

# Oedippus



CLAES U. ELIASSON & MARK R. SHAW

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Prolonged life cycles, oviposition sites,  
foodplans and *Cotesia* parasitoids  
of Melitaeini butterflies in Sweden

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Nr. 21 - 2003

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Publisher: **Gesellschaft für Schmetterlingsschutz e.V.**

Editor: **Dr. Otakar Kudrna Brombergstr. 6, D-97424 Schweinfurt (Germany)**

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Cover design: Siegwald Greubel

GfS Emblem: Bernhard Omert

Drawing of *Coenonympha oedippus*: Kiki Larsen

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Typesetting: Gesellschaft für Schmetterlingsschutz e.V.

Printing: Druckerei W. Trauner, Fröbelstr. 5, D-97645 Ostheim v.d.R.

Price: variable (v. p. 1 of the issue concerned)

ISSN: 1436-5804

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## Prolonged life cycles, oviposition sites, foodplants and *Cotesia* parasitoids of Melitaeini butterflies in Sweden.

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**Keywords:** Sweden; prolonged life cycles; Lepidoptera: *Euphydryas maturna*, *E. aurinia*, *E. iduna*, *Melitaea diamina*, *M. athalia*, *M. britomartis*; Hymenoptera: *Cotesia acuminata*, *Cotesia melitaeorum*.

**Abstract:** Natural oviposition sites and larval foodplants are given for populations of six Melitaeini butterflies (*Euphydryas maturna*, *E. iduna*, *E. aurinia*, *Melitaea diamina*, *M. athalia* and *M. britomartis*) in Sweden, where several of these species are now highly endangered. As an evolutionary response to climatic factors, five (all except *M. britomartis*) exhibit partially biennial, triennial or quadriennial life cycles, and their development and hibernation ecology is analysed. For one species (*E. maturna*) the evidence that the phenomenon is partly under genetic control is strong. The high habitat quality necessary for the survival of these Melitaeini is discussed, as is the occurrence and influence of species of *Cotesia* (Hymenoptera: Braconidae) specialised as parasitoids of Melitaeini.

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Price: 9,-- EUR

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## 1 Introduction

Partly because of the strongly colonial population biology of many species, and the threat to population survival that is often a consequence of land use change, the Melitaeini has become one of the most studied groups of butterflies in the world (MOONEY *et al.* 1981, WILLIAMS 1981, STAMP 1981, PORTER 1982, Brower 1984, MURPHY & WHITE 1984, EHRlich 1987, ELIASSON 1991, 2001c, WARREN 1992, HANSKI, KUUSAAARI & NIEMINEN 1994, BOWERS & WILLIAMS 1995, LEI & HANSKI 1997, KOMONEN 1997, WAHLBERG 1997, 1998, KUUSAAARI 1998, AHLEN 1999). It is widely recognised that a considerable number of Melitaeini species are now threatened at national or global levels, and arguably the Melitaeini is one of the most threatened of all groups of butterflies in the northern temperate climatic zone. All European Melitaeini species are represented on at least one of the European countries' "red lists" of threatened species (SWAAY, WARREN & GRILL 1997), and two of the species of this study –

*Euphydryas maturna* (LINNAEUS, 1758) and *E. aurinia* (ROTTEMBERG, 1775) – are on the EU Habitat Directive, annexes 2 and 4 (European Economic Community 1991, 1992). Each member state in which such species occur is obliged to contribute to the network "Natura 2000" through the protection of an adequate number of sites to ensure the species' survival.

The first steps towards a conservation program for *Euphydryas maturna* and *E. aurinia* in Sweden, Västmanland, were taken during 1998. Three major networks of habitat-patches in the centre of the metapopulations of both species were suggested as preservation areas (ELIASSON 1999b). These were accepted by the Swedish Environmental Protection Agency and the Government in 1999. The first nature reserve (41 ha) was officially designated in 2000, and restoration of the habitat was completed in 2000-2001 (ELIASSON 2000, 2001c, f). Nation-wide action plans for *E. maturna* and *E. aurinia* have recently been commissioned by the Swedish Environmental Protection Agency (ELIASSON in prep. a, b), and a nation-wide action plan for *Melitaea britomartis* ASSMANN, 1847, is underway (ELIASSON in prep. c).

High requirements for habitat quality, and the specialisation to a social life of the pre-adult stages, seem to be general features of the Melitaeini. Several of the species seem unable to adapt to even small changes of land use. In this paper we address one of the group's special traits as seen in Sweden, that of adaptation to unpredictable annual changes in the length of the period with sufficient temperatures for egg and larval development by a prolonged life cycle strategy, and discuss the ways in which this raises the species' requirements for habitat quality.

Prolonged life cycles of Melitaeini butterflies have previously not been well documented, mention in the literature usually being made without any quantitative or circumstantial data. Lowland species known to have at least partially biennial life cycles in Europe outside Sweden are *Euphydryas maturna* and *Melitaea diamina* (LANG, 1789) (FRIEDRICH 1986, BINK 1992, WAHLBERG 1998). The subalpine and alpine taxa *Euphydryas aurinia glaciegenita* VERITY, 1928, *Euphydryas cynthia* (DENIS & SCHIFFERMÜLLER, 1775), *Euphydryas intermedia* (MÉNÉTRIÉS, 1859) and *Melitaea asteria* (FREYER, 1828) have been regarded as having regularly biennial life cycles in the Alps (LUCKENS 1985, GEIGER 1987). The partially triennial life cycle of *E. maturna* was recently discovered in two natural rearings of pre-hibernation broods and has so far only been verified from Sweden (ELIASSON 1991, STOLTZE 1996; the former source was incorrectly referred to as field observations of caterpillars in three different sizes by WAHLBERG (1998), to which a correction has been made (ELIASSON 1999c)).

In this paper we give some information on the proportions of one-year life cycle to multiennial life cycles for all but one of the seven Swedish Melitaeini species. Investigated species are *Euphydryas iduna* (DALMAN, 1816), *E. maturna*, *E. aurinia*, *Melitaea diamina*, *M. athalia* (ROTTEMBERG, 1775) and *M. bri-*

*tomartis*. The seventh species, *Melitaea cinxia* (LINNAEUS, 1758), is widespread in southern Sweden but it was not investigated. All species except *E. iduna* have been reared from eggs and early instar larvae under natural or semi-natural conditions, with full length hibernation periods and natural photoperiods. An increasing knowledge of the demands of each species for particular conditions during diapause and hibernation has lowered the mortality rate in captive rearings and lately offered the opportunity to record the proportions of individuals having annual, biennial, triennial and quadriennial life cycles in the broods. That the biennial to multiennial life cycles exist in the wild has been confirmed in all three species in which it was tested (*E. maturna*, *E. aurinia*, *M. diamina*) through unmanipulated rearings in large outdoor cages.

For several of these species previous information on the foodplants chosen for oviposition has not been distinguished from the foodplants of post-hibernation caterpillars, and in several cases even this information as given in handbooks has proved to be erroneous. Therefore modern field-based records of the natural foodplants of each species are presented.

Two gregarious species of *Cotesia* (Braconidae: Microgastrinae) parasitoids are associated with larvae of the butterflies at the study sites, and their presence in wild-collected larvae is recorded, together with brief notes on the outcome of exposures of "wrong host" larvae to the species of *Cotesia* concerned.

Data on each of the six Melitaeini species studied are presented separately. A brief outline of distribution, followed by data on oviposition plants, foodplants of post-hibernation caterpillars, natural and experimentally obtained data on parasitism of caterpillars, and the detailed analysis of breeding results are given for each species.

## 2 Environment and organisms

### 2.1 The impact of climate on the butterfly fauna in Scandinavia

Populations of Scandinavian butterfly species fluctuate strongly in response to the weather of the previous year. This rather well known, but poorly documented, fact indicates the enormous importance of sufficient temperatures and/or hours of sunshine for the development of pre-adult stages in butterfly species. With the strong influence of an oceanic climate in the northern temperate zone, a rapid decline in species diversity can be observed from the less humid eastern parts towards the more humid western parts of Scandinavia. The distribution patterns of butterfly species in Scandinavia, compared with climate maps, indicate the importance of sunshine to foraging and ovipositing butterflies and in creating a sufficient micro-climate for egg and larval development (LUNDQVIST 1953-1971, NORDSTRÖM 1955). However, it should be noted that temperatures at ground level are probably more important than the air temperatures measured at standard height at weather observations stations, which are the usual bases for climate maps. In fact the measured average annual precipita-

tion, as an approximate correlate of the number of days with overcast skies, gives a better indication of the distribution pattern of most butterfly species in Scandinavia, when correlated to the length of the vegetation period. In Sweden, at the latitude of 59-60°, the number of butterfly species exhibiting strictly one year life cycles abruptly declines at an approximate annual precipitation of >700 mm (LUNDQVIST 1953-1971, NORDSTRÖM 1955), although to some degree the local topographic structure of a broken landscape may compensate for higher regional precipitation.

Species of Melitaeini have gregarious pre-hibernation larvae, which are dependent on sunshine to reach a higher body temperature than is provided by surrounding air temperatures. This is of crucial importance for their metabolism (PORTER 1982). They are particularly vulnerable to insufficient solar radiation in the first two instars. All the Melitaeini species (*Euphydryas maturna*, *E. aurinia*, *Melitaea diamina* and *M. athalia*) in the study site in Västmanland usually enter diapause (and hibernation) in the late third or the early fourth instar, which they reach at the end of the vegetation period. If caterpillars of *E. maturna*, *E. aurinia* and *M. diamina* are still in their second instar in September, they will not be able to perform the necessary preparations to withstand winter conditions and successfully hibernate. In the cold and rainy summers of 1987, 1993, 1998 and 2000 nearly 100 % mortality in all broods of pre-hibernation larvae of these species resulted at the study site in Västmanland. In the warmest summers caterpillars of *E. maturna* initiated diapause in early August (ELIASSON 1991, 1995c).

Many butterfly and moth species of Fennoscandia may have adapted to a short vegetation period and unpredictable summer weather by biennial development through prolonging their larval stage, or through a high percentage of repeated hibernations in their pupal stage. In the northern taiga zone and the subalpine and alpine zones, a two-year life cycle is believed to be a common survival strategy for numerous species, but it has so far only been verified for a limited number of them. It is most conspicuous in Fennoscandia in the satyrid butterfly *Oeneis jutta* (HÜBNER, 1806), and the noctuid moth species of the genus *Xestia*, as the adults of these species are known to appear within large territories in either even or odd years only (MIKKOLA 1976, DOUWES 1980, SCOTT 1986, MIKKOLA & KONONENKO 1989). About half of the investigated *Erebia* species in the Alps also have a biennial development and mainly appear in odd years (WIPKING & MENGELKOCH 1994). A similar developmental strategy was not suspected in more southern Scandinavian populations of *Euphydryas aurinia*, *Melitaea diamina* and *M. athalia*, as they all appear in fair numbers in both even and odd years in the same local populations.

### 2.2 The Melitaeini and Braconidae taxa discussed

*Cotesia* CAMERON, 1891

*Cotesia acuminata* (REINHARD, 1880)

*Cotesia bignellii* (MARSHALL, 1885)  
*Cotesia melitaearum* (WILKINSON, 1937)  
*Euphydryas* SCUDDER, 1872  
*Euphydryas aurinia* (ROTTEMBURG, 1775)  
*Euphydryas aurinia beckeri* (HERRICH-SCHÄFFER, 1851)  
*Euphydryas aurinia glaciegenita* VERITY, 1928  
*Euphydryas cynthia* (DENIS & SCHIFFERMÜLLER, 1775)  
*Euphydryas iduna* (DALMAN, 1816)  
*Euphydryas intermedia* (MÉNÉTRIÉS, 1859)  
*Euphydryas maturna* (LINNAEUS, 1758)  
*Euphydryas maturna maturna* (LINNAEUS, 1758)  
*Euphydryas maturna staudingeri* (VNUKOWSKY, 1929)  
*Euphydryas maturna tenuireticulosa* VARGA & SÁNTHA, 1973  
*Melitaea Fabricius*, 1807  
*Melitaea asteria* (FREYER, 1828)  
*Melitaea athalia* (ROTTEMBURG, 1775)  
*Melitaea athalia lachares* FRUHSTORFER, 1919  
*Melitaea athalia norvegica* AURIVILLIUS, 1888  
*Melitaea britomartis* ASSMANN, 1847.  
*Melitaea cinxia* (LINNAEUS, 1758)  
*Melitaea diamina* (LANG, 1789)  
*Melitaea didyma* (ESPER, 1779)  
*Melitaea phoebe* (DENIS & SCHIFFERMÜLLER, 1775)

For certain Melitaeini taxa we are tentatively using subspecific names in order to differentiate between definable phenotypes known to inhabit different habitats and/or have different life histories.

### 2.3 The main study site

The main study site is in the province Västmanland, near the towns Nora and Lindsberg. *Euphydryas maturna* is here restricted to a network of suitable patches in a roughly circular forested and hilly area surrounded by lakes. The species is found at altitudes between 90 and 225 m above sea level. The total area covering all distribution patches is approximately 100 km<sup>2</sup> (ELIASSON 1991, 1995c, 1996b, 2001c). In several patches *E. maturna* flies with *E. aurinia*, *Melitaea diamina* and *M. athalia* (ELIASSON 1995a, d, 1996a). The typical habitat of these species in the study area is clearings or small mires in mixed spruce-broadleaf forest along small streams, on slightly calcareous moraine (Carboniferous limestone). The suitability of the habitats is often time-limited. The average annual precipitation at Lindsberg and Nora is 650-700 mm. The mean temperature for the month of July (1901-1960) is +16-17°C. The average length of the period with snow cover is 130 days per winter season (LUNDQVIST 1953-1971, BERGSTEN 1958).

## 3 Methods

### 3.1 Field methods

Field studies of developmental stages of *Euphydryas maturna* and the locally monophagous parasitoid *Cotesia acuminata* were made in all local populations available. However, more extensive data have been collected from three local populations. The studies were made continuously from the end of the caterpillars' hibernation period until the end of the vegetation period in 1992-1994. In the following years (1995-2002) observations were made mainly during the spring and autumn periods. Notes were made in the field of all records of caterpillars, pre-pupae, pupae and parasitised hosts during the spring period. Parasitised hosts were tagged so as to follow individual development in the field. In autumn notes were made of all webs, their individual positions, observed instars and number of adult parasitoids. Random collecting of egg clusters or early instars of *E. maturna* for breeding were mainly made in seasons with insufficient temperatures for completing growth to the hibernating instar. Field studies of developmental stages of *E. aurinia* and *Melitaea diamina* and the narrowly oligophagous parasitoid *Cotesia melitaearum* were made in parallel with the studies of *E. maturna*, but less effort was made to obtain extensive data on these species. In order to obtain parasitoids from post-hibernation caterpillars of *E. aurinia*, cages (40 x 25 x 25 cm with a top opening 25 x 15 cm) with caterpillars were returned to the location from which they originated. Also caterpillars of *E. maturna* on the "wrong" food plant were exposed to parasitism using this method. To obtain parasitoids from pre-hibernation caterpillars of *M. athalia*, females were put in cages for oviposition at the site where they were collected and the resulting larvae collected one month later. Field studies of developmental stages of *M. britomartis* were made during short periods in 1996, 1998 and 2000 in two separate distribution areas. Field studies of developmental stages of *E. iduna* were made on one occasion in 1995. Temperatures were measured inside webs of *E. aurinia* and *E. maturna* in parallel with ambient temperatures with a thermometer with thin wire thermocouples (Fluke 52 K/J).

### 3.2 Terminology

In practice it is often impossible to be sure how many separate females may have contributed progeny to what becomes a single unit of aggregation – a web. The term web is therefore used in this work to refer simply to the unitary aggregation of caterpillars and/or eggs seen in the field, from an unknown number of females. However, egg clusters deposited by different females are usually easy to separate even in cases where they have been deposited edge to edge. Only a short separation in time between the oviposition of two egg clusters will be noticed through gradual changes in egg colour. Aggregations collected as eggs or first to second instar caterpillars will in general present the most reliable information on the number of females involved. The term brood is used to refer to an unitary aggregation from one female (without implying a stage). The term batch

refers to the aggregation which may be a mix of broods, bred as a unit in captivity.

### 3.3 Breeding methods

Batches of caterpillars were bred from egg clusters collected from the wild (*Euphydryas maturna*, *E. aurinia*), from egg clusters deposited by captive females in cages (*Melitaea athalia*, *M. britomartis*), and from webs located and collected in the original habitat in August resulting from single or several egg clusters (*E. maturna*, *E. aurinia*, *M. diamina*). A few batches were collected in post-hibernation stages (*E. aurinia*, *E. iduna*). Most rearings have been conducted outdoors, either on bushes and low plants growing in a garden (*E. maturna*, *M. athalia*, *M. britomartis*), or in a bathtub filled with soil and plants (*E. maturna*, *E. aurinia*, *M. diamina*). Caterpillars were transferred to cages before they split up into smaller groups (*M. athalia*, *M. britomartis*, *M. diamina*) or immediately before the initiation of diapause for hibernation (*E. maturna*, *E. aurinia*), when especially caterpillars of *E. maturna* that have entered their fourth instars are liable to leave the nests to diapause with caterpillars in their second hibernation or solitarily. The cages used were transparent plastic containers (190 × 180 × 180 mm) covered with a clear plastic film, which allows some evaporation. These cages were kept indoors in artificial light and were given the natural photoperiod of that particular date. Caterpillars of *E. maturna* in diapause in their webbing were transferred to paper rolls (made of tightly folded paper) and caterpillars still feeding would usually later join these groups freely. In the other species, pre-hibernation caterpillars were gathered from their pockets of tightly woven silk within the webs (*E. aurinia*), or among folded dry leaves of other plants than the foodplants (*M. athalia*, *M. diamina*, *M. britomartis*), and were transferred to paper rolls. It is very important to give caterpillars that have ceased feeding sufficient time to dehydrate before they are removed from a heating light. The paper rolls were closed with a gauze before the caterpillars were placed in a cold and damp earth-chamber (potato-cellar) on a grate over some water in a bucket. Hibernation was terminated by bringing the cages out in April or May, as soon as foodplants were available. The same plastic containers were used for post-hibernation caterpillars, but usually covered with gauze to avoid occasional overheating of caterpillars at ambient temperatures above +20°C. Cages were moved every day with the sun to maximise the caterpillars' opportunities to bask. Caterpillars with a multiennial life cycle were able to seek protection in the same paper rolls used at their first hibernation. After one moult in this position they would come to a complete rest from late May or early June. Caterpillars in diapause were not separated from active caterpillars until the latter were in the last instar or later. The paper rolls with caterpillars in diapause were again sealed and placed on a grate over water in a shady but well aired place. In late autumn they were transferred to the earth-chamber. When the paper rolls have to be changed in autumn, as the result of mouldering frass and shed larval skins, it is very important to sprinkle the

frass and shed larval skins, it is very important to sprinkle the new paper rolls with water. If this precautionary measure is not performed the entire brood will surely die from drought. Particularly *M. diamina* and *E. aurinia* are vulnerable to even a short period of insufficient humidity in diapause and hibernation. A larger batch of caterpillars seems to withstand such events better than single caterpillars or smaller groups. The perfect balance between an environment dry enough to avoid mould and humid enough to enable a high survival rate is particularly hard to maintain in sealed containers. The survival rate of *M. diamina* and *E. aurinia* seems to be higher when hibernation takes place in semi-natural outdoor cages, but scores are difficult to make in this environment and these broods (and those of *E. maturna* reared under similar conditions) have been excluded from the tables. Lately paper rolls have been replaced with plastic rolls filled with various species of tree lichens, which prevents condensation while seeming to maintain a higher and less variable humidity than the paper rolls. All bred caterpillars were protected from further parasitism, and parasitoid cocoons from collected broods were always removed before adult parasitoids emerged.

### 3.4 Interpretation of the breeding results

The following notes apply to tables 1-7:

There is a general chronology from left to right: each successive D, S and R relates to a successive year (the years are indicated by 1, 2, 3 or 4 immediately following R).

**Year** = the year of collection. This is also the first year of the life cycle except when collections of post-hibernation larvae were made. These are recognisable by the figures for D being scored "na" (= data not available), and in all such cases the first year of the life cycle would have been the year prior to the year of collection.

**Instar** = collections were made either as eggs (= ova) or as various mixes of instars (e.g. from first to fourth instars (= 1-4) in the pre-hibernation collections and in third to fifth instar (= 3-5) in post-hibernation collections).

**B** = number of broods mixed together. Each brood is presumed to have originated from at least one separate female.

**D** = number of larvae attempting diapause. Larvae entering diapause in summer are scored here whether or not they were still alive at the onset of winter.

**S** = number surviving diapause and hibernation. The criterion for survival was the ability to resume feeding and defaecating.

**P** = number of parasitised larvae. The figures refer to hosts from which the parasitoid(s) erupted to form cocoons. The actual number of parasitised pre-hibernation larvae might be higher, but dissections of larvae that died in hibernation were not undertaken.

**R** = remaining healthy larvae (S minus P and minus mortality during the active feeding period). The score is of larvae that can subsequently be scored ei-

ther as attempting to reach the adult stage in the same year, or as attempting to enter diapause.

1-4 = number of larvae attempting to reach the adult stage. This includes all larvae reaching the pre-pupal, pupal or adult stage immediately after being scored as part of R. The numbers 1-4 relate to the year class as follow: 1 = number of larvae with one-year life cycle; 2 = number of larvae with biennial life cycle; 3 = number of larvae with triennial life cycle; 4 = number of larvae with quadriennial life cycle.

Breeding series in which the life cycle covers several years are very likely to be broken by some accident. The most usual cause of failure has been insufficient humidity for the caterpillars during diapause (including hibernation). Mortality during the active feeding period has in general been low, but some cases of accidental overheating have occurred. A small loss in many broods during the active period was caused by failure in moulting, which occurred most commonly in small caterpillars. Several breeding series were deliberately broken to provide livestock for introduction experiments. In Tables 2, 3, 5, and 6 the first figure given for the percentage of healthy larvae attempting diapause (D/the proceeding R) gives a direct measure of the proportion having a multiennial (biennial or more) life cycle. This is of particular help in the broods with a low survival rate during the second (or subsequent) diapause period. The percentage of larvae surviving diapause and the feeding period (R/(D-P)) each year is presented to give a general view of the variations in the success of maintaining a high survival rate in the broods (under captive conditions P = zero for all except the first year: in the wild P might recur as a drain on the host population in each succeeding year). The percentages of the total sum of adults presents the proportions of individuals with 1, 2, 3, 4 year life cycles respectively, based on the total number of caterpillars attempting to reach the adult stage. Although carrying the presumption that sources of mortality are not distorting, these proportions give the best available estimate of what we believe is at least partly a genetically influenced division of individuals, from the same broods, into life cycles of various lengths. Thus although none of these presentations can be expected to reflect the actual division between one to multiennial life cycles in wild broods, they do describe the possibilities that each species has of altering the generation length.

## 4 Results and discussion

### 4.1 General biology of the Melitaeini species in Sweden

A general understanding of the biology of Melitaeini is a necessary background to this work. The following outline depends heavily on our own field observations (ELIASSON 1991, 1995a, b, c, d, 1996a, 1998a, b, 1999a, 2001c, 2002a, b, c); other publications describe similar work in other countries (PORTER 1982, FRIEDRICH 1986, BINK 1992, EBERT 1993, WAHLBERG 1997, 1998, 2000).

Adults emerge when the leaves of their foodplants have grown to their full size. For lowland species in Scandinavia the flight period usually falls within the month of June, but for some lowland species (*Melitaea athalia*, *M. britomartis*) and for arctic species (*Euphydryas iduna*) the flight period may last until late July. Oviposition takes place on the underside of sun-exposed leaves. Eggs are placed in smaller (c. 50-100) (*M. diamina*, *M. athalia*, *M. britomartis*) or larger (c. 200-300) (*E. matura*, *E. aurinia*) clusters. Females often oviposit on a leaf on which eggs have already been placed by a preceding female (a well documented phenomenon for several *Euphydryas* species: STAMP 1982, WILLIAMS 1984, ELIASSON 1991). If the growth of the leaf selected for oviposition is not yet completed, further expansion will split the egg mass, which can lead to great loss of eggs. Egg development takes 10-20 days (*M. athalia*, *M. britomartis*, *M. diamina*) or 20-30 days (*E. matura*, *E. aurinia*), much depending on the weather. Predation rates of observed eggs have been very small. Larval development to the third instar, the earliest instar in which most species can hibernate, takes a minimum of 12 days (*M. athalia*, *M. britomartis*, *M. diamina*) to 20 days (*E. matura*, *E. aurinia*) given the most favourable weather conditions. The caterpillars feed and moult gregariously in nests of folded leaves covered with a dense water-resistant silk web. In some of the species the caterpillars gradually give up their gregarious life in their late second or early third instars, long before hibernation (*M. athalia*, *M. diamina*) but others hibernate gregariously in a conspicuous nest of webbing and leaves (*E. matura*, *E. aurinia*). Most caterpillars will pass through one moult in the position chosen for hibernation. Predation and other mortality rates of pre-hibernation caterpillars are in general more than 50%. After hibernation the caterpillars of all species can live solitarily and no new webs are made around foodplants. The fourth to sixth instars are the darkest in all species and these caterpillars spend a longer time basking between feeding periods. Pupation takes place after the sixth instar and the pupa is formed in warm sun-exposed positions, hanging from the cremaster. The pupal stage lasts a minimum of 10 to 15 days. Predation rates of post-hibernation caterpillars and pupae are not well known. Caterpillars undergoing repeated diapause show a stronger (*E. matura*, *E. aurinia*) or weaker (*M. athalia*, *M. diamina*) tendency to gather for social diapause (which continues unbroken into hibernation), forming large groups. Caterpillars in repeated social diapause often create a thin protecting web (*E. matura*, *E. aurinia*); some of this web is probably used for a safer foothold in an upside down position (*E. matura*) and some webbing usually covers entrances. Caterpillars with repeated diapause feed only in spring and they enter diapause before caterpillars attempting to reach the adult stage have completed their growth.

A majority of Melitaeini species oviposit on plants containing iridoid glycosides (JENSEN, NIELSEN & DAHLGREN 1975, BOWERS 1983, WAHLBERG 1998). These components are sequestered by feeding caterpillars and may serve to protect

pupa and adults, making them unpalatable to birds (BROWER 1984, WIKLUND & TULLBERG 1985, BOWERS & WILLIAMS 1995).

## 4.2 *Euphydryas maturna maturna* (LINNAEUS, 1758)

### 4.2.1 Distribution

The nominate race of *Euphydryas maturna* associated with ash *Fraxinus excelsior* is locally distributed in Sweden, France, Belgium, Germany, Poland, Estonia, Czechia, Slovakia, Austria and Hungary. It is possibly also distributed in parts of White Russia and Ukraine, bordering the above mentioned countries. Scattered populations in south-eastern Europe are associated with related *Fraxinus* species. From Finland, and eastwards to Transbaykal and north Mongolia, in the Ural Mountains reaching the Polar Circle, the two subspecies *E. maturna tenuireticulosa* and *E. maturna staudingeri* are more widely distributed (VARGA & SÁNTHA 1973, LUKHTANOV & LUKHTANOV 1994, J. KULLBERG pers. comm.). Recent research in Finland suggests that they are probably mainly associated with herbs (WAHLBERG 1998). The local populations of *E. maturna tenuireticulosa* usually do not persist for more than a few years in a distribution-patch and have therefore been considered difficult to study (I. HANSKI pers. comm.).

In Sweden *Euphydryas maturna* is now restricted to the provinces Västmanland and Uppland, though formerly it had a scattered distribution in the two most southern provinces and in five provinces to the north and east of the larger lakes (NORDSTRÖM 1955, ELIASSON 1991, 1995c, 1996b, 1999b, 2001c, d, 2002a, f, PALMQVIST 1997, BLOMQVIST, ELIASSON & MARTINSON 2002). In the province Uppland it was rediscovered in 2001 after 14 years with no records (ELIASSON 2001c, ELIASSON, MARTINSON & BLOMQVIST 2001). Its status in Sweden has been classified as Critically Endangered (GÄRDENFORS 2000). The current threats are habitat fragmentation and browsing by moose (*Alces alces*) when the moose population is high enough to inhibit the natural regeneration of saplings. Loss of habitat quality has occurred in the past due to drainage, air-spread herbicides and changes in land use (especially tree plantation of small pastures in forests). It is, nevertheless, often the most common butterfly in its restricted distribution-patches.

### 4.2.2 Oviposition, foodplants and larval development

Prior to this work, oviposition in Sweden had been recorded only on *Fraxinus excelsior* (AURIVILLIUS 1887, HENRIKSEN & KREUTZER 1982, GUSTAFSSON 1970). At the initial stage of this study it was discovered that *Viburnum opulus* was a regularly used plant for oviposition (ELIASSON 1991). Between 1992 and 2002 a large number of larval webs ( $n = 3564$ ) have been located in Västmanland and of these a smaller number were found on *Viburnum* and the majority on *Fraxinus* (ELIASSON 1995c, 1996b, 1999b, 2001c, 2002a, ELIASSON, AHLEN & KINDVALL 2002). In two habitat patches where *Viburnum* is fairly

common, the average distribution of webs to this bush was 6.8% ( $n = 117$ ) and 7.8% ( $n = 489$ ) between 1992-2000. Two exceptional cases of oviposition on *Syringa vulgaris* were recorded in 1992 and 1993 at the same spot. The two plants *Melampyrum pratense* and *Veronica longifolia* on which oviposition has recently been recorded in Finland (WAHLBERG 1998, 2000) are with certainty not used (or are used so rarely that we have been unable to detect it in the course of comprehensive vegetation searches) as oviposition plants in Västmanland in Sweden. The only oviposition plant in common between WAHLBERG's populations of southeast Finland and ours of central and eastern Sweden appears to be *Viburnum opulus* (BLOMQVIST, ELIASSON & MARTINSON 2002, ELIASSON 2002a). In 1992 we found a single egg cluster on this bush, which is rather rare in Finland, as the result of one week's investigation close to the Russian border. The place is only a few kilometres from the study site described by WAHLBERG (1998). This brood was bred to the adult stage, eliminating the possibility of incorrect determination. A single occasion on which a brood of first instar caterpillars was found by us on an undetermined *Melampyrum* species (*M. sylvaticum* or *M. pratense*) in Sweden is interpreted as the occasional result of browsing moose. This brood was found beneath a bush of *Fraxinus* which had recently lost more than 50% of the leaves to browsing. As the caterpillars were first determined as *Melitaea athalia* they were collected and continuously bred on the same foodplant. The growth rate on this plant was very slow and when caterpillars reached their second instar and were recognised as *Euphydryas maturna* they were offered *Fraxinus* as an alternative food. All caterpillars immediately started to feed on *Fraxinus* and the growth rate increased rapidly. This observation seems at variance with WAHLBERG's results, but data on the ecology and biology of the populations in Finland remain sparse. Both the pre-hibernation and later instar larvae in Sweden can also be reared on *Valeriana sambucifolia* and *Veronica spicata*, on which they maintain a fast growth rate. Some other potential foodplants that have been tested with poor results and some less likely foodplants for oviposition that have been listed in the literature have been discussed elsewhere (ELIASSON 1991, WAHLBERG 1998).

Post-hibernation larvae were mainly found feeding on swelling buds of *Fraxinus* and *Viburnum* (ELIASSON 1991, 1995c, 2001c). Caterpillars feeding on *Valeriana sambucifolia*, *Melampyrum sylvaticum*, *M. pratense*, *M. nemorosum* and more rarely on *Salix caprea*, *Lonicera xylosteum* and *Vaccinium myrtillus* have been recorded in nature and this feeding mainly takes place before the buds of *Fraxinus* become edible (ELIASSON 2001c). In captivity caterpillars also accept buds of *Syringa* and *Lonicera caprifolium*, and leaves of *Plantago media* and *P. lanceolata* (ELIASSON 1991). Under prolonged favourable conditions the first hibernation is preferentially made in the fourth instar, but more often the caterpillars are forced to hibernate in their third instar. The second diapause period (including hibernation) is made in fourth to fifth instars and any subsequent diapause periods in the fifth instar. During the hibernation period and in spring,



before caterpillars have resumed their metabolism, they are very tolerant of being submerged in water. In an experiment at the termination of hibernation a number of fourth instar caterpillars ( $n = 28$ ) were allowed to sink in a glass jar filled with water at a constant temperature of  $+4^{\circ}\text{C}$ . These survived 72 hours well beneath the water surface and most of them ( $n = 25$ ) later developed normally. Four caterpillars survived ten days with the same treatment during an interruption in their hibernation. When these were brought out of the water and into indoor temperatures they moved to new positions for renewal hibernation. One individual in a group of eleven fourth instar caterpillars even survived compression in an ice cube for a week. This caterpillar survived another month in hibernation, but was from the start touched by external mould and later died. Tolerance to submersion is believed to be an important consideration in the conservation of habitats, and occasional flooding may even have a positive impact if it reduces predation of the diapausing caterpillars.

The results of transect counts in each of the years 1992-2002 indicate that the length of the feeding period of *Euphydryas maturna* caterpillars in spring is not dependent on ambient temperatures. This was to be expected as *E. maturna* caterpillars bask between each feeding period, a process known to be crucial for raising body temperatures in *E. aurinia* in south England (PORTER 1982). Basking *E. aurinia* caterpillars in England could reach a body temperature of  $+35$ - $37^{\circ}\text{C}$  in springtime, while vegetation temperatures remained only slightly above ambient. Food assimilation was optimal at  $35^{\circ}\text{C}$  (PORTER 1982). In Västmanland measurements of temperature inside webs of *E. maturna* ( $n = 50$ ) were performed in sunny weather at various development stages of the pre-hibernation caterpillars. The average temperature in webs was  $+30.2^{\circ}\text{C}$  (range =  $+24.1$ - $41.9^{\circ}\text{C}$ ). Air temperatures were measured in parallel with temperatures in webs and the mean temperature difference was  $9.4^{\circ}$ . The measurements were conducted during the period 31.vii-07.ix in 1992 and air temperatures were between  $+13.9^{\circ}$ - $23.3^{\circ}\text{C}$ . The results indicate that temperatures are elevated during this period of food assimilation in broadly similar ways in *E. maturna* and *E. aurinia*. The lower average temperature measurements in *E. maturna* webs may be partly due to wind exposure. The third instar pre-hibernation caterpillars of *E. maturna* are darker than the same instar of *E. aurinia*, which probably compensates for the temperature reduction caused by wind exposure. The caterpillars of this instar exhibit a somewhat different behaviour whereby *E. maturna* is more liable to bask on the outside of the web. At temperatures above  $37^{\circ}\text{C}$  caterpillars of *E. maturna* leave the web and take up positions outside the web on the shaded side. At temperatures above  $+17^{\circ}\text{C}$  third instar *E. maturna* caterpillars will also feed at night-time until c. 22.00 hrs.

#### 4.2.3 Interactions with *Cotesia* parasitoids

The gregarious parasitoid *Cotesia acuminata*, with two generations per year, mainly ovipositing in the first two host instars before hibernation and the sixth

instar in early summer (ELIASSON 1995c, 1996b, 2001c), causes significant mortality of *Euphydryas maturna* in Sweden (cf. Table 1). *Cotesia bignellii* (MARSHALL, 1985) (K.J. HEDQVIST det.) was a mis-identification and is not the host-specific parasitoid of *E. maturna* as earlier stated (ELIASSON 1991) but rather it is a parasitoid of *E. aurinia*, and it has not yet been found in Sweden (although it occurs in Finland). *Cotesia acuminata* has been found to be the only important parasitoid attacking the caterpillars of *E. maturna* in Sweden (Table 8). Experimental rearings from unmated females have given rise to all-male progeny, showing that *C. acuminata* has the usual haplo-diploid sex determination mechanism of Hymenoptera. Females of *C. acuminata*, that had been reared in spring from 3-4<sup>th</sup> instar larvae of *E. maturna* following their diapause (i.e. from hosts in which the parasitoid larvae had overwintered), were introduced experimentally to unparasitised 5<sup>th</sup> instar larvae of *E. maturna* ( $n = 6$ ) destined for further diapause, into which they oviposited. After overwintering in the host, parasitoid larvae erupted the following year and produced cocoons from which the adult parasitoids emerged at the same time of year as their parents. This demonstrated that the parasitoid is able to adapt to the host's diapause patterns and assume a one-year life cycle on occasion. In nature the one-year life cycle of the parasitoid seems to be relatively rare in most years, but an obvious dominance of 5-6<sup>th</sup> instar hosts among those parasitised was observed in the springs of 1994 and 2001 (ELIASSON, AHLEN & KINDVAL 2002).

A single individual of *Cotesia melitaeorum* has been found among a large number of *C. acuminata* ( $n = 542$ ) emerging in spring from parasitised hosts ( $n = 138$ ) collected from broods of pre-hibernation larvae ( $n = 442$ ) in 1993-1994 and from older dispersed parasitised hosts ( $n = 23$ ) collected in nature in 1994. In captivity *C. melitaeorum* (which is similarly a gregarious and haplo-diploid species, in which unfertilised eggs give rise to male progeny) reared from *Euphydryas aurinia* will successfully oviposit and develop in all post-hibernation instars of *E. maturna*, but this host/parasitoid relation has not yet been found in nature at the Swedish sites, apart from the single reared individual detailed above (Table 8). However, a brood of *E. maturna* deliberately placed on *Valeriana sambucifolia* in the habitat of both parasitoid species during the caterpillars' first and second instars, and then collected for rearing, gave three hosts from which only *C. melitaeorum* emerged. The general failure of *C. melitaeorum* to involve *E. maturna* in its host range in Sweden is at first sight puzzling, especially as in south-east Finland the post-hibernation caterpillars of *E. maturna* are parasitised by both *C. acuminata* and *C. melitaeorum* (KOMONEN 1997). It does not seem to result from lack of synchrony in Sweden as the first generation adults of *C. melitaeorum* emerge only 1-2 weeks earlier than *C. acuminata* in spring – a difference that may suggest some disadvantage in comparison with the (locally) monophagous *C. acuminata*, but which seems not so great as to suggest prohibitive asynchrony. The single specimen of *C. melitaeorum* detailed above was from a small pre-hibernation brood of *E. mat-*

urna (Table 1, batch 3) on a branch of *Viburnum* overhanging a small stream, drooping beneath the surrounding ground level. This detail suggests that the failure of *C. melitaearum* to make as significant use of *E. matura* at the Swedish sites as was purported in south-east Finland (WAHLBERG 1998) may be connected with differences in the feeding environments (manifested as foodplants) used by *E. matura* in the two areas. Further research is needed on this point, especially in Finland (where it appears that possibly only one brood of *C. melitaearum* was reared). There is an interesting possibility that the success of *E. matura* in Västmanland has depended on its avoiding feeding on low plants in the vegetation zone occupied by the usually co-occurring *E. aurinia*, *Melitaea diamina* and *M. athalia*, the first two of which are regular hosts of *C. melitaearum*. Instead, *E. matura* has specialised in shrub and tree foliage and buds that, in terms of an evident absence of *C. melitaearum*, represents "enemy free space". In Uppland, where *E. matura* co-occurs only with *M. athalia*, which is probably incapable of supporting a population of *C. melitaearum* in the absence of more suitable hosts, the post-hibernation caterpillars seem invariably to feed on the low plant *Melampyrum* (*C. WIKLUND* pers. comm., data from 1975 and 1977).

The normally white cocoons of the two *Cotesia* species are arranged in a different fashion (*C. acuminata* in strict order; *C. melitaearum* in disorder) in relation to the host and can easily be determined when found in nature, in practically all cases of more than two cocoons. Hosts of *C. acuminata* are induced to choose very conspicuous positions on sun-exposed trees, rocks and fallen branches in spring as sites in which to produce their parasitoids, and are easy to find.

The average brood size of *C. acuminata* from 3-4<sup>th</sup> instar hosts ( $n = 507$ ) was 4.6 in breedings in 1993-1994, and 5.0 in 1994-1995 ( $n = 1053$ ). Brood size variation in these hosts was 1-15. The average brood size of *C. acuminata* in 5-6<sup>th</sup> instar hosts ( $n = 46$ ) collected in nature in spring 1994 was 15.9 (range 9-44). The mean brood size was 25.1 (range 8-63) in 5-6<sup>th</sup> instar hosts ( $n = 23$ ) of the second (summer) generation of the parasitoid. Hosts of the second generation are induced (by parasitoid larvae) to stay active but only sparingly feeding until the middle or close to the end of the butterfly's flight period. After this prolonged development period parasitoid larvae erupt to form cocoons. The cocoon stage (from formation of cocoons to emergence of adults) lasts 6-9 days in the first generation under the most favourable conditions. Adult parasitoids of the second generation may remain fully developed inside the cocoons for a longer time (> 21 days from the formation of cocoons, emerging from hosts in cages between 20 June and 19 July in 1993). PORTER (1983) observed a similar behaviour in *C. bignellii*. Adult females of *C. acuminata* are normally to be observed attending the egg clusters of *Euphydryas matura* from half-way through the egg development period.

Different sizes of caterpillars can often be observed in wild broods, but larvae of *Cotesia acuminata* inducing a faster growth rate in parasitised individuals

usually cause the difference. These caterpillars continue to feed after their moult to the fourth instar when unparasitised caterpillars are already in diapause. Caterpillars larger than average in wild broods were selected from many separate webs in six networks of patches in the period 1993-1994 ( $n = 202$ ). The survival rate after hibernation was 82.2% and the rate of parasitism in surviving caterpillars was 96.4%. The remaining caterpillars ( $n = 6$ ) entered a second diapause period. In two collected webs (Table 1, batches 10 and 12) the larger caterpillars ( $n = 166$ ) were separated. Their survival rate after hibernation was 72.3% and 100% of survivors ( $n = 120$ ) proved to be parasitised. The survival rate of all caterpillars ( $n = 687$ ) in batches 10 and 12 was 69.3% and the rate of parasitism 32.1%.

At the end of the feeding period of pre-hibernation caterpillars (with the majority in diapause) the conspicuously larger caterpillars are typically found feeding together with the very smallest caterpillars, with a retarded growth rate. These smallest caterpillars are believed to be victims of super-parasitism, i.e. having been oviposited into by more than one female parasitoid, each contributing its normal number of eggs. If this is the case it is certainly a disadvantage also to the parasitoids, as these caterpillars usually remain in their second instar until the end of the vegetation period and are unable to withstand hibernation. However, some caterpillars with a retarded growth rate were separated and given special treatment with artificially warmer conditions. These caterpillars exhibited an extreme behaviour with a higher proportion of time spent on producing webbing than on feeding and basking. Only a few of the caterpillars with retarded growth rate from 1994 survived diapause ( $n = 11$ ) and all proved to be parasitised. The average number of parasitoids emerging from the hosts was 11.2, which is about double the brood size for normal hosts after the first hibernation (average 5.0;  $n = 1053$ ). Broods in which parasitism was absent grew more evenly and typically all individuals diapaused in the same instar.

The pre-hibernation caterpillars of *Euphydryas matura* have an efficient defence against the ovipositing *Cotesia acuminata*. When the gregarious caterpillars are attacked they jerk their anterior halves violently from side to side in unison. If a caterpillar detects the position of the parasitoid it will strike in its direction. Caterpillars are able to open their jaws to deliver a drop of oral secretion about the size of their head, which, particularly in the web-producing pre-hibernation stages, contains a strong cement. Adults of *C. acuminata* can be severely handicapped by a slight touch of this oral secretion. The strategy of *C. acuminata* to locate the egg clusters of *E. matura* before the eggs eclose gives it an opportunity to attack the host during a defenceless developmental stage. The young caterpillars are attacked at the moment of emergence, just outside or still inside the eggshells. Later the parasitoid tends to avoid all direct confrontation with its host, and this starts as soon as the caterpillars have moved away from the eggshells to the upper (opposite) side of the leaf. Subsequently all attempts at oviposition into hosts before their first hibernation are made more or less haphazardly through the web and are believed to be generally unsuccessful.

In contrast to pre-hibernation caterpillars, the post-hibernation instars of *E. maturna* from Sweden seem to have a very inefficient defence against attacks by the first generation of *C. acuminata*. Swedish 5-6<sup>th</sup> instar caterpillars are, in captivity, remarkably slow in their reactions to physical contact by females of *C. acuminata* and *C. melitaeorum* in comparison with post-hibernation *E. maturna* from Hungary, or in comparison with post-hibernation *E. aurinia* from Sweden. The Swedish *E. maturna* caterpillars will not react to a parasitoid walking on their spines, but react violently when oviposition is over and the damage is done. The caterpillars of Hungarian *E. maturna* are more easily disturbed by parasitoids. The caterpillars from Hungary belong to south-eastern populations with only a one-year life cycle (E. MEGLÉCZ pers. comm.), and they were studied in parallel with Swedish *E. maturna* in Sweden. The pre-pupal stage is not attacked in either case, and observed parasitoid attacks on caterpillars attempting to reach the adult stage yielded no progeny if the caterpillar was within 3-4 days of reaching its pre-pupal state (ELIASSON, 2001c).

Our local rearings of other Melitaeini strongly suggest that *Euphydryas maturna* is the only host of *Cotesia acuminata* in Västmanland (Table 8). This is consistent, too, with the observation that three collections of *E. maturna* broods (Table 1, batches 17-18), from two recent introduction sites that had pre-existing populations of *Melitaea athalia*, proved to be unparasitised. Elsewhere in Europe *Cotesia* reared from several species of Melitaeini have been recorded as *C. acuminata*, in particular from *Melitaea phoebe*, *Melitaea didyma* and possibly *M. athalia*. Recent DNA (M. KANKARE & M.R. SHAW in prep.) and morphological (M.R. SHAW in prep.) analyses suggest, however, that *M. phoebe* may support a distinct *Cotesia* species very close to *C. acuminata* rather than *C. acuminata* itself, and that this is certainly the situation regarding the *Cotesia* reared from *M. didyma* (with some doubtful records of the same taxon from *M. athalia*). Adults of what appear to be the true *C. acuminata* have been collected on webs of *E. intermedia* in Switzerland by C.U. ELIASSON, which suggests that *C. acuminata* should be regarded as narrowly oligophagous, although locally entirely monophagous in the areas of Sweden inhabited by *E. maturna*.

#### 4.2.4 Breeding results (Tables 1 and 2)

Survival rates of *Euphydryas maturna* caterpillars have in general been high during the first diapause and hibernation period, which lasts only 7-8 months. A high survival rate is more difficult to maintain during the subsequent unbroken periods of summer diapause and subsequent hibernation, which last 10-11 months. Taking the "long series before 1995" data of Table 2 it is therefore evident that at least a triennial life cycle was the most dominant at that time in the wild *E. maturna* population in Västmanland. When the difficulties of breeding are considered it also seems likely that the actual proportion with a quadriennial life cycle might have been higher than the proportion with a biennial life cycle.

The proportion of caterpillars with a one-year life cycle is remarkably low throughout a long period (1992-1998) compared with the proportions of one-year life cycle in the other Melitaeini species studied (Tables 3-6). There is an evident change in the data for the *E. maturna* series after 1995, with a higher proportion having a biennial life cycle. However, this result is probably due to a boost in the relative proportion of parents with a biennial life cycle reflected in the 1996 and 1997 collections, and in that sense it is believed to be a merely temporary phenomenon. Thus the two batches 19 and 20 from 1996 most probably were the progeny of 1994 adults, which was the best reproduction year in the period 1992-1997. The cold summer of 1993 caused a total reproductive failure at the altitudes where these broods were collected, and the summers of 1994-1996 had severe drought periods causing a high mortality rate of caterpillars in diapause, affecting the entire *E. maturna* population. The drought is probably the reason for the high proportion with a biennial life cycle in batch 21. Many local populations in environments with insufficient ground humidity went extinct during this period. These two circumstances make it unlikely that individuals originating before eggs laid in 1994 would have had significant participation in overall reproduction in 1996. In batch 18, from an introduction site where all reproducing *E. maturna* individuals indubitably had a biennial life cycle, a very strong dominance of a biennial life cycle is seen to have been carried on by their progeny. Thus batches 18-20 very clearly indicate that the proportions having a one-year life cycle and multiennial life cycles are to an extent genetically controlled, and this raises the expectation that proportions may change within a local population, if a changed proportion of caterpillars predisposed to one year or multiennial life cycles successfully reach the adult stage. Depending on the strength of reinforcing circumstances, such changes may at least hypothetically become permanent, though the stochastic climatic influence on *E. maturna* populations would be likely to be destabilising in the long run. The counts of webs in all distribution patches after the 1994-1996 drought period showed that a limited periodicity had been established and reinforced by the poor reproduction results in 1998 and 2000. Despite favourable weather conditions during the oviposition period and the subsequent development period in 2002, the counted number of webs ( $n = 217$ ) was markedly lower than in 2001 ( $n = 653$ ). This indicates that throughout this period the proportion of the population with triennial life cycle had probably remained low in relation to a dominant proportion with biennial life cycle, and that the low proportion with one-year life cycle had been of limited importance in the wild population (ELIASSON, AHLÉN & KINDVALL 2002).

For the *Euphydryas maturna* populations of south-east Finland, WAHLBERG (1998) suggests that larvae growing in a warm place will develop to adults in one year, whereas in colder areas they will return to diapause and require two years. Such a presumption of developmental plasticity of *E. maturna* caterpillars is not supported by our extensive data on breeding *E. maturna* under various conditions in Sweden. The methods and data presented by WAHLBERG (1998)

for estimating the impact of exposure to solar radiation (in two separate patches, one warm and one cool) on the length of the life cycle were far from ideal, and seem open to other interpretations. With reference especially to the warm group, the relatively small numbers that were still in evidence at the end of the observation period, when all detectable larvae were collected for rearing, may indicate merely that more (and many) larvae from that faster-growing group had removed themselves from observation in order to enter a second diapause before the end of the monitoring period. This would leave largely (or perhaps only) those few attempting to reach the adult stage at the time of collection. As the larvae did not retain their marks throughout, there is also the possibility that inward and outward migration from the arena (10 × 10m) could have confused the results if incomers were of an older year class.

FRIEDRICH (1986) gives breeding information from an unknown area, probably Germany. He states that caterpillars that diapause (and hibernate) in the third instar the first time usually diapause a second time in the fourth instar, while caterpillars that diapause in the fourth instar the first time usually diapause just once. Our results can only to a very limited degree relate to this, as the number of caterpillars with a one-year life cycle has always been very low (Table 2). The bred caterpillars have in general entered the first diapause (and hibernation) period early in the fourth instar, and the fewer that did so in the third instar have had a lower survival rate during diapause. The only indication in the Swedish breedings that caterpillars with a one-year life cycle might be recognised from their larger size came from two small broods in which there was a strong possibility that the majority of caterpillars had left the webs before the collection date on 12 August 1994 (Table 1, batch 11). After hibernation the larger caterpillars (n = 25) were separated to detect the rate of parasitism. In contrast to the batches with larger caterpillars detailed in section 4.2.3, only 11 caterpillars proved parasitised and 12 attempted to reach the adult stage. It is, however, difficult to interpret these results in view of the possibility that the collected caterpillars were residual and not representative of their broods as a whole.

It has been suggested that female larvae of a related species, *Euphydryas intermedia*, may need a longer feeding period than male larvae, and that this would lead to a division with females having a longer development cycle (LUCKENS 1985). Although in the populations of *E. maturna* we studied the data for sex ratios are not available for all batches or for all individuals in batches, the following examples point to there being no significant difference in the sex ratio between different lengths of the life cycle. In 1994 batches 6-9 gave 7 males and 6 females with a one-year life cycle. In 1998 batch 19 gave 58 males and 50 females with a biennial life cycle and batch 12 gave 4 males and 4 females with a quadriennial life cycle (the figures in each case include all individuals which successfully reached the adult stage). WAHLBERG (1998) came to the same conclusion from wild collected caterpillars from south-east Finland, and this corresponds to our own breeding results from our single egg cluster from south-east Finland which in 1994 gave 10 males and 13 females with biennial life cycle.

Wild-collected sixth instar caterpillars, pre-pupae and pupae (n = 107) in Sweden 1992-1994 also gave an even sex ratio (males, n = 47; females, n = 41), which suggests that parasitism and other major mortality factors are not selective (ELIASSON 2001c).

### 4.3 *Euphydryas aurinia* (ROTTEMBERG, 1775)

#### 4.3.1 Distribution

This species is widely distributed in the lowlands of the temperate climate zone and in mountains of the southern temperate and subtropical climate zones from west Europe to China and Korea. In Europe *Euphydryas aurinia aurinia* is usually associated with *Succisa pratensis*. In Spain and North Africa *E. aurinia beckeri* is associated with *Lonicera* species, and in the higher European mountain ranges *E. aurinia glaciegenita* mainly with *Gentiana* species (DOUWES 1971, GEIGER 1987, BINK 1992, EBERT 1993, STOLTZE 1996).

In Sweden the nominate race of *Euphydryas aurinia* was formerly locally distributed in all southern, central and eastern provinces to 62° latitude (NORDSTRÖM 1955). Since 1980 it is only found in six provinces including the Baltic Islands (RYRHOLM 1995, ELIASSON 1995a, 1996a, 1999b, d, 2002b, d, e, PALMQVIST 1997, FRYCKLUND 2002, LINDBERG & FORSLUND 2002a, LINDMARK, RIPLER & ELIASSON 2002, SJÖBERG 2002, BERGSTEN & FRYCKLUND in prep.). The species has been classified as Vulnerable according to the new IUCN definitions (GÄRDENFORS 2000). The current threats are habitat fragmentation and changes in land use (especially tree plantation of pastures in forests). Losses of habitats and habitat quality have occurred in the past due to drainage and reforestation. It is, nevertheless, often one of the most common butterflies in its restricted distribution-patches.

#### 4.3.2 Oviposition, foodplants and larval development

Oviposition, with one exception, has only been recorded on *Succisa pratensis* in Sweden: Västmanland 1989-2002 (n = 1018); Gästrikland 1994-1996 (n = c. 20); Dalarna 1989-1991 (n = c. 10); Gotland 2001-2002 (n = 146). It seems unlikely that the species selects other plants for oviposition in Sweden, unless an abnormal situation occurs: two webs were found on *Knautia arvensis* in Västmanland in August 2003. Post-hibernation larvae have mainly been found feeding on the same plant (EKLÖV & CEDERBERG 1992, HÖJER 1995, ELIASSON 1995a, 1996a, 2001a, J. GUSTAFSSON & C. KÄLLANDER pers. comm.), but occasional feeding on *Valeriana sambucifolia* has also been seen in nature. In captivity caterpillars also accept leaves of *Lonicera caprifolium*. The position of the pupa is always close to the ground, often on withering grass and herbs or on stems of *Calluna vulgaris*. It is in general hard to find except when a newly eclosed butterfly reveals its location. On a single occasion two pupae, from late developed caterpillars, were found in unusual positions in Västmanland. In each

case the pupa was attached to a thin web connecting the outer edges of a leaf of *Rubus saxatilis*. In this position the pupa could make use of the solar heating of the upper side of the parabola-shaped leaf.

In Västmanland parallel measurements of the temperature inside the webs of *Euphydryas aurinia* ( $n = 28$ ) and ambient temperature were performed in sunny weather at various development stages of the pre-hibernation caterpillars. The average temperature in *E. aurinia* webs was  $+35.9^{\circ}\text{C}$  (range =  $+24.6$ - $47.0^{\circ}\text{C}$ ). The measurements were conducted during the period 31. vii-07. ix in 1992 and the air temperatures were between  $+13.9$ - $23.3^{\circ}\text{C}$ . Measurements of the temperature inside groups of basking caterpillars on eight webs were made after their hibernation in mid-April, when 25-50% of the habitat was still snow-covered. During sunshine, the temperatures increased to between  $+23.0$ - $34.2^{\circ}\text{C}$ , when ambient temperatures increased to between  $+12.7$ - $13.9^{\circ}\text{C}$ . This indicates that Swedish caterpillars in early spring can reach a body temperature close to the optimal temperature of  $+35^{\circ}\text{C}$  regarded by PORTER (1982) to allow for most efficient metabolism in the population he studied in S. England.

The hibernating caterpillars are very tolerant of submergence in water. In a test whereby 50 caterpillars were submerged for three days, and the water at the end of the period was frozen to a solid block of ice, 20% of the caterpillars managed to survive. At indoor temperatures the surviving caterpillars proved able to move around and seek new positions for diapause: however, all were touched by external mould (which is why they had been selected for this possibly sacrificial experiment) and later died.

#### 4.3.3 Interactions with *Cotesia* parasitoids

The only larval parasitoid of *Euphydryas aurinia* which was detected in the Swedish populations studied in Västmanland and Gotland is the gregarious braconid *Cotesia melitaearum*, a species regarded to have a relatively wide host range among Melitaeini species (NIXON 1974, M.R. SHAW unpublished) to which it is specialised (Table 8). Although recent DNA analysis (M. KANKARE & M.R. SHAW in prep.) has raised the possibility that *C. melitaearum*, as currently understood, in the western Palaearctic region might in fact be an aggregate of closely related species, each with a more restricted host range, there is no evidence to contradict our presumption in this paper that the Swedish populations encountered with their various hosts all belong to a single species. *Cotesia melitaearum* has been reared from *E. aurinia* very widely in Europe, including Finland (KOMONEN 1997). In Sweden (as elsewhere) this parasitoid has two generations per year, ovipositing in the first three instars of pre-hibernation larvae and the fifth to sixth instars of post-hibernation larvae (ELIASSON 1995a, 1996a). The pre-pupal stage is not attacked. Parasitoid larvae erupt to form cocoons in early spring before caterpillars fully leave the web and may be formed in the web or in very close proximity to it. This often takes place when 10-20%

of the habitat is still covered with snow. Cocoons are regularly found on the underside of the top leaves in the leaf litter covering the ground; in the study sites most often on leaves of birch, *Betula* species. The cocoons of the second generation are more difficult to find in nature, but two cocoon masses with host remains have been found inside small chambers made up of web and the fresh top leaves of 20 cm high birches. A third cocoon mass has been found on the upper side of a leaf of the low plant *Convallaria majalis*, resembling its flower bud. Parasitised hosts of the second generation have also been obtained by placing caterpillars in fourth to fifth instars in a cage with an open top in the place from where they originated. In addition to producing second generation parasitoids, when the experiment was terminated c. 40 caterpillars had entered diapause. Although the survival rate after hibernation was very low, progeny of *C. melitaearum* emerged from one of these caterpillars in the spring of the following year (i.e. in a univoltine mode). Generally the rate of parasitism of pre-hibernation larvae has been low (Table 3). The average number of cocoons in the first generation from parasitised 3-4<sup>th</sup> instar larvae ( $n = 24$ ) was 1.7, with brood size variation 1-5. The average number of cocoons in the second generation from parasitised 5-6<sup>th</sup> instar larvae ( $n = 14$ ) was 14.9 with brood size variation 6-32. (When this information was compiled many samples had to be excluded because hosts tend to move around after parasitoid larvae have started to emerge to form cocoons, and the parasitoid broods became confused). The parasitoid's pupal stage in the first generation lasts 8-12 days at indoor temperatures. Second generation *C. melitaearum* adults have emerged 10-12 days after the formation of cocoons during the flight period of the host butterfly in mid June. This is a difference worth noting in comparison with the more narrowly host-specialised *C. acuminata*, which remains fully developed in the cocoons for a longer period.

*Cotesia acuminata* would not develop in post-hibernation larvae of *Euphydryas aurinia* (Table 8), despite experiments in which apparent oviposition was observed twice when seven caterpillars in their fifth instars were exposed. Six of these caterpillars reached the pupal stage; the other died, but without evidence of having been successfully parasitised. The parasitoids used in this experiment originated from *E. maturna* collected at the same locality as the *E. aurinia* larvae.

Post-hibernation caterpillars of *Euphydryas aurinia* reacted immediately to disturbance by both species of *Cotesia* in small experimental boxes of clear transparent plastic (10 × 10 × 5 cm). They sometimes chased the parasitoid and made repeated attempts to hit it with oral secretion. Very often a successful oviposition by *C. melitaearum* ended with the parasitoid entirely (and, at least under captive conditions, fatally) caught inside a blob. Observations were made of parasitoids that had their antennae bitten off and of caterpillars that sucked up their own drop of oral secretion from the plastic after a failed attack, probably in order to be able to defend themselves again quickly.

#### 4.3.4 Breeding results (Table 3)

The partially biennial life cycle of *Euphydryas aurinia* has previously been unknown from north-west Europe (DOUWES 1971, PORTER 1982, 1983, GEIGER 1987, BINK 1992, EBERT 1993, STOLTZE 1996). It is possible that this is a unique feature of the Scandinavian *E. aurinia* population and the subalpine *E. aurinia glaciegenita* distributed in the Alps and the Pyrenees (GEIGER 1987, ELIASSON 1995a, 1996a, 2002b). The breeding results in Table 3 show that approximately 50% of the caterpillars may attempt a second diapause period. Although in most breedings the proportion is smaller, this indicates that a partially biennial life cycle is probably important to the long-term survival of *E. aurinia* in Västmanland. The survival rates after the first hibernation, but in particular after the second diapause and hibernation periods, are both low compared to breeding results of *E. maturna*. This suggests that the proportion of resulting adults that would be found to have a biennial or longer life cycle would be much higher than that recorded in Table 3 with more successful breeding results. The single caterpillar attempting a third diapause period in batch 1 was perfectly healthy through the last summer in diapause, but died during hibernation. Thus it seems possible that an unknown proportion of *E. aurinia* has a triennial life cycle, but that this is not yet revealed because of the low diapause survival rates achieved in the breedings. The drought during the summers of 1994-1996 seem to have affected the proportions of caterpillars entering a second diapause period (Table 3; batches 5-8), and the main reason is probably a higher mortality rate of caterpillars with repeated diapause, affecting the genetically influenced proportions of one-year to multiennial life cycles in much the same way as is discussed in the section on *E. maturna* (4.2.4).

Breedings of *Euphydryas aurinia* in an outdoor cage (bath tub c. 0.8 m<sup>2</sup> filled with cut-out pieces of natural habitat) have also given a high proportion of caterpillars attempting a second diapause and hibernation period (in 1995 c. 27.4 %, n = 68; but estimates were uncertain owing to unknown mortality and escape rates, and the results are not included in Table 3). Here observations were also made of natural social behaviour of the caterpillars attempting a second diapause period. The same position was not chosen every year (n = 3), but a single locus never failed to attract more than 90% of the caterpillars forming a tight group beneath a thin web at the edge of a tuft or beneath a piece of wood. Caterpillars of *E. maturna* and *Melitaea diamina* joined *E. aurinia* in the same social diapause position.

Populations of *Euphydryas aurinia* with an apparently exclusively one-year life cycle were present (but are now extinct) no more than 20 km east of the studied populations living sympatrically with *E. maturna* and *Melitaea diamina* in Västmanland (C.U. ELIASSON unpublished, F. IVERSEN & P.S. NIELSEN pers. comm.). The average annual precipitation in this area is 550-600 mm and in Nora and Lindesberg 650-700 mm (LUNDQVIST 1953-1971). The adults were markedly later on the wing in these populations without a partly biennial life

cycle. Although few, the caterpillars attempting a second diapause period in batches 5-6 in Table 3, from Uppland and Gästrikland provinces, indicate that a biennial life cycle is probably also important to the north and north-east of Västmanland, in spite of a lower average annual precipitation in these areas. *E. aurinia* in south Sweden probably has a strictly one-year life cycle.

#### 4.4 *Euphydryas iduna* (DALMAN, 1816)

##### 4.4.1 Distribution

The nominate race is distributed in boreal, subalpine and alpine regions with moderate to low levels of annual precipitation. It occurs from the upper level of the subalpine birch forest to approximately 1000 m above sea level in Fennoscandia. In Finnmark and the Kola Peninsula it can be found at sea level. In the Scandinavian mountains the distribution reaches its southernmost point at 66° latitude (NORDSTRÖM 1955). The distribution of the nominate race includes a few scattered records from polar and sub-polar Ural, Taymyr and North Yenisey (LUKHTANOV & LUKHTANOV 1994). The species has been classified as Near Threatened according to the new IUCN definitions (GÄRDENFORS 2000). The current threats are vegetation changes caused by global warming and worn-out soil layers due to over-browsing by reindeer (*Rangifer tarandus*) on patches with thin and early-melting snow. The frequency of butterflies is extremely variable, but usually a few years with high abundance come in a row (J. GUSTAFSSON & C. KÄLLANDER pers. comm.).

##### 4.4.2 Foodplants and larval development

Very few reliable records of pre-adult development have been published (NORDMAN 1942, HARRYSSON 1970, DOUWES 1971, HENRIKSEN et al. 1982). Most of them are records of finding the pre-pupae. Only one article presents reliable observations of foodplants in nature (NORDMAN 1942). The plant(s) selected for oviposition is not known with certainty. In 1995 one pupa and 14 post-hibernation larvae were found on a wind-exposed subalpine heath, at 400 m above sea level in northern Sweden, near Torne träsk. The same spot was investigated daily between 4 and 10 July and 13 caterpillars were found solitarily, feeding on flowers and the upper leaves of *Bartsia alpina* (Scrophulariaceae) between 4 and 7 July. A single caterpillar was found feeding on *Pedicularis hirsuta* (Scrophulariaceae). The pupa was attached to a rock with a vertical side. The first adults of both sexes were on the wing at this locality from 7 July. The caterpillars ceased feeding on 12 July and after one moult they initiated diapause in probably their fourth and fifth instars (n = 13). At the time of this event the caterpillars were still exposed to the day length of the natural environment. NORDMAN (1942) mentions *Bartsia alpina*, *Vaccinium uliginosum*, *V. myrtillus* and flowers and leaves of several *Salix* spp. as foodplants of the two caterpillars found (probably by sweeping) at Kilpisjärvi in Finland on 19 June and a few

days later. At the same place the adults emerged after 12 July. The experience with post-hibernation larvae in 1996 was that none of the *Vaccinium* spp. mentioned above nor *Salix* spp. available at more southern latitudes (*S. caprea* and *S. cinerea*) were accepted as foodplants. The caterpillars could stay alive, but without growing much, by feeding on *Valeriana sambucifolia*, *Plantago media*, *Melampyrum nemorosum* and *Veronica chamaedryas*. Very rapid growth first started when they were offered *Pedicularis palustris*. The potted plants were consumed down into the roots. Soon after, four caterpillars died, probably because no more *P. palustris* could be offered. Six caterpillars passed through one moult on 27 May 1996 in positions selected for diapause. After hibernation the last caterpillar died on 14 June 1997 after passing through one more moult on 4 June (Table 4). The caterpillars were bred under artificial light in the day length of more southern latitudes. It seems probable that this species has a biennial and triennial life cycle in nature. In the Torne Träsk area the species was locally common as adults in 1994 and 1996. The most suitable plant for oviposition would seem to be the perennial *Bartsia alpina*. Larger plants make dense stands of dark green to violet coloured leaves and flowers. The smaller leaf and plant size of other related subalpine plants would make them seem less probable as plants for oviposition if *Euphydryas iduna* has a gregarious pre-hibernation development.

#### 4.5 *Melitaea diamina* (LANG, 1789)

##### 4.5.1 Distribution

The species has a patchy distribution in the temperate climate zone from the mountains of north Spain and Italy to Japan, but only rarely exceeding 60° latitude in Siberia. It is mainly a lowland species but reaches 2000 m above sea level in the Alps (DOUWES 1971, GEIGER 1987, BINK 1992, EBERT 1993, LUKHTANOV & LUKHTANOV 1994).

The former distribution in Sweden ranges from the southernmost provinces to 63° latitude, including almost all mainland provinces with a few exceptions (NORDSTRÖM 1955). Since 1980 it is only found in eight provinces, with no preference for provinces to the east in contrast with most of the Melitaeini species. It is, besides *Melitaea athalia*, the only lowland species distributed in the Norwegian fjords (NORDSTRÖM 1955, ELIASSON 1995d, 1998b, 2002c, RYRHOLM 1995). The species has been classified as Near Threatened according to the new IUCN definitions (GÄRDENFORS 2000). The current threats are habitat fragmentation and changes in land use (tree plantation of small pastures in forests). Losses of habitats and habitat quality have occurred in the past due to drainage and re-forestation. It usually occurs in small numbers in its restricted distribution-patches.

##### 4.5.2 Oviposition and foodplants

In this study oviposition in nature was recorded only on sterile plants of *Valeriana sambucifolia* in Västmanland in the period 1992-1997 (n = 16) (ELIASSON 1995d, 1998b, 2002c). The post-hibernation larva (n = 1) was only found once in nature, and was then feeding on this plant. The same plant was exclusively chosen (n = >20) in a semi-natural environment in an outdoor cage (bath tub c. 0.8 m<sup>2</sup>). In captivity caterpillars refused to accept other plants such as *Melampyrum* spp., *Veronica* spp. or *Plantago* spp., which are mentioned in the older literature. *Valeriana* spp. seem also to be the only important foodplants in populations of *Melitaea diamina* in Germany, Switzerland and Finland (GEIGER 1987, EBERT 1993, WAHLBERG 1997).

##### 4.5.3 Interactions with *Cotesia* parasitoids

The oligophagous gregarious parasitoid *Cotesia melitaeorum*, which attacks a relatively wide range of Melitaeini, is the only larval parasitoid of *Melitaea diamina* we recorded (Table 8) (ELIASSON 1995d, 1998b). This parasitoid has two (to three) generations per year, ovipositing in the first three instars of pre-hibernation larvae and the fifth to sixth instars of post-hibernation larvae. The adult parasitoid can emerge in autumn from cocoons resulting from third instar hosts before hibernation, but more often the parasitoids remain within the host through its hibernation to erupt after host hibernation. This partial autumnal generation of *C. melitaeorum* has also been found to occur in Finland (LEI & HANSKI 1997) and Gotland when the host is *M. cinxia*, but we have not found it to occur when the host is *Euphydryas aurinia* in Sweden despite very extensive rearings. The average number of cocoons in the first generation from fourth instar caterpillars (n = 20) was 3.7 with brood size variation 1-8. The *M. diamina* host of the second generation of *C. melitaeorum* was only found once in nature, a fifth instar larva on 23 June from which 19 parasitoid larvae erupted to form cocoons on 7 July. Populations of *M. diamina* typically co-occur with other Melitaeini species, consequently sharing the parasitoid *C. melitaeorum* and no doubt resulting in greatly complicated population dynamics.

In captivity the individual post-hibernation larvae destined to pupate in a brood of *Melitaea diamina* tend to grow with a less even pace than the individual larvae in broods of *E. aurinia* and *Euphydryas maturna*. A few caterpillars have pupated as late as 1 July, while the majority of the same brood pupated 4-5 weeks earlier, or initiated diapause seven weeks earlier. It seems possible that these late caterpillars might be susceptible to attack by second generation *C. melitaeorum*, resulting from *E. aurinia* hosts, which may emerge as adults in mid June.

The young pre-hibernation caterpillars respond to disturbance by *Cotesia* parasitoids in a similar way to caterpillars of *Euphydryas maturna* and *E. aurinia* (described in section 4.2.3 for *E. maturna*). From the late second instar, caterpillars drop to the ground, rather than trying to defend themselves. Later instars of

*Melitaea diamina* are sluggish in comparison with *E. aurinia* caterpillars, and seem to have little means of self-defence. In the majority of habitat patches with both *E. aurinia* and *M. diamina* the latter occurs at a much lower population density than in habitat patches where only *M. diamina* can be found. It seems possible that the presence of *C. melitaeorum* in these shared patches is tending to distort the combined population of Melitaeini species towards *E. aurinia*, both because on average it reaches its pre-pupal stage first and because the late instar larvae of *M. diamina* are easier to attack.

Two sixth instar caterpillars exposed to *Cotesia acuminata* and with observations made of apparent oviposition pupated normally, which indicates that *Melitaea diamina* is not a suitable host for this parasitoid species (Table 8). Parasitoids and caterpillars used in this experiment originated from the same locality. An investigated population of *M. diamina* in Finland appeared to have no parasitoids (WAHLBERG 1997).

#### 4.5.4 Breeding results (Table 5)

The partially biennial life cycle of *Melitaea diamina* has previously been recorded only by BINK (1992), from an unknown area of north-west Europe (possibly south Sweden). A population recently investigated in Finland seems to have only a one-year life cycle (WAHLBERG 1997). The proportion of caterpillars from Västmanland attempting a second diapause and hibernation period is close to 50% of the caterpillars surviving the first hibernation and feeding period. This indicates that a partly biennial life cycle is important to the long-term survival of the species in Västmanland. Under captive conditions the survival rate during the second diapause and hibernation period was rather low (similar to the results with *Euphydryas aurinia*). The percentage of caterpillars attempting to reach the adult stage after their second hibernation was high compared with the number of caterpillars attempting to reach the adult stage after the first hibernation in batch 1 (the only batch with caterpillars surviving the second hibernation). The ratio of caterpillars surviving the first diapause and feeding period to those attempting to reach the adult stage is quite similar in batches 1-3. Batch 4, in which the proportion having an annual life cycle was much higher, came from a recently colonised habitat patch 3 km north of previously known populations. All parasitoids (*Cotesia melitaeorum*) emerging from this single brood of caterpillars were males, presumably progeny of one or more unmated females. Broods from unmated females are rarely found in nature, and in fact this brood is the only example (of either *Cotesia* species) from all breedings of Melitaeini species in the present work (excluding very small broods resulting from early instar hosts). This may suggest very recent colonisation by *C. melitaeorum*, such that the newly established *M. diamina* population was previously unaffected by parasitism and that caterpillars with a one-year life cycle, in need of a longer feeding period, would have had a higher chance of survival. The impact of drought during the summers of 1994-1996 on mortality rates of caterpillars

in diapause of the preceding generations of this *M. diamina* brood could also have selected for an increase of the proportion with a one-year life cycle. As in *E. maturna*, this type of change in the proportions of the population having different lengths of the life cycle thus suggests a degree of genetic control, though in the case of *M. diamina* the evidence is admittedly less clear.

Breedings in an outdoor cage (bath tub c. 0.8 m<sup>2</sup>) of larvae from two egg batches from the south of the province Dalarna proved that the partly biennial life cycle also exists in this population although, because of a high escape rate of caterpillars, quantitative data could not be collected. However, several were found during their second diapause period and one caterpillar was seen after a second hibernation.

### 4.6 *Melitaea athalia* (ROTTEMBERG, 1775)

#### 4.6.1 Distribution

The species is widespread in the temperate climate zone from Spain and England to Yakutien and China, but only rarely exceeding 60° latitude in Siberia. It is mainly a lowland species but reaches 2000 m above sea level in the Alps (DOUWES 1971, GEIGER 1987, BINK 1992, EBERT 1993, LUKHTANOV & LUKHTANOV 1994).

The species is found in all provinces of Sweden and it is in recent times the only Melitaeini species which is still widespread. North of 61° latitude, predominantly as *Melitaea athalia lachares* FRUHSTORFER, 1919, it becomes local. Further north, including the mountains from 61° latitude, it is very local, here as the distinctively smaller *M. athalia norvegica* AURIVILLIUS, 1888. In some places it can be found at subalpine levels (NORDSTRÖM 1955, DOUWES 1971). In several provinces it is one of the commonest butterfly species. It is rarely seen in great abundance in the same distribution-patches for more than one year at a time.

#### 4.6.2 Oviposition, foodplants and larval development

Oviposition has been recorded by us only once in nature in Västmanland. The plant selected was *Melampyrum nemorosum* and eggs were deposited under leaves near the flowers. Females in cages will also accept *Melampyrum sylvaticum*, *M. pratense*, *Veronica chamaedryas* and *Plantago lanceolata*. The latter is an unusual plant in most habitats in Västmanland, but more common by the coast in Uppland and Södermanland. The most used plants for oviposition in Sweden are probably *Melampyrum* species. The small webs made by pre-hibernation larvae are very hard to locate and the broods split in their late second or early third instars. The post-hibernation larvae have been found by us remarkably few times in nature: once feeding on *Plantago media*, twice at the initiation of the pre-pupal stage and once fully in the pre-pupal stage. The post-hibernation larvae will also accept *Digitalis purpurea*. In captivity at both pre-



and post-hibernation stages the individual larvae in a brood of *Melitaea athalia* tend to grow at very different rates. This is probably the main reason why adults can be observed from June until late August in rainy seasons.

#### 4.6.3 Interactions with *Cotesia* parasitoids

The gregarious parasitoid *Cotesia melitaeorum* has been obtained from *Melitaea athalia* exposed to parasitoids in nature during the first to second larval instars (Table 6, batch 2). We have no data on parasitism in post-hibernation larvae in nature, but post-hibernation caterpillars have been exposed to oviposition by *C. melitaeorum* and *C. acuminata* in small experimental boxes of clear transparent plastic (10 × 10 × 5 cm) (Table 8). Despite numerous observations, made in two separate years, of apparent oviposition by *C. melitaeorum* in fourth to sixth instar caterpillars (n = 16), these continued to grow without a higher rate of mortality or parasitoids developing. Thirteen caterpillars pupated during the same year and two caterpillars that survived an artificial hibernation also proved not to be parasitised. On one of those occasions caterpillars of *Euphydryas maturna* (n = 10) were exposed to the same parasitoid females resulting in five cases of successful parasitism. Caterpillars of *M. athalia* in third to sixth instars (n = 40) were exposed to *C. acuminata* in two separate years. Only three ovipositions were observed. Two of the presumed hosts gradually ceased feeding and died in their sixth instars. No evidence of parasitoid progeny was found on dissection of these caterpillars. The remaining caterpillars all successfully reached the pupal stage. The negative results of parasitism by *C. melitaeorum* of post-hibernation caterpillars is at first sight surprising, and it appears that the older caterpillars of this species are able to prevent the development of the parasitoid. The broods of caterpillars from separate years were reared on different foodplants (*Digitalis purpurea*, *Plantago media*, *Melampyrum nemorosum*) and the parasitoids used came from *E. maturna*, *E. aurinia* and *M. athalia*. Thus *M. athalia* seems to be an insufficient host resource to support populations of *C. melitaeorum*, and this parasitoid probably is not distributed in all patches where the widespread and common *M. athalia* can be found. This is consistent with the apparently slow colonisation by *C. melitaeorum* of the newly established *M. diamina* population (at a site at which *M. athalia* was the only pre-existing potential host) discussed in an earlier section (4.5.4).

#### 4.6.4 Breeding results (Table 6)

The partially biennial life cycle of *Melitaea athalia* has not previously been recorded from north-west Europe. In broods from Västmanland (batches 1-3) the average proportion of caterpillars surviving the first diapause and feeding period that attempted a second diapause is smaller than in *Euphydryas aurinia* and *M. diamina*. The proportion is similar in batch 4 from the coast in north Uppland at 60° latitude. Batch 5 from 59° latitude on the coast of Södermanland

had an entirely one-year life cycle, and the partially biennial life cycle may occur only at more northern latitudes or in areas with a climate less favourable to the development of the early life stages (higher annual precipitation). Although the series of natural hibernations of batch 4 was broken by one artificial hibernation, the results indicate that *M. athalia* probably also has a partially triennial life cycle. In the present work most attention was focused on the rare species, and this explains the rather poor results with *M. athalia*, which in fact is easy to breed.

#### 4.7 *Melitaea britomartis* ASSMANN, 1847

##### 4.7.1 Distribution

The species has a restricted distribution in the temperate climate zone from north Italy and Germany to Japan, not exceeding 59° latitude in Siberia. It is a lowland species (DOUWES 1971, GEIGER 1987, BINK 1992, EBERT 1993, LUKHTANOV & LUKHTANOV 1994).

In Sweden *Melitaea britomartis* was formerly restricted to the east coast and a few inland regions between 57-62° latitude, with low annual precipitation. It was still relatively widespread in five separate regions in the mid 1970s. During this period it had an outbreak and probably colonised some remote inland areas and temporarily established a small population on the island of Öland. A very rapid decline of populations was noted in the 1980s and the bad summer weather of 1987, with its low air temperatures and few hours of sunshine, seems to have eradicated most populations between 59-62° latitude. Investigation of previously colonised areas proved that foodplant density is rapidly decreasing. Lately *M. britomartis* is only found in four very restricted and widely separated areas (RYRHOLM 1994, 1995, ELIASSON 1995b, 1998a, 1999a, 2001b, PALMQVIST 1996, 1997, 1998, 1999, 2000, 2001, FRANZEN *et al.* 2002, LINDBERG & FORSLUND 2002b, RIPLER & ELIASSON 2002, J.-O. BJÖRKLUND, C. KÄLLANDER, I. SVENSSON, S. TORSTENIUS and B. WICKHOLM pers. comm.). The species has been classified as Critically Endangered according to the new IUCN definitions (GÄRDENFORS 2000). The current threats are habitat fragmentation and changes in land use (tree plantation of small pastures in forests). Losses of habitats and habitat quality have occurred in the past due to a rapidly declining need for unfertilised pastures in forests. It was once one of the most common butterfly species in its restricted distribution-patches. An introduction made in 1999 to a previously used distribution-patch (in the 1940s) in Uppland, with butterflies from Småland, was still observed here in 2002 (C. ELIASSON in prep. c, I. FRYCKLUND pers. comm.).

##### 4.7.2 Oviposition and foodplants

Oviposition has previously been observed on *Veronica spicata* in Södermanland and on *Plantago lanceolata* in Småland (NORDSTRÖM 1947, HENRIKSEN &

KREUTZER 1982). In 1996 two egg clusters were found on the island of Utö in Södermanland in late July on small plants of *P. lanceolata* growing in very sun-exposed positions on rocks. The plants used for oviposition in one of the populations in the interior of Småland were investigated in 1998. Two ovipositions were observed on *Veronica chamaedrys* and three more egg clusters were found on this plant. No egg clusters were found on *P. lanceolata*, but several females were observed for long periods on tufts of this plant, apparently investigating the quality of potential foodplants. Females in flight and in search of oviposition plants seemed first to be attracted by small solitary rocks in sun-exposed positions, and then to investigate whether foodplants were available (ELIASSON 1999a). In spring a small number of post-hibernation-caterpillars were swept from *P. lanceolata* in the Småland locality (P. KOCH-SCHMIDT pers. comm.). Former populations in Dalarna and Gästrikland, now extinct, and one remaining population in Västmanland probably only oviposit on *V. chamaedrys*, as *V. spicata* is not found here and *P. lanceolata* is rare (ELIASSON 2001b, RIPLER & ELIASSON 2002, C. KÄLLANDER and B. WICKHOLM pers. comm.). Females from Södermanland accepted *P. lanceolata*, *V. spicata* and *V. chamaedrys* for oviposition in cages. An introduction made in 1997 to a habitat accepted by females, but without the above mentioned foodplants, resulted in oviposition of four egg clusters on *Veronica officinalis*. Those broods died in their first instar, so it appears that this common plant is not a suitable foodplant.

#### 4.7.3 Interactions with *Cotesia* parasitoids

Although collections of larvae from the wild have been very limited, *Melitaea britomartis* appears to be incapable of supporting *Cotesia melitaeorum* (Table 8), at least to the extent that is found for *M. athalia* (see section 4.6.3). Not only has no parasitism been detected in the field, but also experiments involving post-diapause 4-5<sup>th</sup> instar *M. britomartis* larvae (n = 3) and *C. melitaeorum* (from *Euphydryas aurinia*) resulted in apparent oviposition into all three larvae, but no progeny resulted and all larvae went on to pupate successfully. Similar trials with *C. acuminata* resulted only in rejection after brief antennation. In both situations the respective *Euphydryas* hosts were avidly, and successfully, attacked concurrently.

#### 4.7.4 Breeding results (Table 7)

The pre-hibernation caterpillars from Södermanland (batch 1) ceased feeding and entered diapause in their late second or early third instars. So far *Melitaea britomartis* is the only Melitaeini species in Sweden that has been proved to be able to survive hibernation in its second instar. The majority, however, hibernated early in their third instars. With an early development period (May to mid June) of the post-hibernation larvae and pupae in captivity in 1997, the offspring of these adults (batch 2) ceased to feed and entered diapause (which lasted until hibernation) in late third or fourth instars. The pre-hibernation lar-

vae from Småland were in third (n = 236) and fourth (n = 105) instars when they entered diapause. Approximately the same proportions of mixed instars were also recorded in nature on Utö in Södermanland, in late August 2000, near the end of the vegetation period (in September). This butterfly has a long flight period in Sweden, sometimes starting as early as mid June and usually continuing to the end of July (NORDSTRÖM 1947, HENRIKSEN 1982, ELIASSON 1995b, 1998a, 2001b, RIPLER & ELIASSON 2002). No indications of a partially biennial life cycle were evident from the nine broods from separate females (batches 1, 3). In the coastal habitat of Utö, *M. britomartis* lives sympatrically with *M. cinxia* and they oviposit on the same foodplants. Investigations of the population of *M. cinxia* on Åland, which is further to the north in the Baltic sea, have suggested that this species has a strictly one-year life cycle (KUUSSAARI 1998).

## 5 General discussion

### 5.1 The possible influence of day length on the initiation of diapause

In central Europe larvae of the burnet moth *Zygaena trifolii* (ESPER, 1783) (Zygaenidae) respond to variations of temperature and photoperiod during their first feeding period by initiating diapause in different instars (3-6) or by direct development to adults (WIPKING 1988, 1995): in South Europe this species is partially bivoltine, but in Germany the development of caterpillars may span several years. Although the possible influence of variations in photoperiod at key stages on the length of the life cycles of the Melitaeini species was not investigated thoroughly, it seems unlikely to be important, at least for *E. maturna* for which we have the most data, on the following grounds. Breedings were performed over a long sequence of years with various weather conditions, and weather definitely influenced larval growth rate. However, the young pre-hibernation caterpillars always diapause in the fourth instar if they are given sufficient warmth, whether they reach this instar in early August or in September (times when photoperiod variation is large). The feeding period of post-hibernation caterpillars that re-enter diapause is so short, and may fall within such varying periods of the month of May, that the change in photoperiod during the feeding period could not of itself have an important impact on the initiation of subsequent diapause periods. The lengths of the short period between eruption of parasitoid larvae from hosts and the re-entering of diapause by caterpillars have been 10-12 days in all years of breeding. Broods in which the first diapause was artificially broken in January or February and which were then bred indoors (exposed to solar radiation at windows) at the natural photoperiods pertaining behaved in the same way as caterpillars in which the first diapause was broken in April and May: after a short feeding period and a single moult, the caterpillars attempting further diapause periods returned to diapause. Furthermore, if caterpillars that initiate diapause in May are kept dark and at low temperatures (+4-10°C) for the following 90 days, they will resume feeding and

may develop to adults, given summer temperatures and exposure to solar radiation or artificial light, despite a shorter photoperiod (ELIASSON 1991).

## 5.2 The importance of habitat quality

A brief description of the habitats of *Euphydryas maturna*, *E. aurinia* and *Melitaea diamina* in Västmanland is given in section 2.3. Each species has a different tolerance to the habitat's decreasing sun exposure due to the re-growth of natural forest. The first species to disappear from a clearing is *E. aurinia* (2-5 years), whilst *M. diamina* may persist longer (5-10 years). *E. maturna* prefers a later stage of re-forestation, which creates wind-shielded bushes (>0.5 m) for the pre-hibernation caterpillars, and it persists longest (10-25 years) in a clearing where the three species co-occur. Analysis of habitat qualities that improve the survival rates of caterpillars during diapause (particularly *E. maturna*) indicates above all the importance of constant ground humidity. An inclined topography with surfacing ground water and a soil plentiful in stones and rocks pushed from the ground to the surface by winter frost creates many hiding places and prevents flooding. Frequent communities of peat moss (*Sphagnum* spp.) helps to maintain the humidity, especially in a sloping terrain (ELIASSON 1991). It is of utmost importance that the ground lacks the nutrients to support a higher and thicker herb layer (e.g. including *Urtica*, *Sonchus*, *Anthriscus*). In a nutrient-rich environment the assemblage of withering plants creates favourable conditions for a rich fauna of snails (Mollusca) and other invertebrates that cause a faster compostation of dead plant materials, in which diapausing caterpillars may hide. The artificial breeding farm, where many observations have been made, is situated in a clearing in a nutrient-rich and humid forest of ash (*Fraxinus*) and alder (*Alnus*), next to a stream. Released *E. maturna* have persistently refused to oviposit here in the period 1988-1999. The best habitats for the survival of caterpillars in diapause also have a strong attraction for ovipositing butterflies. Sweden was struck by severe drought in three successive summers (1994-1996) and at that time the counts of webs very clearly pointed out failing areas (with respect to populations in the preceding years) without sufficient ground humidity. The butterfly was eradicated in an overwhelming majority of dry places (AHLEN 1999, ELIASSON 1999b, 2001e, 2002e, ELIASSON, AHLEN & KINDVALL 2002).

The following list of plants characteristic of the typical habitat may help to identify viable environments for restoration for any of the three species *Euphydryas maturna*, *E. aurinia* and *Melitaea diamina*. It only includes the plants on the more acid soils where all three species co-occur. None of the plants has colonised the habitat after clear-felling, but rather they constitute the natural under-growth of the mainly mixed spruce and pine forest, with broadleaf trees confined to a patchy distribution along streams or in other wet places. Some areas were pastures two centuries ago. All habitats are covered with moraine or fine sand at the bottom of valleys, but parts of the habitats also have naked

acidic bedrock of three different types. The presence of plants indicating a slightly richer soil in the list below is due either to a wide belt of Carboniferous limestone in the northern part of the study area (where only *E. maturna* occurs) which has turned the moraine (to the south) slightly calcareous, or to smaller pockets with basic minerals in the acidic bedrock. The influence of these basic minerals is usually not observable outside areas with surfacing ground water and flood areas along the small streams (ELIASSON 1991, 1999b). Asterisk (\*) indicates the most frequently visited flowers or buds by adults of *Euphydryas maturna*, *E. aurinia* and *Melitaea diamina* in the study site in Västmanland.

*Sphagnum* spp., *Pteridium aquilinum*, \**Picea abies*, *Pinus sylvestris*, *Juniperus communis*, *Salix caprea*, *Salix myrsinifolia*, *Myrica gale*, *Betula pubescens*, *Betula pendula*, *Alnus glutinosa*, *Alnus incana*, *Anemone nemorosa*, *Trollius europaeus*, \**Ranunculus acris*, *Filipendula ulmaria*, *Rubus saxatilis*, \**Rubus idaeas*, \**Rubus nessensis*, *Rosa majalis*, *Rosa dumalis*, \**Potentilla erecta*, \**Fragaria vesca*, \**Sorbus aucuparia*, *Prunus padus*, \**Polygala vulgaris*, *Geranium sylvaticum*, \**Frangula alnus*, *Daphne mezereum*, *Hypericum maculatum*, *Viola palustris*, *Angelica sylvestris*, *Calluna vulgaris*, \**Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Trientalis europaea*, *Fraxinus excelsior*, *Galium uliginosum*, *Prunella vulgaris*, *Mentha arvensis*, \**Veronica officinalis*, *Melampyrum pratense*, *Melampyrum sylvaticum*, *Euphrasia stricta*, *Rhinanthus serotinus vernalis*, \**Viburnum opulus*, \**Valeriana sambucifolia*, *Succisa pratensis*, *Campanula rotundifolia*, *Solidago virgaurea*, \**Cirsium palustre*, *Cirsium helenioides*, *Leontodon autumnalis*, \**Scorzonera humilis*, *Deschampsia cespitosa*, *Agrostis capillaris*, *Calamagrostis epigejos*, *Molinia caerulea*, *Dactylorhiza maculata*,

## 5.3 Advantages and disadvantages of prolonged life cycles.

The rearings from Västmanland, Uppland and Gästrikland proved that all four lowland Melitaeini species with a geographical distribution in the interior of Sweden, north of 59-60° latitude, have a significant portion of caterpillars undertaking a second (or more) hibernation (Tables 1-3, 5-6). Two lowland Melitaeini species in Sweden, of which one was investigated by us (Table 7), are confined to coastal areas or areas with a low precipitation. Both have strictly one-year life cycles and probably this is also the case for at least two of the four species in the first group (Tables 3, 6) in more southern and coastal areas. The causal connection of natural selection and the genetically influenced division between smaller and larger proportions of prolonged life cycles is possibly covered by the suggestions below.

Advantages, consequent on partially biennial or multiennial life cycles, which we suggest may be of importance to the long-term survival of the Melitaeini species, are:

1. Caterpillars diapausing in the fifth instar (after the second hibernation) will produce adults faster than caterpillars diapausing in 3-4<sup>th</sup> instars (after the first hibernation). The offspring of the earliest emerging butterflies will have a better chance to complete their development to an instar capable of surviving the first hibernation.
2. Cold and rainy seasons may lead to local extinctions (to various extents) or even population extinction of one-year individuals when the early instar pre-hibernation caterpillars fail to reach the instar in which they are able to withstand hibernation. Caterpillars from previous years, able to diapause following a shorter feeding period, may counteract extinctions and prevent genetic drift.
3. The year after an extremely cold and rainy season, with general population crashes in insects that depend on insolation, offers caterpillars coming out of their second (or subsequent) diapause period a relatively enemy-free environment (to various extents). This situation may promote a population outbreak for the Melitaeini species, leading to more long-distance colonisations of suitable environments.
4. Our observations on *Euphydryas maturna* and *Cotesia acuminata* suggest that the lifetime exposure to parasitism may be reduced. This is because, after the first diapause, the feeding period of caterpillars that will diapause again is shorter, and takes place largely at a time when the parasitoid adults are not active, than that of caterpillars attempting to become adults after a single diapause, whose feeding necessarily extends through a period of adult parasitoid activity. In the subsequent year, the caterpillar that have already diapaused twice start larger and require a shorter feeding time (again, while parasitoid adults are scarce) to become immune to parasitism by *Cotesia* as they approach pupation than those which have attempted to complete their growth after a single diapause. The caterpillars that enter second (and subsequent) diapauses relatively early in summer are possibly found by *Cotesia* but appear to be protected from parasitism to a large extent by virtue of their dehydration, and possibly also aggregation, both of which result in their spines surrounding them with impenetrable density.

Likewise the disadvantages of a partially biennial or multiennial life cycle are:

5. Some potential mortality factors are likely to pose undiminished (if stochastic) threats, such that a longer pre-adult existence results in a greater risk.
6. Each additional diapause period (of 10-11 months) may cause high losses in less suitable (dry) habitats. Similarly during the non-frozen time of the year diapausing caterpillars must be able to find spots where they are less disturbed by intruders (e.g. Mollusca) or threatened by (unknown) predators. These demands on habitat quality may exclude some environments that would be suitable for populations with a one-year life cycle.
7. Limitations in the spatial distribution of populations highly dependent on repeated diapause periods (as described in 6) may render migration less successful.

8. Populations with one-year life cycles and less exacting demands on habitat quality may be more successful in colonising areas free from the specialised parasitoids than populations with prolonged life cycles. This may promote more frequent (local population) outbreaks, generating a higher rate of migration from populations with one-year life cycles.

The suggestions above may be applicable to each regional metapopulation with a network of distribution areas with different types of habitats and during a long time sequence with climatic variation. If the risk of weather-based reproduction failure diminishes, the proportion of one-year life cycles should increase. This is probably the case in populations of *Euphydryas aurinia*, *Melitaea diamina* and *M. athalia* below 59-60° latitude, and may account for the restricted distribution of *M. britomartis* if, as our data suggest, it invariably has a one-year life cycle. The extremely low proportion of *E. maturna* with a one-year life cycle in Västmanland (Tables 1 and 2), and the fact that this species does not share the threat of parasitism from *Cotesia melitaeorum* with the other three species, have made us suspect that *Cotesia acuminata* may have a selective influence on the prolonged life cycle. Extensive data (C.U. ELIASSON unpublished) on the relationship between *Cotesia acuminata* and *E. maturna* will hopefully shed light on this question. It is remarkable that one of the two remaining populations of *E. maturna* in Sweden today mainly thrives in a climate where a reproduction failure on average happens as often as every fourth year.

#### 5.4 Conclusions

In north-west Europe *Euphydryas maturna* is today one of the most endangered butterfly species and included in the EU Habitat Directive (annexes 2 and 4) (European Economic Community 1991, 1992, GÄRDENFORS 2000). It was not considered to be threatened in Finland and Estonia according to the former red list status and IUCN definitions (SWAAY, WARREN & GRILL 1997). The ecology of the *E. maturna* populations in north-west Europe compared with east Europe (east of the Baltic sea) seems to be so different that the results of ecological studies of the two (or more) subspecies should not be mixed. The difference is between a stenotopic taxon and a taxon that rarely occurs in the same distribution-patch for more than two years in a row. *Euphydryas aurinia* is less threatened than *E. maturna* in north-west Europe, but has very high demands on habitat quality, and is therefore also included in the EU Habitat Directive (Annex 2). It may disappear very abruptly from a region (from a large population size) as a result of a few years of interruptions in the land management or to natural or man-made forestation. This is what is happening to *Melitaea britomartis* in Sweden today and the species is now on the brink of extinction. In Västmanland, *E. maturna*, *E. aurinia* and *M. diamina* live sympatrically – a fact that definitely indicates that these species' demands on habitat quality are very similar. The colder and more wet climate of northern to central Scandinavia is not only a threat to the annual success of reproduction of Melitaeini species, it also

helps to create the necessary humidity of the environment in which repeated diapause periods can be successful. *Cotesia acuminata*, being entirely dependent on *E. maturna* in Sweden, should be recognised as equally endangered and fully encompassed in nature conservation initiatives for the butterfly, not least because of its undoubted roles in the evolutionary and population ecology of its host.

## 6 Acknowledgements

We thank JAN-OLOF BJÖRKLUND, Rainer BLOMQVIST, Ingemar FRYCKLUND, Jan GUSTAFSSON, Kenth MARTINSON, Peter KOCH-SCHMIDT, Jaakko KULLBERG, Clas KÄLLANDER, Mats LINDEBERG, Hans LINDEMARK, Göran RIPLER, Ingvar SVENSSON, Peter STREITH, Stig TORSTENIUS, Bengt WICKHOLM and Christer WIKLUND for additional information concerning foodplants and modern distributions, Johan AHLÉN and Oskar KINDVALL for participation in the monitoring survey of larval webs from 1998, Finn IVERSEN and Per STADEL-NIELSEN for their confirmation of strictly one year life cycles in *Euphydryas aurinia*, Ilkka HANSKI for information concerning *E. maturna* as a study-object, Emese MEGLÉCZ for a brood of caterpillars of *E. maturna* from Hungary, and Maaria KANKARE for sharing the results of DNA investigations of the relevant *Cotesia* species on a wider scale. Björn CEDERBERG, Clas KÄLLANDER, Oskar KINDVALL and Christer WIKLUND all made valuable comments on the manuscript at various stages in its preparation, Rainer MATHES and Peter STREITH translated the summary into German, and Otakar KUDRNA has been most helpful towards configuring the manuscript for publication in *Oedippus*. We are most grateful to Lindesbergs community and Lindesbergs Bostäder AB for the donation of land for preserving *E. maturna* and *E. aurinia*. The research on *E. maturna* and *E. aurinia* was funded by grants from the World Wide Fund for Nature in the period 1992-1995. Publication of this paper was made possible by a grant from the Swedish Environmental Protection Agency (Naturvårdsverket).

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## 8 Zusammenfassung

Das Ziel der vorgestellten Untersuchung ist es, Erkenntnisse für eine erfolgreiche Naturschutzarbeit zu gewinnen und vor allem die Eiablageplätze und Raupenfutterpflanzen von sechs Melitaeini-Arten – namentlich *Euphydryas aurinia*, *E. iduna*, *E. maturna*, *Melitaea athalia*, *M. britomartis* und *M. diamina* – in Schweden zu erkunden. Einige dieser Arten sind dort sehr gefährdet. Fünf von ihnen – alle außer *M. britomartis* – haben partielle zwei-, drei- oder vierjährige Entwicklungszyklen; ihre Überwinterungsökologie und Raupenentwicklung werden im Detail untersucht (mit unterschiedlicher Gründlichkeit, aber mit besonderen Hinweisen zu *E. maturna*). Klimatologische Faktoren, die offensichtlich einen Schmetterlingslebenszyklus beeinflussen, werden diskutiert; für *E. maturna* werden Beweise präsentiert, dass dieses Phänomen teilweise genetisch gesteuert ist. Eine hohe Habitatqualität ist eine wichtige Voraussetzung für das Überleben der Melitaeini-Arten.

Zwei Microgasterinae-Arten (Hymenoptera: Braconidae), *Cotesia acuminata* und *C. melitaeorum*, beide spezialisierte Parasitoiden auf Melitaeini-Arten, treten in den untersuchten Gebieten auf; sie zeigen eine marginale Überschneidung ihrer Wirte. Eine besondere Eigenschaft dieser Parasitoiden ist es, dass mehrere aufeinander folgende Generationen auf einer einzigen Generation des Wirts leben, ihre Eier aber auf unterschiedlich alte Raupenstadien ablegen. Infolgedessen sind sie wichtig für die Populationsdynamik der befallenen Falterarten. Wir geben eine kurze Zusammenfassung vom Auftreten und dem Lebenszyklus der Parasitoiden, außerdem berichten wir von einigen experimentellen Manipulationen.

In Schweden legt *E. maturna* Eier nur an *Fraxinus excelsior* und *Viburnum opulus* ab. Die Raupe frisst nach ihrer Überwinterung auch an Kräutern wie *Valeriana sambucifolia* und *Melampyrum* spp., bevorzugt aber, an Sprösslingen von *Fraxinus excelsior* zu fressen, soweit diese zugänglich sind. Das ist ein großer Unterschied zu *E. maturna* (ssp. *tenureticulosa*) in Finnland, wo die Eiablage an *Melampyrum pratense*, *Viburnum opulus* und *Veronica longifolia* erfolgt. Die beiden oben genannten Parasitoiden können sich in Raupenstadien von *E. maturna* vor und nach der Überwinterung entwickeln; in einer großen Anzahl von vor und nach der Überwinterung gesammelten Raupen entwickelten sich sehr wenige *Cotesia melitaeorum* Individuen gegenüber Hunderten Generationen von *C. acuminata*. In einer Brut Raupen jedoch, die bewusst im ersten Raupenstadium auf *Valeriana* platziert wurde, entwickelte sich nur *C. melitaeorum*. Dies deutet an, dass in diesem Fall der Futterplatz eine wichtige Determinante der Parasitierung ist. *E. aurinia* und *M. diamina* – mit der gesamten Raupenentwicklung an *Succisa pratensis* bzw. *Valeriana sambucifolia* – sind in derselben Gegend regelmäßige Wirte von *C. melitaeorum*. Experimentell durchgeführte Eiablagen von *C. acuminata* an Raupen von *E. aurinia*, *M. athalia* und *M. diamina* ergaben nicht größere Nachkommen an Parasitoiden. Die häufigere und weiter verbreitete Art *M. athalia* legt in Schweden Eier meistens an *Melampyrum* spp. ab; sie scheint als Wirt für *C. melitaeorum* ungeeignet zu sein. Die Parasitoiden können sich erfolgreich in Raupenstadien vor der Überwinterung entwickeln, nicht jedoch in Raupenstadien nach der Überwinterung.

Sehr wenige zuverlässige Aufzeichnungen der präimaginalen Entwicklungsstadien von *E. iduna* sind publiziert worden. Wir meinen, dass die am häufigsten gewählte Pflanze *Bartsia alpina* ist, da wir dreizehnmal Raupen nach der Überwinterung auf dieser Pflanze und nur einmal auf *Pedicularis hirsuta* fanden. Wahrscheinlich hat *E. iduna* einen zweijährigen oder dreijährigen Entwicklungszyklus; die Zucht zum Imaginalstadium ist uns aber leider nicht ganz gelungen.

In Schweden legt *M. britomartis* Eier auf *Veronica spicata*, *V. chamaedrys* und *Plantago lanceolata* ab. *M. britomartis* scheint einen strikten einjährigen Entwicklungszyklus zu haben. Im Gegensatz zu allen anderen von uns studierten Melitaeini-Arten kann die Raupe im zweiten Stadium überwintern; meistens überwintert sie jedoch im dritten oder vierten Stadium, so wie

es auch bei den anderen Arten der Fall ist. Sie scheint nicht regelmäßig von *Cotesia* spp. parasitiert zu werden. Wir fanden weder Parasitismus in der Natur, noch brachten wir experimentell durchgeführte Eiablagen von *C. melitaeorum* und *C. acuminata* positive Ergebnisse.

Das Raupenzuchtergebnis von Populationen mit teilweise mehrjähriger Entwicklungszyklus stammt in der Hauptsache aus Västmanland nördlich der großen Seen. Im Gegensatz zu *E. aurinia*, *M. athalia* und *M. diamina*, Arten die einen Hohen Anteil Raupen mit einjährigem Lebenszyklus haben, hat *E. matura* einen sehr niedrigen Anteil mit einjährigem Lebenszyklus. In den Jahren 1994 bis 1996 wurde die ganze Population im Västmanland durch Trockenheit negativ beeinflusst. Bis dahin war ein dreijähriger Entwicklungszyklus dominierend und auch ein vierjähriger Zyklus war möglich. Zuchtexperimente in der Gefangenschaft haben das bestätigt. Nach der Trockenperiode dominierte ein zweijähriger Lebenszyklus, aber der kleine Anteil der Population mit einjährigem Entwicklungszyklus blieb konstant.

Bei *E. aurinia*, *M. athalia* und *M. diamina* wird der Anteil mit zweijährigem Entwicklungszyklus von den Raupen bestimmt, die eine Diapause nach einem Jahr einleiten. Bei *E. aurinia* und auch bei *M. athalia* ist nur ein kleinerer Anteil bereit, eine dritte oder vierte Diapause einzuleiten. *E. iduna* hat wahrscheinlich einen zweijährigen oder dreijährigen Entwicklungszyklus, wie es die Diapausen der Raupen anzeigen.

Alle Melitaeini-Arten sind für die Entwicklung der Eier und Raupen von Sonnenschein stark abhängig. Das ist besonders gut manifestiert durch die längeren Zeitabschnitte zwischen den Fressperioden, in denen die Raupen sich sonnen. Es ist gefunden worden, dass die optimale Temperatur für den Metabolismus in einer britischen Population von *E. aurinia* beträgt 35° C. Unsere Messungen in 50 Nestern von *E. matura* und in 28 Nestern von *E. aurinia* brachten dasselbe Ergebnis. Wir stellen daher fest, dass die optimale Temperatur für den Metabolismus von *E. matura* ebenfalls 35° C beträgt.

*E. aurinia*, *E. matura* und *M. diamina* bevorzugen Lebensräume mit hoher Bodenfeuchtigkeit. Ihre Populationen sind meistens individuenreich in sehr nassen Gebieten, oft in der Nähe kleiner Wasserläufe. Eine besonders interessante Anpassung zeigten Raupen von *E. aurinia* und *E. matura*, die während der Diapause sogar längere Zeit unter Wasser überleben konnten.

In Nordwesteuropa ist *E. matura* eine der am stärksten gefährdeten Tagfalterarten. *E. matura* ist u.a. deshalb in die FFH Richtlinie der EU aufgenommen. In Finnland und Estland galt *E. matura* gemäß der alten Roten Liste und der IUCN Gefährdungskategorien als nicht gefährdet. Die Ökologie der nordwesteuropäischen Populationen von *E. matura* ist offensichtlich so unterschiedlich von der Ökologie der osteuropäischen Populationen (d.h. östlich des Ostsee), dass die Resultate ökologischer Studien über diese Populationen nicht miteinander vermengt werden sollten. Hinzu kommt, dass einige Populationen streng bodenständig sind, während die anderen selten mehr als zwei Jahren auf einer Stelle halten. Es handelt sich wohl um zwei (oder mehr) unterschiedliche Unterarten.

*E. aurinia* ist in Nordwesteuropa offensichtlich weniger gefährdet als *E. matura*, stellt aber hohe Ansprüche in die Habitatqualität und ist wohl deshalb auch in die FFH Richtlinie der EU aufgenommen. *E. aurinia* scheint aus einer Region abrupt zu verschwinden, wenn die land- bzw. forstwirtschaftliche Bodennutzung grundlegend geändert wird. Das geschieht gegenwärtig auch *M. britomartis* in Schweden; diese Art im Aussterben begriffen zu sein. In Västmanland leben *E. matura*, *E. aurinia* und *M. diamina* nebeneinander – eine Tatsache, die zeigt, dass die Ansprüche dieser Arten an die Habitatqualität sehr ähnlich sind. Das kältere und feuchtere Klima in Nord- und Zentralskandinavien gefährdet wohl insgesamt den jährlichen Entwicklungszyklus der Melitaeini-Arten, sorgt jedoch andererseits für die notwendige Feuchtigkeit während der Diapausen.

*C. acuminata*, in Schweden völlig von *E. matura* abhängig, sollte ebenfalls als gefährdet anerkannt und voll in den Schutz der Lebensräume dieser Tagfalterart einbezogen werden, vor allem deswegen, weil *C. acuminata* unbestritten an der Evolution und Populationsbiologie seines Wirts teilnimmt.

Die ersten Arbeiten in einem Artenschutzprogramm für *E. aurinia* und *E. matura* in Västmanland, wurden 1998 aufgenommen. Drei größere Lebensraumverbunde mitten der Metapopulationen beider Arten, wurden gemäß der FFH Richtlinie der EU als Schutzflächen vorgeschlagen. Diese sind vom Natur- und Umweltschutzamt der schwedischen Regierung akzeptiert worden. Das erste Naturschutzgebiet (41 ha) wurde offiziell im Jahr 2000 ausgewiesen. Die Wiederherstellung des Habitats wurde in den Jahren 2000-2001 abgeschlossen. Nationale Aktionspläne für *E. aurinia* und *E. matura* sind neuerdings vom schwedischen Natur- und Umweltschutzamt erarbeitet worden. Ein nationaler Aktionsplan für *M. britomartis* ist in Vorbereitung.

## 9 Tables and figures

Tables 1 – 8 are not arranged in ascending order. The reasons are practical: page saving layout; the editor offers his apology to readers. Figures 1 – 4: the author of all photographs is C.U. Eliasson.

**Table 5. Breeding results of complete broods of *Melitaea diamina* from Sweden: Västmanland, Nora and Lindesberg.**

**Year** = the year of collection. **Instar** = instars in which collection made. **B** = number of broods mixed together. **D** = number of larvae attempting diapause (including hibernation). **S** = number surviving diapause. **P** = larvae parasitised by *Cotesia melitaeorum*. **R** = remaining healthy larvae (S minus P and minus mortality during the active feeding period). **1-2** = number of larvae attempting adult stage (reaching pre-pupal, pupal or adult stage); **1** = number of larvae with one year life cycle; **2** = number of larvae with biennial life cycle.

Batch	Year	Instar	B	P	D	S	P	R	1	D	S	R	2	D
1.	1992	1, 3	2	0	50	40	8	32	9	23	8	8	8	0
2.	1994	2	2	0	28	20	0	3	1	2	0			
3.	1995	1, 2	3	0	160	30	10	20	8	12	0			
4.	1997	3	1	4	70	52	11	33	25	8	0			
1-4. Sum			8	4	308	142	29	88	43	45	8	8	8	0
Percentage of healthy larvae attempting diapause (D/R)										51.1		0		
Percentage of larvae surviving diapause and feeding period (R/(D-P))										31.5		17.8		
Percentage of total sum of adults (n = 51)									84.3		15.7			

Collecting and breeding by C.U. Eliasson.





**Table 3. Breeding results of complete broods and collected post-hibernation larvae of *Euphydryas aurinia***

Year = the year of collection. Instar = the mixes of instars involved in batches. B = number of broods mixed together. D = number of larvae attempting diapause (including hibernation). S = number surviving diapause. P = larvae parasitised by *Cotesia melitaeorum*. R = remaining healthy larvae (S minus P and minus mortality during the active feeding period). 1-2 = number of larvae attempting adult stage (reaching pre-pupal, pupal or adult stage); 1 = number of larvae with one year life cycle; 2 = number of larvae with biennial life cycle.

Batch	Year	Instar	B	D	S	P	R	1	D	S	R	2	D	S
1.	1992	4-5	na	na	12	0	12	5	7	1	1	0	1	0
2.	1993	4-5	na	na	32	0	21	9	12	7	7	7	0	
3.	1993	1-2	5	327	150	0	150	35	115	15	1 <sup>na</sup>	7	0	
4.	1994	2-4	5	303	263	14	215	147	68	27	7	7	0	
5.	1996	4	na	na	18	3	11	7	4	0				
6.	1998	4	na	na	80	2	62	58	4	0				
7.	1999	3	2	174	101	0	81	68	13	9	7	7	0	
8.	1999	4	1	79	61	0	46	42	4	1	0			

Batches 3, 4, 7, 8. Percentage of larvae surviving diapause (S/(D-P))

66.2

26.0

1. Series before 1995

1, 2, 4. Percentage of healthy larvae attempting diapause (D/R)

35.1

1-4. Percentage of healthy larvae attempting diapause (D/R)

50.8

1, 2, 4. Percentage of total sum of adults (n = 175)

92.0

8.0

6.7

na

2. Series after 1995

5-8. Percentage of healthy larvae attempting diapause (D/R)

12.5

5-8. Percentage of total sum of adults (n = 182)

96.1

3.8

Batches 1, 2, 5, 6 = post-hibernation larvae collected from unknown number of broods (collection in general made from webs in early spring which should not contain caterpillars from previous hibernations); 1-4 = Sweden, Västmanland, Nora and Lindesberg; 5 = Sweden, Uppland, Östfora; 6 = Sweden, Gästrikland, Hade; 7 = Sweden, Västmanland, Vikar; 8 = Sweden, Västmanland, Nora. <sup>1</sup>Larvae used in parasitoid experiment. na = data not available. Collecting and breeding by C. U. Eliasson.

**Table 4. Breeding results of collected post-hibernation larvae of *Euphydryas iduna* from Sweden, Torne lappmark, Abisko.**

Year = the year of collection. Instar = collection made as third to fourth instars. B = number of broods mixed together. D = number of larvae attempting diapause (including hibernation). S = number surviving diapause. P = larvae parasitised by *Cotesia* spp. R = remaining healthy larvae (S minus P and minus mortality during the active feeding period). 1-2 = number of larvae attempting adult stage (reaching pre-pupal, pupal or adult stage); 1 = number of larvae with one year life cycle; 2 = number of larvae with biennial life cycle. na = data not available.

Batch	Year	Instar	B	D	S	P	R	1	D	S	R	2	D	S	R
1.	1995	3-4	na	na	14	0	13	0	13	11	7	0	7	1	0
Percentage of healthy larvae attempting diapause (D/R)									100			100			
Percentage of larvae surviving diapause and feeding period (R/(D-P))									53.8						

Collecting and breeding by C.U. Eliasson.

**Table 6. Breeding results of complete broods of *Melitaea athalia***

Year = the year of collection. Instar = collection made as either ova or first to second instars. B = number of broods mixed together. D = number of larvae attempting diapause (including hibernation). S = number surviving diapause. P = larvae parasitised by *Cotesia melitaeorum*. R = remaining healthy larvae (S minus P and minus mortality during the active feeding period). 1-3 = number of larvae attempting adult stage (reaching pre-pupal, pupal or adult stage); 1 = number of larvae with one year life cycle; 2 = number of larvae with biennial life cycle; 3 = number of larvae with triennial life cycle.

Batch	Year	Instar	B	D	S	P	R	1	D	S	R	2	D	S	R	3	D	S	
1.	1994	ova	1	24	24	0	24	18	6	0									
2.	1995	1-2	1	22	22	14	8	3	5	0									
3.	1996	ova	2	76	57	0	35	33	2	0									
1-4.	1994	ova	2	102	102	0	43	28	15	14	13	1	12	6	5	3	2	0	
5.	1996	ova	3	156	156	0	89	89	0										
1-4.	Sum		6	224	205	14	110	82	28	14	13	1	12	6	5	3	2	0	
1-4. Percentage of healthy larvae attempting diapause (D/R)													25.5		92.3		40.0		
1-4. Percentage of larvae surviving diapause and feeding period (R/(D-P))													52.4		46.4		41.7		
1-4. Percentage of total sum of adults (n = 86)													95.3		1.2		3.5		

Batch 1-3 = Sweden, Västmanland, Lindesberg; 4 = Sweden, Uppland, Gräsö; 5 = Sweden, Södermanland, Utö. <sup>1</sup>In batch 4 the second hibernation was artificial (three months at a temperature just above freezing). Collecting and breeding by C. U. Eliasson.

**Table 7. Breeding results of complete broods of *Melitaea britomartis***

**Year** = the year of collection. **Instar** = collection made as ova. **B** = number of broods mixed together. **D** = number of larvae attempting diapause (including hibernation). **S** = number surviving diapause. **P** = larvae parasitised by *Cotesia* spp. **R** = remaining healthy larvae (S minus P and minus mortality during the active feeding period). **I** = number of larvae attempting adult stage (reaching pre-pupal, pupal or adult stage); **1** = number of larvae with one year life cycle.

Batch	Year	Instar	B	D	S	P	R	1	D
1.	1996	ova	4	198	111	0	90	90	0
2.	1997	ova	2	40	22	0	22	22	0
3.	1998	ova	5	341	273	0	271	271	0

Percentage of larvae surviving

diapause and feeding period (R/(D-P)) 66.1

Percentage of total sum of adults (n = 383)

100

Batch 1-2 = Sweden, Södermanland, Utö; 3 = Sweden, Småland, Nybro, Millemåla. Collecting and breeding by C.U. Eliasson.

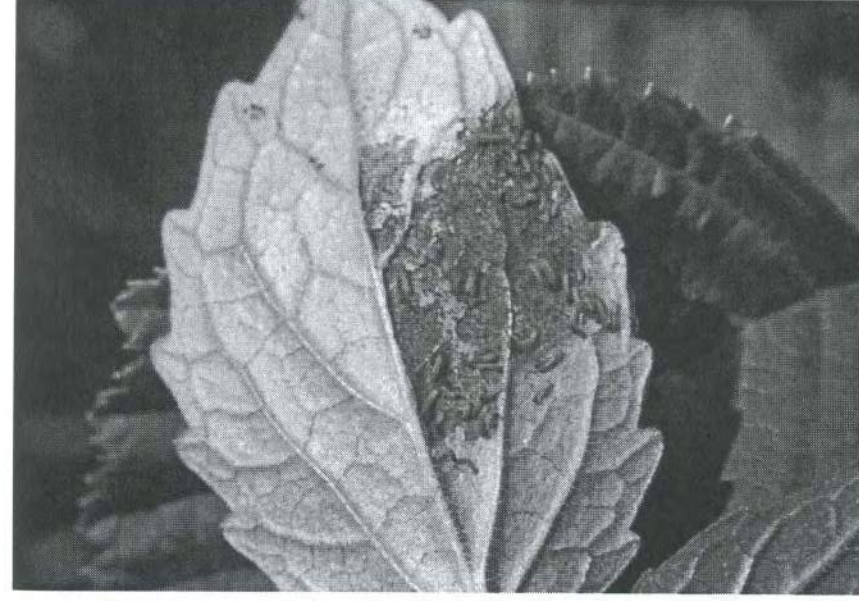


Fig. 2. *Melitaea diamina*: 1<sup>st</sup> instar larva on *Valeriana sambucifolia*.

**Table 8. Host relations of the three *Cotesia* species in Fennoscandia specialised as parasitoids of *Melitaeini* species.**

Only the hosts occurring in Fennoscandia are included: a = natural rearings in Sweden, b = natural rearings elsewhere in Fennoscandia, c = experimental rearing successful (done in Sweden), d = experimental rearing unsuccessful (done in Sweden). Letters in brackets = (rarely). The *C. acuminata* used in experiments originated from *E. maturna*. *Cotesia melitaeorum* were from *E. aurinia* except that additionally individuals from early instar *M. aethalia* were used with later instar *M. aethalia* from the same brood.

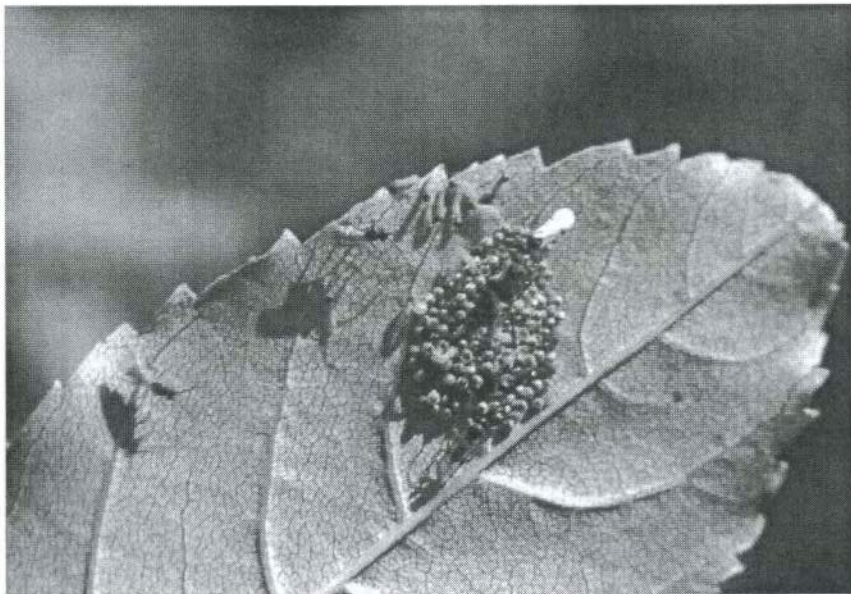
Host species	<i>C. melitaeorum</i>		<i>C. acuminata</i>		<i>C. bignellii</i>
	(a)	(b)	(a)	(b)	(c)
<i>Euphydryas maturna</i>			a	b	c
<i>Euphydryas aurinia</i>	a	b	c		
<i>Euphydryas idana</i>				d	b
<i>Melitaea diamina</i>	a			d	
<i>Melitaea aethalia</i>	(a)	(b)	d	d	d
<i>Melitaea britomartis</i>			d		d
<i>Melitaea cinxia</i>	a	b			



Fig. 1. *Melitaea aethalia*: a web with 1<sup>st</sup> instar larvae on *Melampyrum nemorosum*.



**Fig. 3.** *Cotesia acuminata* attending an egg cluster of *Euphydryas maturna* more than a week before hatching of larvae.



**Fig. 4.** *Cotesia acuminata* attacking larvae of *Euphydryas maturna* breaking through the egg shells.