# Quantifying the impact of insect predators and parasitoids on populations of the apple ermine moth, *Yponomeuta malinellus* (Lepidoptera: Yponomeutidae), in Europe

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## Abstract

Life tables were developed to assess the significance of natural enemies on the dynamics of apple ermine moth, *Yponomeuta malinellus* Zeller, in southwestern Germany and to select parasitoid species for use in the biological control of this pest in Canada. During the study from 1993 to 1995 the abundance of *Y. malinellus* varied from 1.5 to 4.3 tents per 100 leaf clusters indicating that this was a non-outbreak population. From the life tables it was evident that the impact of egg predators accounted for 25–43% of the total generational mortality of *Y. malinellus*, more than any other known mortality factor. Percent parasitism varied from 18 to 30%, but the impact of parasitoids in relation to the total generational mortality of *Y. malinellus* from the life tables was remarkably constant at 11–14%. The loss of potential fecundity had an important influence on the generational mortality of *Y. malinellus*, but declined from 27% to 15% over the course of this study. This decline corresponded with a rise in the net rate of increase $R_0$ from 1.35 in 1993 to 6.8 in 1995, despite the impact of insect predators and parasitoids on the generational mortality. *Yponomeuta malinellus* was attacked by five different obligate primary parasitoids, a single obligate hyperparasitoid, and three facultative hyperparasitoids. Of these, the oligophagous egg–larval parasitoid *Ageniaspis fuscicollis* Dalman (Encyrtidae) and the oligophagous larval–pupal and pupal parasitoid *Herpestomus brunnicornis* Gravenhorst (Ichneumonidae) were selected as potential biological control agents for Canada due to a minimal degree of interspecific competition.

## Introduction

The apple ermine moth, *Yponomeuta malinellus* Zeller, is a member of the small genus *Yponomeuta* Latreille in the family Yponomeutidae (Lepidoptera) and is widely distributed throughout the Palaearctic region. Recently, *Y. malinellus* was accidentally introduced into British Columbia (Parker & Schmidt, 1985) and Washington State, and by 1991, the distribution of *Y. malinellus* had extended into northwestern Oregon (Unruh *et al.*, 1993). In Europe, during the early part of the century, *Y. malinellus* was considered to be among the most destructive defoliators of apple, a pest second in importance to the notorious codling moth (*Cydia pomonella*

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(Linnaeus), Lepidoptera: Tortricidae) (Faes, 1928; Janecke, 1933). More recently, it has come to be regarded as a minor pest of apples under current management practices in Europe (Galli & Höhn, 1992). *Yponomeuta malinellus* does not pose a serious threat to conventional apple production in North America if an early cover spray is used for codling moth control. However, the replacement of insecticide treatment of this latter pest with alternative control measures, such as mating disruption, is already being implemented in large demonstration plots in western North America (Unruh *et al.*, 1993). In this case, *Y. malinellus* represents a significant threat to apple production in the absence of its coevolved natural enemies (Unruh *et al.*, 1993).

*Yponomeuta malinellus* is univoltine, and lays batches of 30–50 eggs on apple trees from July to September (Parott & Schoene, 1912; Thorpe, 1929; Minkiewicz, 1943; Pag, 1959). Hatching takes place in early autumn and the first-instar larvae enter diapause and overwinter in a communal hibernaculum beneath the covering of the egg batch (Ruzaev, 1929; Pag, 1959). In early April, first instar larvae emerge from the hibernacula to mine the adjacent developing leaves (Pag, 1959; Junnikkala, 1960). From the second to the fifth instar, the larvae feed externally of the foliage from within a characteristic communal tent (Pag, 1959; Junnikkala, 1960). During heavy infestations, the tents may envelop the entire tree, resulting in total defoliation and affecting fruit production for several years following an outbreak (Parker & Schmidt, 1985). The mature larvae spin cocoons that are suspended in rows or clusters within, or adjacent to, the larval tents. Pupal development lasts 10–14 days and adult emergence occurs from July to early September (Minkiewicz, 1943; Pag, 1959).

Although natural enemies have not always been implicated in the natural control of small ermine moth populations in Europe (e.g. Junnikkala, 1960; Mowat & Clawson, 1995), there is evidence that parasitoids have played a major role in the dynamics of populations in at least some regions (Eremenko, 1974; Pyörnilä & Pyörnilä, 1979). Thus, at the request of Agriculture and Agri-Food Canada, *Y. malinellus* populations were intensively sampled in southwestern Germany to determine the impact of natural enemies on the generational mortality of this potential pest in its region of origin and to select potential parasitoids for use in a classical biological control programme in Canada.

## Material and methods

### *Field sites*

Samples of *Y. malinellus* were collected from two sites in southwestern Germany, where populations had been consistently observed in previous years (Burghause, 1993, personal communication). The first collection site, located at Biebesheim, was a 1.5 km$^2$ grass covered apple orchard situated 100–200 m from the Rhine River. It contained unpruned, unevenly spaced (10–20 m), 8 m high trees, ranging from 50 to 60 years old, and was used for a life table study. The second collection site was located near Giessen-Wettenberg. This orchard contained unpruned, evenly spaced (10 m) in a row, 3–4 m high trees, in a grass–annual weed ground cover and was used for additional assessments of parasitism.

### *Estimates of* Y. malinellus *fecundity*

Pupae of *Y. malinellus* were collected from both Biebesheim and Giessen-Wettenberg, each year from 1993 to 1995, and kept in rearing cages (30×30×57 cm) under laboratory conditions at 20°C, 16:8 L:D, 70–80% rh to await emergence. Newly emerged moths were collected randomly from the rearing cages and deep-frozen at –22°C for 24 h to determine the sex ratio and potential fecundity. Potential fecundity was determined by dissection of female abdomens in 70% alcohol to count the total number of mature, pigmented and unpigmented eggs. A second set of mated females was collected randomly from the rearing cages and kept singly in sleeve cages (20×30 cm) on several apple trees in Delémont, Switzerland, to obtain data on realized fecundity under field conditions. At the end of the oviposition period (July 1 to early August), all egg batches were counted for each female and the number of eggs in each batch was recorded. The latter was estimated accurately in the field, without destroying the egg batches, using a microscope mounted on a tripod.

### *Estimates of mortality factors in different developmental stages of* Y. malinellus

Freshly laid egg batches of *Y. malinellus* are light yellow in colour and can be detected in the field, but change within a couple of days to a red and then brownish colour and can no longer be easily detected. Due to the difficulty of monitoring naturally-laid egg batches in the field, mortality of *Y. malinellus* egg batches was studied using experimental populations on trees in a small apple orchard in Delémont, Switzerland. Ten *Y. malinellus* adults were placed in each of a series of sleeve cages (20×35 cm) over branches of the apple trees and left to oviposit for four to five weeks from July 1 each year. After removal of the sleeve cages, all egg batches on the branches were marked with coloured pins and the number of eggs in each batch counted. The egg batches and subsequent egg-batch hibernacula were counted each month from August through to March to monitor their loss due to predation. In March, the egg batches were removed from the branches and the number of live overwintered first instar larvae counted. The loss of egg batches and hibernacula and the difference between the number of eggs in a batch and the number of overwintered first instar larvae in March were combined as egg and hibernaculum mortality.

Sampling was carried out at the two field sites in southwestern Germany from late April to mid June each year, to estimate the number of individuals of *Y. malinellus* and the extent of mortality at each of five life stages (L2–L5 and cocoons). The sample unit most suitable for studying populations of small ermine moths is the leaf cluster (e.g. Leather & Mackenzie, 1994), as it represents a distinct unit of food resource and all juvenile stages of *Y. malinellus* are found on it. Ten trees selected at random were sampled at each site. Each tree crown was divided into an upper and lower canopy and each half was divided into four equal quadrants according to the four cardinal points of the compass. This provided eight sampling sections within the tree crown. From each section a single branch was selected at random and 30 leaf clusters were examined to determine the number of *Y. malinellus* tents and the number of individuals in each tent. Sampling occurred when the insects were at the mid point of each life stage and selected branches

were marked to avoid reselection during the assessment of other host life stages. Mortality at each of the life stages was estimated from the differences in *Y. malinellus* abundance in each of the successive samples.

On each sampling occasion, the *Y. malinellus* tents sampled were collected from the field to determine rates of parasitism. Individual tents were placed, with fresh apple foliage, in plastic containers (10 × 10 × 8 cm) with a gauze lid and the *Y. malinellus* were reared outdoors at Delémont, Switzerland until adult moths and parasitoids had emerged. Rearing containers were checked every two days until pupation to supply fresh apple foliage if necessary. After pupation, rearing containers were checked daily to count the number of moths and parasitoids emerging. Percent parasitism was estimated from the number of parasitoid adults (divided by the mean clutch size per host, one for solitary species) divided by the total number of adult moths and parasitoid adult clutches and multiplied by 100. The estimate of parasitism was based on parasitoid adults emerged, and so may not reflect parasitoid attack rates, although there was no reason to suspect that there was differential mortality of healthy and parasitized hosts.

### *Construction of life tables*

For the study site at Biebesheim, life tables were constructed for 1993, 1994 and 1995 with the following columns: $l_x$ the number of *Y. malinellus* present in each life stage, $d_x$ the number of *Y. malinellus* dying during each life stage, $Fd_x$ the factor(s) responsible for the *Y. malinellus* mortality at each life stage, and the corresponding marginal death rate, apparent mortality, and k-value. More detailed descriptions of columns used are given in Southwood (1978) and Bellows *et al.* (1992).

Percent loss of *Y. malinellus* egg batches and hibernacula was used both as a mortality factor (due primarily to predation) in the egg stage and to calculate, from the number of first instar larvae, the number of *Y. malinellus* eggs. The results of the sampling programme described above were used to obtain data on the number of individuals of *Y. malinellus* in each larval stage. Although parasitism could be detected from the rearing of *Y. malinellus* samples at all larval stages, parasitoid-induced mortality ('parasitism') in the life tables was estimated from the fifth instar larval and cocoon samples only. The number of hosts in the pupal stage was estimated by subtracting the number of hosts killed by larval parasitoids in the fifth instar from the number of *Y. malinellus* cocoons sampled on the final sampling date. The number of *Y. malinellus* adults in the life table was estimated from the number reared from the sampled cocoons. Fecundity estimates of *Y. malinellus* were introduced into life tables from estimates of sex ratio and 'potential fecundity' (from dissection) of emerged females, and 'realized fecundity' from individual females in sleeve cages. The net reproductive rate ($R_0$) was estimated as the ratio of the expected egg population in the following generation to the egg population at the beginning of the generation. Values of $R_0$ less than one indicate declining populations, while values greater than one indicate increasing populations. The total generational mortality (K) was calculated from the sum of the individual k-values associated with each life stage, allowing each stage mortality or each mortality factor to be expressed as a percentage of the generational mortality ($100k_i/K$).

## Results

### *Estimates of* Y. malinellus *fecundity*

The following sex ratios of *Y. malinellus* (proportion of females) were determined: 0.47 (n = 184) in 1993, 0.51 (n = 415) in 1994, and 0.49 (n = 106) in 1995. From dissection of emerging *Y. malinellus* females the mean fecundity was 115 ± 4.5 SE (n = 19) and ranged from 72 to 153 eggs, giving 153 as an estimate of the potential fecundity. The mean realized fecundity of emerging females in the field was 52 (±5.9 SE, n = 22) in 1993, 75 (±9.4 SE, n = 20) in 1994, and 107.3 (±8.3 SE, n = 20) in 1995. The number of eggs per batch in the field was on average 39.3 (±1.2 SE, n = 195) in 1993, 41.4 (±1.1 SE, n = 238) in 1994, and 48.6 (±2.7 SE, n = 42) in 1995.

### *Estimates of mortality factors in different developmental stages of* Y. malinellus

Predation of *Y. malinellus* egg batches and hibernacula by unknown insect predators started soon after oviposition. It was determined that mortality caused by insect predators reached 64% in 1992/93, 64% in 1993/94 and 65% in 1994/95. Although no systematic observations were made of the predators responsible, both the European earwig, *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae), and larvae of *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) were observed to feed on egg batches and hibernacula.

The sampling programme provided estimates each year of *Y. malinellus* tents per 30 leaf clusters, individuals per tent and percent parasitism (separately for each parasitoid species present) for each larval instar of *Y. malinellus* both for Biebesheim (table 1) and for Giessen (table 2). Nine parasitoid species of the hymenopteran families Ichneumonidae (five species), Encyrtidae (one species), Eulophidae (one species), and Elasmidae (one species) and of the dipteran family Tachinidae (one species) were identified (table 3). Five of the parasitoid species were obligate primary parasitoids, but *Mesochorus* sp. (Hymenoptera: Ichneumonidae) was an obligate hyperparasitoid and *Baryscapus evonymellae* (Bouché) (Hymenoptera: Eulophidae), *Elasmus albipennis* Thompson (Hymenoptera: Elasmidae) and *Itoplectis maculator* Fabricius (Hymenoptera: Ichneumonidae) acted as facultative hyperparasitoids. Parasitism by several of the parasitoid species at Giessen appeared not to occur as early in the life cycle as at Biebesheim and two of the parasitoids, *Eurysthaea scutellaris* Robineau-Desvoidy (Diptera: Tachinidae) and *Agrypon canaliculatum* Ratzeburg (Hymenoptera: Ichneumonidae), were entirely absent from Giessen.

Primary parasitoid species with the same pattern of host utilization can be grouped into parasitoid guilds to represent the structure of the parasitoid community. From the stage-specific patterns of parasitism (tables 1, 2) five parasitoid guilds of *Y. malinellus* were recognized: (1) egg–larval endoparasitoid, (2) larval–prepupal endoparasitoid, (3) larval–pupal endoparasitoid, (4) larval/prepupal ectoparasitoid, and (5) pupal endoparasitoid (fig. 1). The polyembryonic egg–larval endoparasitoid *Ageniaspis fuscicollis* Dalman (Hymenoptera: Encyrtidae) which attacked host eggs, was detected in all larval instars, and killed the host during the final larval instar. This univoltine species mummifies the final instar larvae and produces 80 parasitoid

Table 1. Host abundance and percentage of apple ermine moth, *Yponomeuta malinellus*, attacked by parasitoids in relation to host stage at Biebesheim, Germany, from 1993 to 1995.

1993

| Stage | Host abundance No. tents/ 30 leaf clusters | Hosts/ tent | % Parasitoids present in Biebesheim | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Ageniaspis fuscicollis* | *Diadegma armillatum* | *Eurysthaea scutellaris* | *Herpestomus brunnicornis* | *Baryscapus evonymellae* | *Mesochorus* sp. | *Elasmus albipennis* | *Agrypon canaliculatum* | *Itoplectis maculator* |
| L1 | | | | | | | | | | | |
| L2 | 0.6 ± 0.1 | 34.7 ± 4.2 | | | | | | | | | |
| | n = 80 | n = 48 | 0.1 | 0.2 | | | | | | | |
| L3 | 0.6 ± 0.07 | 29.8 ± 2.3 | | | | | | | | | |
| | n = 80 | n = 51 | 0.1 | 12.4 | | 0.1 | | 0.3 | | | |
| L4 | 0.9 ± 0.1 | 21.2 ± 1.5 | | | | | | | | | |
| | n = 80 | n = 72 | 0.4 | 6.3 | 0.1 | 0.7 | 0.8 | 2.2 | | | |
| L5 | 0.9 ± 0.1 | 18.3 ± 1.4 | | | | | | | | | |
| | n = 80 | n = 72 | 0.3 | 20.7 | 0.8 | 1.4 | 0.8 | 1.8 | | | |
| Cocoons | 0.65 ± 0.08 | 16.9 ± 1.8 | | | | | | | | | |
| | n = 80 | n = 52 | 1.5 | 5.3 | 0.6 | 3.4 | 9.7 | 0.8 | 3.4 | 0.3 | 0.3 |

1994

| Stage | Host abundance No. tents/ 30 leaf clusters | Hosts/ tent | % Parasitoids present in Biebesheim | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Ageniaspis fuscicollis* | *Diadegma armillatum* | *Eurysthaea scutellaris* | *Herpestomus brunnicornis* | *Baryscapus evonymellae* | *Mesochorus* sp. | *Elasmus albipennis* | *Agrypon canaliculatum* | *Itoplectis maculator* |
| L1 | 0.7 ± 0.09 | 42.3 ± 2.1 | | | | | | | | | |
| | n = 80 | n = 54 | | | | | | | | | |
| L2 | 0.5 ± 0.07 | 35.6 ± 2.7 | | | | | | | | | |
| | n = 80 | n = 39 | 0.4 | | | | | | | | |
| L3 | 0.48 ± 0.06 | 25.5 ± 2.1 | | | | | | | | | |
| | n = 80 | n = 38 | 0.3 | 1.0 | | | | | | | |
| L4 | 0.46 ± 0.06 | 25.2 ± 2.3 | | | | | | | | | |
| | n = 80 | n = 37 | 1.0 | 1.9 | 0.8 | 0.5 | 1.5 | | | | |
| L5 | 0.48 ± 0.07 | 24.9 ± 3.4 | | | | | | | | | |
| | n = 80 | n = 37 | 1.1 | 7.2 | 2.7 | 4.0 | 3.7 | | | | |
| Cocoons | 0.55 ± 0.09 | 18.7 ± 1.7 | | | | | | | | | |
| | n = 80 | n = 43 | 1.5 | 4.4 | 3.0 | 6.6 | 9.8 | | 0.1 | | 0.1 |

1995

| Stage | Host abundance No. tents/ 30 leaf clusters | Hosts/ tent | % Parasitoids present in Biebesheim | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Ageniaspis fuscicollis* | *Diadegma armillatum* | *Eurysthaea scutellaris* | *Herpestomus brunnicornis* | *Baryscapus evonymellae* | *Mesochorus* sp. | *Elasmus albipennis* | *Agrypon canaliculatum* | *Itoplectis maculator* |
| L1 | 1.25 ± 0.11 | 35.9 ± 2.3 | | | | | | | | | |
| | n = 80 | n = 100 | 1.8 | | | | | | | | |
| L2 | 1.13 ± 0.11 | 32.8 ± 2.4 | | | | | | | | | |
| | n = 80 | n = 96 | 1.0 | 0.2 | | | | | | | |
| L3 | 1.53 ± 0.13 | 24.3 ± 2.0 | | | | | | | | | |
| | n = 80 | n = 110 | 1.0 | 1.2 | | 0.1 | | 0.05 | | | |
| L4 | 1.34 ± 0.11 | 25.0 ± 1.5 | | | | | | | | | |
| | n = 80 | n = 107 | 1.5 | 3.4 | 0.6 | 2.0 | 0.04 | 0.2 | | | |
| L5 | 1.24 ± 0.12 | 26.4 ± 2.3 | | | | | | | | | |
| | n = 80 | n = 99 | 2.2 | 2.7 | 0.4 | 4.8 | 0.1 | 0.3 | | | |
| Cocoons | 1.21 ± 0.12 | 25.2 ± 2.6 | | | | | | | | | |
| | n = 80 | n = 97 | 1.6 | 1.4 | 1.0 | 9.6 | 5.4 | 0.2 | 1.4 | | 0.1 |

Table 2. Host abundance and percentage of apple ermine moth, *Yponomeuta malinellus*, attacked by parasitoids in relation to host stage at Giessen, Germany, from 1993 to 1995.

1993

| Stage | Host abundance No. tents/ 30 leaf clusters | Hosts/ tent | % Parasitoids present in Giessen | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Ageniaspis fuscicollis* | *Diadegma armillatum* | *Eurysthaea scutellaris* | *Herpestomus brunnicornis* | *Baryscapus evonymellae* | *Mesochorus* sp. | *Elasmus albipennis* | *Agrypon canaliculatum* | *Itoplectis maculator* |
| L1 | | | | | | | | | | | |
| L2 | 0.58 ± 0.11 | 27.7 ± 3.3 | | | | | | | | | |
| | n = 80 | n = 43 | 6.3 | 0.2 | | | | | | | |
| L3 | 0.06 ± 0.08 | 29.4 ± 1.9 | | | | | | | | | |
| | n = 80 | n = 48 | 6.8 | 5.8 | | | | | | | |
| L4 | 0.72 ± 0.1 | 26.5 ± 2.5 | | | | | | | | | |
| | n = 80 | n = 58 | 4.9 | 13.3 | | | 0.4 | | | | |
| L5 | 0.71 ± 0.1 | 20.3 ± 2.1 | | | | | | | | | |
| | n = 80 | n = 56 | 9.2 | 18.2 | | 0.4 | 1.9 | 0.4 | | | |
| Cocoons | 0.63 ± 0.07 | 25.6 ± 2.5 | | | | | | | | | |
| | n = 80 | n = 50 | 6.9 | 12.8 | | 1.1 | 2.9 | 0.2 | 1.4 | | 0.5 |

1994

| Stage | Host abundance No. tents/ 30 leaf clusters | Hosts/ tent | % Parasitoids present in Giessen | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Ageniaspis fuscicollis* | *Diadegma armillatum* | *Eurysthaea scutellaris* | *Herpestomus brunnicornis* | *Baryscapus evonymellae* | *Mesochorus* sp. | *Elasmus albipennis* | *Agrypon canaliculatum* | *Itoplectis maculator* |
| L1 | | | | | | | | | | | |
| L2 | 0.34 ± 0.05 | 29.2 ± 2.3 | | | | | | | | | |
| | n = 80 | n = 27 | 7.0 | | | | | | | | |
| L3 | 0.41 ± 0.06 | 30.1 ± 2.9 | | | | | | | | | |
| | n = 80 | n = 33 | 6.7 | 0.3 | | | | | | | |
| L4 | 0.45 ± 0.07 | 22.9 ± 2.4 | | | | | | | | | |
| | n = 80 | n = 36 | 6.8 | 0.6 | | | | | | | |
| L5 | 0.59 ± 0.07 | 21.6 ± 2.3 | | | | | | | | | |
| | n = 80 | n = 47 | 20.5 | 0.1 | | 2.5 | 2.0 | | | | |
| Cocoons | 0.51 ± 0.07 | 25.9 ± 3.4 | | | | | | | | | |
| | n = 80 | n = 42 | 8.9 | 1.0 | | 5.8 | 2.4 | | | | |

1995

| Stage | Host abundance No. tents/ 30 leaf clusters | Hosts/ tent | % Parasitoids present in Giessen | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *Ageniaspis fuscicollis* | *Diadegma armillatum* | *Eurysthaea scutellaris* | *Herpestomus brunnicornis* | *Baryscapus evonymellae* | *Mesochorus* sp. | *Elasmus albipennis* | *Agrypon canaliculatum* | *Itoplectis maculator* |
| L1 | 0.54 ± 0.06 | 32.8 ± 3.3 | | | | | | | | | |
| | n = 80 | n = 44 | 16.1 | | | | | | | | |
| L2 | 0.4 ± 0.05 | 28.6 ± 3.5 | | | | | | | | | |
| | n = 80 | n = 32 | 4.6 | | | | | | | | |
| L3 | 0.43 ± 0.05 | 27.3 ± 2.9 | | | | | | | | | |
| | n = 80 | n = 34 | 13.0 | | | | | | | | |
| L4 | 0.53 ± 0.06 | 25.0 ± 2.8 | | | | | | | | | |
| | n = 80 | n = 43 | 9.8 | 0.2 | | 1.0 | 0.4 | | | | |
| L5 | 0.64 ± 0.07 | 23.1 ± 3.7 | | | | | | | | | |
| | n = 80 | n = 51 | 16.7 | 0.1 | | 2.7 | 1.3 | | | | |
| Cocoons | 0.58 ± 0.08 | 38.1 ± 5.0 | | | | | | | | | |
| | n = 80 | n = 45 | 18.0 | 0.1 | | 9.5 | 2.3 | | | | |

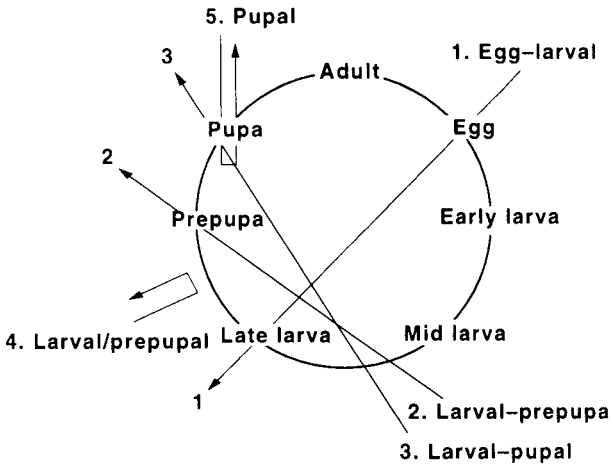
Table 3. Primary parasitoids and hyperparasitoids reared from the apple ermine moth, *Yponomeuta malinellus*, at two sites in Germany from 1993 to 1995.

| Parasitoid and hyperparasitoid species of the apple ermine moth, *Yponomeuta malinellus* | |
|---|---|
| Obligate primary parasitoids | |
| **Ichneumonidae** | **Encyrtidae** |
| *Diadegma armillatum* Gravenhorst | *Ageniaspis fuscicollis* Dalman |
| *Herpestomus brunnicornis* Gravenhorst | **Tachinidae** |
| *Agrypon canaliculatum* Ratzburg | *Eurysthaea scutellaris* Robineau-Desvoidy |
| Obligate hyperparasitoids | |
| **Ichneumonidae** | |
| *Mesochorus* sp. | |
| Facultative hyperparasitoids | |
| **Ichneumonidae** | **Elasmidae** |
| *Itoplectis maculator* Fabricius | *Elasmus albipennis* Thompson |
| **Eulophidae** | |
| *Baryscapus evonymellae* Bouché | |

individuals per host. The solitary larval–prepupal endoparasitoid *Diadegma armillatum* (Gravenhorst) (Hymenoptera: Ichneumonidae) attacked as early as the second larval instar, but as percent parasitism increased in samples up to the fifth larval instar, it appeared able to attack a broad range of larval instars. It killed *Y. malinellus* hosts as prepupae producing an oval, brown cocoon, outside or inside the cocoon of *Y. malinellus* and was itself attacked by the hyperparasitoid *Mesochorus* sp. The gregarious larval/prepupal ectoparasitoid *E. albipennis* attacked *Y. malinellus* as fifth instar larvae protected in a tent or as prepupae in cocoons. *Elasmus albipennis* is also known to act as a facultative hyperparasitoid of the cocoon stage of *D. armillatum* (Dijkerman *et al.*, 1986). The solitary larval–pupal endoparasitoids *E. scutellaris*, *A. canaliculatum* and *Herpestomus brunnicornis* Gravenhorst (Hymenoptera: Ichneumonidae) and the gregarious larval–pupal endoparasitoid *B. evonymellae* attacked *Y. malinellus* larvae from the third or fourth larval instar but only killed their host in the pupal stage. *Baryscapus evonymellae* is also known to be a facultative hyperparasitoid, parasitizing *D. armillatum* and *Mesochorus* sp. (Dijkerman *et al.*, 1986; Graham, 1991). *Herpestomus brunnicornis* continued to attack *Y. malinellus* in the pupal stage which, together with the solitary *I. maculator*, form the pupal endoparasitoid guild. *Itoplectis maculator* is also known to be a facultative hyperparasitoid of other parasitoids developing within *Y. malinellus* pupae (Zwölfer, 1963).

### *Construction of life tables*

Life tables were constructed for the *Y. malinellus* study site at Biebesheim for 1993, 1994, and 1995 (table 4). They include the life stages directly sampled from the field (L1 to cocoon) and were completed, using independent observations from Delémont, for egg and hibernaculum mortality and the realized fecundity of *Y. malinellus* females. The number of *Y. malinellus* eggs was calculated from the number of first instar larvae in leaf mines (L1) and the independent estimates of egg/hibernaculum mortality. The number of *Y. malinellus* pupae was calculated from the number of cocoons sampled in the field minus the number of individuals dying from parasitism as prepupae. The maximum number of eggs in a dissected female of *Y. malinellus*, reared from cocoons collected at Biebesheim, represented the potential fecundity and was used to calculate the potential progeny. The realized fecundity was estimated from emerging females sleeve-caged in Delémont and was used to calculate the actual progeny for the following generation. The net reproductive rate of increase ($R_0$) was




**1. Egg–larval endoparasitoid guild**
*Ageniaspis fuscicollis* (Hymenoptera: Encyrtidae)

**2. Larval–prepupal endoparasitoid guild**
*Diadegma armillatum* (Hymenoptera: Ichneumonidae)

**3. Larval–pupal endoparasitoid guild**
*Herpestomus brunnicornis* (Hymenoptera: Ichneumonidae)
*Agrypon canaliculatum* (Hymenoptera: Ichneumonidae)
*Baryscapus evonymellae* (Hymenoptera: Eulophidae)
*Eurysthaea scutellaris* (Diptera: Tachinidae)

**4. Larval/prepupal ectoparasitoid guild**
*Elasmus albipennis* (Hymenoptera: Elasmidae)

**5. Pupal endoparasitoid guild**
*Itoplectis maculator* (Hymenoptera: Ichneumonidae)
*Herpestomus brunnicornis* (Hymenoptera: Ichneumonidae)

Fig. 1. Parasitoid guilds of the apple ermine moth, *Yponomeuta malinellus*, defined by their pattern of host utilization. Arrows connect the host stage attacked to the host stage killed by the parasitoid, and arrows passing through the host circle indicate endoparasitic development, whereas those remaining outside the circle indicate ectoparasitic development.

estimated from the ratio of the actual progeny to eggs and was 1.35 in 1993, 2.43 in 1994 and 6.8 in 1995.

Parasitism between the fifth instar larval and pupal stages was caused by *A. fuscicollis*, *D. armillatum* and *E. albipennis*. Mortality due to *A. fuscicollis* was estimated from the combined fifth instar larval and cocoon samples, as parasitized larvae often died in rearing. Parasitism due to *D. armillatum* was estimated from the fifth instar larval samples and included hosts from which the obligate hyperparasitoid *Mesochorus* sp. emerged. Parasitism by

Table 4. Life tables for the apple ermine moth, *Yponomeuta malinellus*, in Biebesheim in Germany from 1993 to 1995.

1993

| Stage | Factor | Stage | | Factor $d_x$ | Marginal death rate | Apparent mortality | | k-Value | |
|---|---|---|---|---|---|---|---|---|---|
| | | $l_x$ | $d_x$ | | | Stage $q_x$ | Factor $q_x$ | Stage | Factor |
| Egg | | 7812 | 4960 | | | 0.635 | | 0.438 | |
| | Predation | | | 4960 | 0.635 | | 0.635 | | 0.438 |
| L1 | | 2852 | 1120 | | | 0.393 | | 0.217 | |
| | Unknown factors | | | 1120 | 0.393 | | 0.393 | | 0.217 |
| L2 | | 1732 | 211 | | | 0.122 | | 0.056 | |
| | Unknown factors | | | 211 | 0.122 | | 0.122 | | 0.056 |
| L3 | | 1521 | 21 | | | 0.014 | | 0.006 | |
| | Unknown factors | | | 21 | 0.014 | | 0.014 | | 0.006 |
| L4 | | 1500 | 181 | | | 0.121 | | 0.056 | |
| | Unknown factors | | | 181 | 0.121 | | 0.121 | | 0.056 |
| L5 | | 1319 | 543 | | | 0.412 | 0.230 | | |
| | Parasitism | | | 361 | 0.298 | | 0.274 | | 0.153 |
| | Residual | | | 182 | 0.162 | | 0.138 | | 0.077 |
| Pupae | | 776 | 339 | | | 0.437 | | 0.251 | |
| | Parasitism | | | 128 | 0.194 | | 0.165 | | 0.095 |
| | Residual | | | 211 | 0.301 | | 0.272 | | 0.156 |
| Adults | | 435 | | | | | | | |
| | Sex ratio | 0.467 | | | | | | | |
| Adult female | | 203 | | | | | | | |
| | Potential fecundity | 153 | | | | | | | |
| Potential progeny | | 31059 | 20495 | | | 0.660 | | 0.468 | |
| | Realized fecundity | 52 | | 20495 | 0.660 | | 0.660 | | 0.468 |
| Actual progeny | | 10564 | | | | | | | |
| Ro | | 1.35 | | | | | | | |

1994

| Stage | Factor | Stage | | Factor $d_x$ | Marginal death rate | Apparent mortality | | k-Value | |
|---|---|---|---|---|---|---|---|---|---|
| | | $l_x$ | $d_x$ | | | Stage $q_x$ | Factor $q_x$ | Stage | Factor |
| Egg | | 6332 | 4046 | | | 0.639 | | 0.442 | |
| | Predation | | | 4046 | 0.639 | | 0.639 | | 0.442 |
| L1 | | 2286 | 899 | | | 0.393 | | 0.217 | |
| | Unknown factors | | | 899 | 0.393 | | 0.393 | | |
| L2 | | 1387 | 417 | | | 0.301 | | 0.155 | |
| | Unknown factors | | | 417 | 0.301 | | 0.301 | | 0.155 |
| L3 | | 970 | 37 | | | 0.038 | | 0.017 | |
| | Unknown factors | | | 37 | 0.038 | | 0.038 | | 0.017 |
| L4 | | 933 | 10 | | | 0.011 | | 0.005 | |
| | Unknown factors | | | 10 | 0.011 | | 0.011 | | 0.005 |
| L5 | | 923 | 174 | | | 0.189 | | 0.091 | |
| | Parasitism | | | 83 | 0.095 | | 0.090 | | 0.043 |
| | Residual | | | 91 | 0.104 | | 0.099 | | 0.048 |
| Pupae | | 749 | 346 | | | 0.461 | | 0.269 | |
| | Parasitism | | | 154 | 0.240 | | 0.205 | | 0.120 |
| | Residual | | | 192 | 0.291 | | 0.256 | | 0.149 |
| Adult | | 403 | | | | | | | |
| | Sex ratio | 0.508 | | | | | | | |
| Adult female | | 205 | | | | | | | |
| | Potential fecundity | 153 | | | | | | | |
| Potential progeny | | 31365 | 15990 | | | 0.510 | | 0.310 | |
| | Realized fecundity | 75 | | 15990 | 0.510 | | 0.510 | | 0.310 |
| Actual progeny | | 15375 | | | | | | | |
| Ro | | 2.43 | | | | | | | |

*Continued overleaf*

Table 4—*continued.*
1995

| Stage | Factor | Stage | | Factor $d_x$ | Marginal death rate | Apparent mortality | | k-Value | |
|---|---|---|---|---|---|---|---|---|---|
| | | $l_x$ | $d_x$ | | | Stage $q_x$ | Factor $q_x$ | Stage | Factor |
| Egg | | 10167 | 6578 | | | 0.647 | | 0.452 | |
| | Predation | | | 6578 | 0.647 | | 0.647 | | 0.452 |
| L1 | | 3589 | 438 | | | 0.122 | | 0.056 | |
| | Unknown factors | | | 438 | 0.122 | | 0.122 | | 0.056 |
| L2 | | 3151 | 475 | | | 0.151 | | 0.072 | |
| | Unknown factors | | | 475 | 0.151 | | 0.151 | | 0.072 |
| L3 | | 2676 | 6 | | | 0.002 | | 0.001 | |
| | Unknown factors | | | 6 | 0.002 | | 0.002 | | 0.001 |
| L4 | | 2670 | 53 | | | 0.02 | | 0.009 | |
| | Unknown factors | | | 53 | 0.02 | | 0.02 | | 0.009 |
| L5 | | 2617 | 281 | | | 0.108 | | 0.049 | |
| | Paratism | | | 167 | 0.066 | | 0.064 | | 0.029 |
| | Residual | | | 114 | 0.046 | | 0.044 | | 0.020 |
| Pupae | | 2336 | 1020 | | | 0.437 | | 0.249 | |
| | Parasitism | | | 390 | 0.196 | | 0.167 | | 0.095 |
| | Residual | | | 630 | 0.299 | | 0.270 | | 0.154 |
| Adult | | 1316 | | | | | | | |
| | Sex ratio | 0.491 | | | | | | | |
| Adult female | | 646 | | | | | | | |
| | Potential fecundity | 153 | | | | | | | |
| Potential progeny | | 98838 | 29716 | | | 0.301 | | 0.155 | |
| | Realized fecundity | 107 | | 29716 | 0.301 | | 0.301 | | 0.155 |
| Actual progeny | | 69122 | | | | | | | |
| Ro | | 6.8 | | | | | | | |

*E. albipennis* was estimated from the cocoon samples, but as this species is a facultative hyperparasitoid a proportion of the hosts from which *E. albipennis* emerged were transferred to parasitism by *D. armillatum*, under the assumption that it attacked primary and secondary hosts in proportion to their abundance. Similarly, *B. evonymellae* can be a facultative parasitoid of *D. armillatum* and using the same assumption of proportional attack, a proportion of hosts from which *B. evonymellae* emerged were also transferred to parasitism by *D. armillatum*. Apparent parasitism during the fifth instar larval and prepupal stages reached 27% in 1993, 9% in 1994 and 6% in 1995.

Rates of parasitism in the cocoon stage, due to *B. evonymellae*, *E. scutellaris*, *A. canaliculatum*, *I. maculator* and *H. brunnicornis*, were estimated from the cocoon samples and were based on the number of *Y. malinellus* pupae. Apparent parasitism by *B. evonymellae* and *I. maculator* were proportionally reduced due to potential hyperparasitism of *D. armillatum* and other pupal stage parasitoids respectively. Apparent parasitism in the pupal stage was 17% in 1993, 21% in 1994, and 17% in 1995.

The impact of predation and parasitism on the generational mortality of *Y. malinellus* was determined at Biebesheim in 1993–1995, using the k-values from the life tables. The generational mortality ($K = \Sigma k_i$) was 1.72 in 1993, 1.51 in 1994 and 1.04 in 1995. The percentage of the generational mortality due to loss of potential fecundity, predation of eggs and hibernacula and parasitism ($100k_i/K$) are presented in table 5. Predation had the greatest impact on the *Y. malinellus* population studied, although it equalled the loss of potential fecundity in the first year of the study. The impact of parasitism had the least impact of the known mortalities and this remained remarkably constant over the three-year period. The combined effect of natural enemies at 40–55% of the generational mortality of the *Y. malinellus* population was substantially greater than the loss of potential fecundity at 15–27%.

Table 5. Loss of potential fecundity and impact of natural enemies on the generational mortality of the apple ermine moth, *Yponomenta malinellus*, at Biebesheim in Germany from 1993 to 1995.

| Year | Host fecundity losses (%) | Impact of natural enemies (%) | | |
|---|---|---|---|---|
| | | Egg predators | Parasitoids | Total |
| 1993 | 27.2 | 25.4 | 14.4 | 39.8 |
| 1994 | 20.6 | 29.3 | 10.8 | 40.1 |
| 1995 | 14.9 | 43.3 | 11.9 | 55.2 |
| mean | 20.9 | 32.7 | 12.4 | 45.0 |

## Discussion

We have presented here the results of a life table study to determine the impact of natural enemies on a population of *Y. malinellus* over a three year period in southwestern Germany. This approach was used to provide data for the selection of natural enemies for use in a biological control programme for *Y. malinellus* in Canada.

### *Factors influencing the generational mortality of* Y. malinellus

The abundance of *Y. malinellus* varied from 1.8 to 4.3 tents per 100 leaf clusters in Biebesheim and from 1.5 to 2.2 tents per 100 leaf clusters in Giessen. These densities were generally below the traditional control threshold of 3–5 larval tents per 100 leaf clusters (Baggiolini *et al.*, 1980) and would not have been considered for control treatments as no economic threshold values exist for *Y. malinellus* in central Europe because of its reduced importance today under current pest management practices (Galli & Höhn, 1992).

Insect predation obviously played an important role in the reduction of *Y. malinellus* egg and hibernaculum populations. From the life tables, it is evident that the impact of egg predators accounted for 25–43% of the total generational mortality of *Y. malinellus*, more than any other known mortality factor. Unfortunately, no systematic observations of the predator species responsible for the mortality of egg batches and hibernacula were possible. However, based on the results of this study, and according to Unruh *et al.* (1993) and Smith (1994, personal communication) endemic polyphagous predators in Europe and in the western United States and Canada do produce significant mortality in *Y. malinellus* populations. These generalist predators may be largely responsible for preventing even more damaging levels of *Y. malinellus* in the western United States (Unruh *et al.*, 1993).

Percent parasitism, in the present study, varied from 21 to 26% at Biebesheim and from 18 to 30% at Giessen. However, the impact of parasitoids in relation to the total generational mortality of *Y. malinellus* from the life tables at Biebesheim was remarkably constant at 11–14%. All other studies of *Y. malinellus* in its natural range have considered only percent parasitism. These studies reported values ranging from 30 to 98% (Ruzaev, 1929; Thorpe, 1930; Voukassovitch, 1933; Bilanovski, 1938; Iren, 1952; Vaclav, 1958; Junnikkala, 1960; Balachowsky, 1966; Aleksidze & Bezhanishvili, 1974; Eremenko, 1974; Dijkerman *et al.*, 1986; Tkachev, 1986).

We estimated the average potential fecundity of *Y. malinellus* to be 115, a value that is almost identical to the estimate of 117 for *Y. evonymellus* (Linnaeus) (Lepidoptera: Yponomentidae) (Leather & MacKenzie, 1994). Failure of populations to realize their potential fecundity can be a major factor contributing to changes in numbers of insects between generations (Banerjee, 1979; Courtney & Duggan, 1983; Preszler & Price, 1988; Price *et al.*, 1990). The loss of potential fecundity was a significant component of the life tables of *Y. malinellus*, but declined from 27% to 15% of the generational mortality over the course of this study. Kuhlmann (1995) demonstrated that the fecundity of *Y. malinellus* is significantly influenced by the mean daily temperature during the oviposition period. The number of egg batches laid per *Y. malinellus* female increased significantly with higher mean daily temperatures during the oviposition period.

### *Parasitoid community of* Y. malinellus *and selection of biological control agents*

A natural parasitoid community is defined as an assemblage of primary parasitoid species that attack the population of a particular host species in a given locality (Ehler, 1992; Mills, 1992, 1994a). In the present study, *Y. malinellus* populations were attacked by eight different parasitoid species at Biebesheim and by six parasitoid species at Giessen. The parasitoid species represent five different parasitoid guilds, somewhat less than the eight parasitoid guilds that have been recognized for the Yponomeutidae as a whole (Hawkins & Mills, 1996). Three of the guilds are occupied by a single parasitoid species, with the larval–pupal endoparasitoid and pupal endoparasitoid guilds being occupied by four and two species respectively. The most consistent parasitoid species found attacking *Y. malinellus* throughout its native range are the egg–larval endoparasitoid *A. fuscicollis*, the larval–prepupal endoparasitoid *D. armillatum*, and the larval–pupal or pupal endoparasitoid *H. brunnicornis*. These same parasitoids were responsible for the greatest levels of parasitism at both Biebesheim and Geissen in the present study. Other parasitoids reported from *Y. malinellus* in Europe that were not found during the present study include the tachinids *Bactromyia aurulenta* (Meigen) (Pag, 1959; Dijkerman *et al.*, 1986) and *Bessa selecta* (Meigen) (Pag, 1959), the eulophid *Baryscapus galactopus* (Ratzeburg) (Junnikkala, 1960), and the ichneumonids *Pimpla turionellae* (Linnaeus) (Junnikkala, 1960) and *Agrypon anxium* (Wesmael) (Dijkerman *et al.*, 1986).

In the selection of parasitoids for use in a classical biological control programme, it is important to exclude antagonistic species in the reconstruction of a parasitoid community for the target region of a pest, as they can prevent the most effective parasitoids from realizing their potential as control agents (Waage & Mills, 1992; Mills, 1994b). Considering the natural parasitoid community of *Y. malinellus*, competitive interactions are minimal between the egg–larval parasitoid and the larval–pupal guilds, and of course interspecific competition is excluded between the egg–larval and the pupal parasitoid guilds. *Ageniaspis fuscicollis* is the only member of the egg–larval endoparasitoid and *H. brunnicornnis* in the only member of the pupal endoparasitoid guild that is not a facultative hyperparasitoid. Although *H. brunnicornis* is also a larval–pupal endoparasitoid and can attack *Y. malinellus* from the fourth instar larvae onwards, it preferentially attacks fifth instar larvae and pupae, with a maximum rate of parasitism in the pupal stage. Overlap between *A. fuscicollis* and *H. brunnicornis* is likely to be confined to the fourth larval instar of *Y. malinellus* because *H. brunnicornis* is unlikely to attack a fifth instar host larva that is close to mummification by *A. fuscicollis*. This degree of overlap is minimal and so these two specific parasitoids could be safely introduced simultaneously in a classical biological control programme against *Y. malinellus*. Both parasitoid species are restricted in their host range to the genus *Yponomeuta*, they are univoltine and therefore well-synchronized with the development of their host, and occupy a wide geographic range (for details of *H. brunnicornis* see Kuhlmann, 1996). The ichneumonid *D. armillatum* was not considered as a biological control agent

despite its high impact due to the fact that it is known to be a polyphagous parasitoid of microlepidopteran hosts (Herting & Simmonds, 1982). The egg–larval parasitoid *A. fuscicollis* has already been introduced into Canada and its impact is being determined in British Columbia (Cossentine, 1996, personal communication).

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