates. The larvae disperse in search of food as spring progresses. Towards the middle of May the larvae of one group are spread out within an area of ca. 4 m². The larvae are capable of consuming an entire *Melampyrum* seedling within 20 minutes.

I found 3rd, 4th and 5th instar larvae in the Joutseno region soon after diapause had broken in spring 1996 and 1997. 3rd and 4th instar larvae were generally in close proximity to each other. 5th instar larvae could be found within groups of younger larvae or alone far from any groups recorded in the autumn.

In 1996, I reared 122 *E. maturna* larvae, of which 42 were 4th instar when found. The 80 5th or 6th instar larvae developed to pupae. Of 42 4th instar larvae, only one developed to pupa. The others became inactive and eventually died during winter. In 1997, larvae that were found as 5th instar (25 individuals) soon after diapause had broken were collected and reared under natural conditions. Also 17 3rd or 4th instar larvae were reared under the same conditions. Eleven additional 3rd or 4th instar larvae were allowed to develop in the field for 3 weeks before being collected to be reared (see below). All 5th instar larvae developed to pupae in the rearing, while only 5 of 28 3rd or 4th instar larvae developed to pupae (table 2). However, 7 larvae that died of an unknown disease were all in their 6th instar and thus would have completed development.

The inactive larvae were placed in a large pot with *V. longifolia* and leaf litter and left outside in a shaded place for the summer 1997. The larvae moved occasionally between the leaf litter and the mesh covering the pot, but spent most of their time within rolled up dried leaves. One larva was observed to feed a little in August.

161

Table 2. The fate of *E. maturna* larvae found as different instars in a rearing in spring 1997. 5th instar larvae were noticeably larger than 3rd or 4th when collected soon after winter diapause had broken.

	5th instar larvae (2nd year of development)	3rd and 4th instar larvae (1st year of development)
Number reared	25	28
Died of unknown disease	3	7
Became inactive at the end of May (diapause)	0	16
Developed to pupae	22	5
Parasitized by *Erycia fatua*	8	2
Adult eclosed (♂♂ ♀♀)	9/5	0/3

Table 3. Number of different instar larvae found during 19 days in a warm and in a cool locality.

	Warm group			Cool group		
Date	3rd instar	4th instar	5th instar	3rd instar	4th instar	5th instar
28.04.1997	10	3	0	0	0	0
29.04.	9	4	0	5	1	0
2.05.	10	12	0	8	0	0
3.05.	7	17	0	11	2	0
6.05.	3	22	0	12	2	0
7.05.	2	19	0	8	3	0
8.05.	1	23	0	4	2	0
12.05.	1	14	4	2	3	0
13.05.	0	10	3	0	2	0
14.05.	0	6	3	0	2	0
15.05.	0	5	4	0	2	0
16.05.	0	0	2	0	0	0

To clear up the confusion on the larval development duration (one, two or three year life cycle), I marked larvae individually from two groups in spring 1997 using enamel paint. I had found these groups in the previous autumn, when they were 2nd instar and thus the offspring of adults that flew in 1996. I followed the development of the larvae from 28 April 1997 to 16 May 1997 by recording the position of each larva within a 10 × 10 m grid to the closest centimetre. The positions of the larvae were recorded on 12 days during this period. One group was situated on a very warm southern exposure forest edge, where the sun shone between 09:00 and 18:00. The other group was situated on an eastern exposure forest edge, where the sun shone from 08:00 to 14:00. These groups will be referred to as the "warm"

group and the "cool" group, respectively. I marked a total of
77 larvae in the warm group and 29 larvae in the cool group.
Many individuals were probably marked twice or three times,
because they lost their marks when moulted. The actual number
of larvae in each group is best estimated from the number of
the most common instar marked, 41 4th instar larvae for the
warm group and 15 3rd instar larvae for the cool group.

Larvae in both groups were mainly 3rd instar on 28 April
1997, though I found a few 4th instar larvae in the warm group
on that date (table 3). The warm group larvae grew noticeably
faster than those of the cool group, as one would expect. Larvae
in both groups behaved very secretively during sunny warm days.
They hid under leaves and only came out to feed. I collected
all larvae that I found during 15–16 May 1997 for rearing, because
observations in the field became difficult to make. I found 9 larvae
from the warm group and only two larvae from the cool group,
despite careful searching. The warm group larvae were all 5th
instar and all except one developed quickly to the 6th instar in
the rearing. However, seven of eight 6th instar larvae died of
an unknown disease before pupation (table 2). The two cool
group larvae were 4th instar and fed very little in the rearings.
They became inactive and shed their skin to become 5th instar
towards the end of May.

Larvae in both groups moved over relatively short distances
during the observation period. They moved on average 30 cm
per day mainly in a circular fashion. Since there was a plentiful
supply of *M. pratense* seedlings available, the larvae did not have
to move large distances.

Parasitoids. In Finland the larvae were parasitized by two
braconid wasp species, *Cotesia acuminata* (Reinhard, 1880) and
C. melitaearum (Wilkinson, 1937), and by a tachinid fly *Erycia
fatua* (Meigen, 1824) (Komonen, 1997). The *Cotesia* species most
likely have two broods during one host brood. The first brood
emerges from the larvae in the middle of May. Komonen (1997)
observed three parasitized larvae out of 122 larvae. Three cocoons
of *C. melitaearum* and five cocoons of *C. acuminata* emerged
from two of the observed larvae. Two *Cotesia* larvae emerged
from one host larva but died before pupating and remained
unidentified.

163

The second brood emerged from the larvae in June and remained in a state of aestivation until July (Komonen, 1997). *C. melitaearum* parasitizes *M. cinxia* as well in SW Finland, where it has been studied intensively (Lei *et al.*, 1997; Lei & Hanski, 1997). In this population, the parasitoid can have three broods during one host brood. The first generation emerges in autumn when conditions are good (e.g. a warm autumn). This may be possible in the Joutseno region, though there are no records of an autumn brood.

I observed several *Erycia fatua* females ovipositing on *E. maturna* webs in autumn 1996. The eggs are typically oviposited on the host larvae, after which the fly larvae eat their way into the host and begin development (Tschorsnig & Herting, 1994). In the 1997 rearings a total of 10 *E. fatua* larvae emerged from *E. maturna* pupae and pupated in a few centimetres from them. Of these 7 individuals eclosed. Parasitized butterfly pupae are easily identified, they turn black a few days after pupation. *Erycia fatua* emerged from both larvae that went through a one and a two year development. *Erycia fatua* has been recorded from other Melitaeini species such as *Mellicta parthenoides* (Keferstein, 1851), *M. athalia* (Rottemburg, 1775), *M. britomartis* (Assmann, 1847), *M. deione* (Geyer, [1832]) and *Melitaea cinxia* (cf. Tschorsnig & Herting, 1994).

Adult mate location. The adult flight season extends from the middle of June to the middle of July in Finland (Marttila *et al.*, 1991). *E. maturna* is protandrous, as most butterflies are (Wiklund & Fagerström, 1977). In a capture-mark-recapture study performed in the Joutseno region, males predominated during the first five days of the flight season (Selonen, 1997).

I did not make detailed observations of male mate-locating behaviour, but during the mark-recapture experiment, males were observed to use perching tactic only for mate location. The perching tactic can be identified when males defend small territories in which they wait for receptive females to fly by (Scott, 1974). The territories were usually set up on large *Pteridium aquilinum* leaves or on *Populus tremula* saplings. Some males were recaptured in the same area in several days, usually from the same territory. I did not observe any behaviour indicating the use of the patrolling tactic for mate location.

164

I observed the beginning of only one mating, which lasted over three hours. Related species mate for about an hour (Alcock, 1985; Rutowski & Gilchrist, 1987; Wahlberg, 1995; 1997), suggesting that the *E. maturna* male had mated earlier the same day. I dissected four females collected at the end of the flight period in 1996 for spermatophore count. All females contained only one spermatophore. Two of females examined had a mating plug covering the opening of the bursa copulatrix. It was a hard, colourless substance.

Discussion

Host plant use. The major host plant of *E. maturna* in eastern Finland is *Melampyrum pratense*, a herb occurring over forest edges and in open pine forests. Other recorded host plants in Europe are mostly trees or large bushes. The preliminary results on the host preference of ovipositing females indicates that *E. maturna* from eastern Finland do not accept either *Fraxinus* or *Lonicera* as host plants. *Fraxinus excelsior* is a very rare species in SE Finland, but *L. xylosteum* was common in the study site in Joutseno. In autumn 1997 I found five *E. maturna* groups on *M. pratense* in the western part of its range in Finland, suggesting that *M. pratense* is the major host plant of the butterfly in Finland. There are however observations of *E. maturna* larvae on *L. xylosteum* in southern Finland close to Helsinki (L. Kaila & G. Nordenswan, pers. comm.). All observations of larvae feeding on *L. xylosteum* were made in spring.

The importance of *Veronica longifolia* and *Viburnum opulus* as host plants to *E. maturna* in Finland is not clear. *Veronica longifolia* is a fairly common plant found mainly on shores of lakes and the sea. *E. maturna* is not usually found in these habitats and I assert that *V. longifolia* is not a very important host plant for the butterfly in Finland. *Viburnum opulus* is a rare plant in Finland and thus cannot be very important.

The use of different host plants in different parts of the range has been documented particularly well for *E. editha* (Singer, 1994; Radtkey & Singer, 1995). It is most likely that a similar phenomenon occurs in *E. maturna*. The difference in growth forms of the recorded host plants is exceptional. My observations of females showing prealighting behaviour indicate that females

165

are searching for herb-sized host plants. Furthermore, females tended to alight more on plants with a similar physiognomy to the host plant (i. e. erect plants with lanceolate leaves), like *Epilobium angustifolium* (table 1). The range of *E. maturna* extends from western Europe to the Altai Mountains in Russia. It is possible that eastern populations specialise on herbs, though there are no records of the host plants in the eastern parts of its range to confirm this. Females in the western populations appear to specialise on trees and bushes, though postdiapause larvae are known to feed in the herb layer in these plant associations (Bink, 1992).

All confirmed observations of feeding larvae involved the plants containing iridoid glycosides. This suggests that *E. maturna* is as much a specialist on this group of secondary compounds as are the other Melitaeini species (Bowers, 1983; own observations). This being the case, all reports of larvae feeding on plants that do not contain iridoids (e. g. *Populus tremula, Salix caprea* and *Betula* sp.) are most likely erroneous. It is possible that larvae feeding on these plants in southern and central Europe were misidentified *Callimorpha dominula* (Linnaeus, 1758) (Arctiidae) due to their close similarity in appearance to the larvae of *E. maturna*.

Duration of the life cycle. The larvae of *E. maturna* appear to have a facultative biennial life cycle in Finland. Warm springs and a warm site accelerate growth and thus enable larvae to complete development within one year. Cool sites slow down the growth of larvae and they would risk emerging as adults well after the main flight season if they were to continue development. Thus it would appear adaptive for larvae to defer development until the next year to keep in synchrony with the majority of the population. Also, a later flight season would be selected against as the offspring would not have time to develop to the diapause stage.

Eliasson (1991) suggested a two or even three year life cycle as normal for *E. maturna*. The evidence he presents is that there are three size classes of larvae to be found in the spring (after diapause). My observations suggest a one or two year life cycle for *E. maturna* depending on the growth conditions, though I cannot say which one is more common. The larvae that diapaused

166

twice did so the second time as 5th instar. The largest larvae I found in the spring as soon as diapause had broken were 5th instar and these completed their development the same year. It appears that once a larva develops to the 6th (ultimate) instar, it can no longer enter diapause.

Luckens (1985) suggested that females need a longer period to develop and thus have a biennial life cycle, while males develop in one year in *E. intermedia*. I found this not to be true for *E. maturna*, since females emerged from both once and twice diapaused larvae. The males emerged only from the larvae that had developed over two years in my rearing, but only three individuals that underwent a one-year development survived to the adult stage, making it likely that only by chance were they all females. Both types of *E. maturna* larvae were parasitized by *Erycia fatua*, but it is unknown whether the parasitoid can also go through a two year life cycle.

The developmental plasticity displayed by *E. maturna* larvae requires closer study. The present evidence suggests that northern populations are not always able to complete their development in one year. Bink (1992) states that postdiapause larval development averages 45 days (37–52 days depending on temperature). If this is true for Finnish *E. maturna* postdiapause larvae, a biennial life cycle would be the norm and one year development restricted to very warm springs. The possibility of a perennial life cycle appears to be relatively common in *Euphydryas* species (Ehrlich & Murphy, 1981; Williams *et al.*, 1984; Luckens, 1985; Eliasson, 1991), and is most probably a trait that has evolved only once in the group. If this is the case, an optional biennial life cycle can be seen as a life history strategy for survival in unpredictable environments.

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