

Predator complex of the horse chestnut leafminer *Cameraria ohridella*: identification and impact assessment

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Abstract: The control of *Cameraria ohridella* Deschka and Dimic (Lepidoptera, Gracillariidae) by natural enemies in Europe is poor. Thus, in the past 15 years epidemic population densities of the moth regularly caused a continuous premature defoliation of horse chestnut trees, *Aesculus hippocastanum* L.. Whereas several studies investigated the parasitoid complex of the leafminer and revealed its inefficiency, only little is known about the predators of *C. ohridella*. The aim of this study was to identify the predator complex in European horse chestnut stands by visual observations and exposure experiments and to assess the impact of different predator guilds on *C. ohridella* populations by an exclusion experiment. Of all potential predators observed, only blue tits, *Parus caeruleus* L., great tits, *Parus major* L., marsh tits, *Parus palustris* L. and the southern oak bushcricket *Meconema meridionale* (Costa) were found to prey on the pre-imaginal leafminer stages. Bushcrickets have to our knowledge never before been recorded preying on leafminers; moreover *M. meridionale* showed a measurable negative impact on the *C. ohridella* population. However, birds seem to be of greater importance as predators of *C. ohridella* than arthropods. Predation rates of birds ranged from 2 to 4% of leafminer populations, which is of the same order of magnitude as published parasitism rates. We conclude that the augmentation of tit densities, for example via nesting boxes in chestnut trees, should be considered as a component of an integrated control strategy against the horse chestnut leafminer.

Key words: *Meconema meridionale*, *Parus* sp., biocontrol, density dependence, exclusion experiment, Gracillariidae, predation

1 Introduction

The enemy release hypothesis posits that the invasion success of exotic species is related to the scarcity of natural enemies in the introduced range compared with their native ranges (reviewed in COLAUTTI et al., 2004). This ineffective regulation of invasive species allows the build-up of large population densities. An impressive example of such an invasion is the horse chestnut leafminer, *Cameraria ohridella* Deschka and Dimic (Lepidoptera, Gracillariidae), introduced to Europe in the late seventies (SIMOVA-TOŠIĆ and FILEV, 1985). *C. ohridella* is a pest of unknown origin that causes pre-mature defoliation of the white flowering horse chestnut tree, *Aesculus hippocastanum* L. (Hippocastanaceae). Detailed information on the biology and distribution of this leafmining species has been published by SKUHRAVY (1998), HELLRIGL (2001), SEFROVA and LASTUVKA (2001) and FREISE and HEITLAND (2004). The leafminers' larvae drill almost exclusively into leaves of *A. hippocastanum* and feed between the two

epidermis layers. At high densities, leafminers defoliate trees already in summer (reviewed in BACKHAUS et al., 2002, <http://www.cameraria.de>). Even though the natural enemy complex of *C. ohridella* includes native parasitic wasps (=parasitoids), pathogens and predators (HEITLAND et al., 1999; BACKHAUS et al., 2002), these antagonists are insufficiently adapted and not able to regulate the leafminer's population density. Even after 20 years of moth infestation typical parasitism rates are merely 0–10% (GRABENWEGER and LETHMAYER, 1999; HEITLAND et al., 1999), rates very low compared to other leafminer species (ASKEW and SHAW, 1979; MAIER, 1984; HAWKINS, 1993). Altogether about 20 species of parasitoids are known to develop on *C. ohridella*, mostly generalistic chalcidoids (GRABENWEGER, 2003). However, whereas parasitoids are quite well studied, the predatory species of *C. ohridella* in Europe were never properly investigated and their impact on leafminer populations is unknown. In general, ants, birds and spiders are assumed to be the most important

predators of leafminers (Szöcs, 1959; FAETH, 1980; MAHDI and WHITTAKER, 1993; KORICHEVA et al., 1994; SKUHRAVY, 1998; HEITLAND et al., 1999; ZEGULA et al., 2002).

The first aim of this study was the identification of *C. ohridella*'s main predators by field observations in urban horse chestnut sites. Second, we exposed leafminer-infested leaves to potential predators under laboratory, semi-field and field conditions. In a third part, we estimated the impact of the predatory avian and wandering-insect guilds on a population of *C. ohridella* in an exclusion experiment in the field over one season. In this exclusion experiment we also investigated density-dependent processes of these two guilds at two different spatial scales.

2 Materials and Methods

2.1 Field observations of predators

The purpose of this field study was the identification of *C. ohridella*'s predators under natural conditions. Horse chestnut trees at 24 locations in Austria (seven locations), Croatia (six), Czech Republic (three), Hungary (three), Italy (three) and Slovakia (two) were examined visually for traces of predation such as holes in the surface of mines from 2001 to 2003. At each location, a minimum of 20 leaves of the lower crown of three to five trees was examined once at the end of the first generation of *C. ohridella* (mid to end of June). At 10 sites ('Prater' and 'Zentralfriedhof' in Vienna A, Enns A; 'Maksimir' and 'Podsused' in Zagreb HR, Samobor HR; 'Miramare' and 'Monte Valerio' in Trieste I, Brixen I, Bratislava SK) mines emptied by predators were found and knockdown samples were collected in the lower canopy twice a day, and between 09.00 and 12.00 in the morning and 21.00 and 23.00 in the evening. Arthropods were killed with ethyl acetate and stored in 70% alcohol. All predatory specimens were separated from the catch and counted. Predators with outstanding abundance of several taxonomic orders were determined and designated for further testing in exposure experiments (see below).

Additionally, detailed observations were conducted at two horse chestnut sites ('Vierfeld' and 'Tiefenau') in the city of Bern, Switzerland, from May 23 to October 30, 2001. Each site consisted of more than 40 *A. hippocastanum* trees. At each site, two horse chestnut trees were observed for 1 h in weekly intervals. Each tree was scanned for half an hour from a distance of about 20 m for predatory birds (optical instruments: Swarovski binoculars 10 × 42, Weso 660 telescope 28 × 60). Afterwards, we investigated the trees for another 30 min for predatory arthropods in the lower crown using a 3-metre-high ladder.

2.2 Exposure of *Cameraria ohridella* to potential arthropod predators

We offered *C. ohridella*-infested horse chestnut leaves to some of the most abundant arthropod predators under laboratory, semi-field and field conditions. This allowed us to assign the damage of mines to specific predators.

2.2.1 Egg predation test with a predacious mite

The ability of the predacious mite *Euseius finlandicus* Oudemans (Acari, Phytoseiidae) to feed on *C. ohridella* eggs was tested in detached leaf arenas (modified after HELLE and

OVERMEER, 1985) in May 2001. One single horse chestnut leaflet with a minimum of 20 *C. ohridella* eggs was fixed on a piece of wet foam and set up in a small plastic dish. The margins of the leaflet were covered with wet tissue paper as a barrier for the mites, which were placed in the centre of the leaf surface. One mite was released per arena and kept there until it died. The behaviour of the mites was recorded twice a day for approximately 15 min. Concurrently, eggs were checked for traces of predation. The experiment was conducted in five replicates in a climatic chamber at 25°C, L/D 16/8 h and 60% rh.

2.2.2 Leaf cage experiments under semi field conditions

In 2003, 10 *A. hippocastanum* trees (height 1 m) reared by the Viennese city garden management were potted in plastic containers and set up in a small yard at the Institute of Plant Protection in Vienna. They were infested with adult *C. ohridella* emerging from dry leaves and protected in a gossamer tent from herbivory by other species. Single leaflets of these trees were enclosed inside plastic leaf cages without being cut off the stem. The leaf cages consisted of rectangular transparent plastic containers (19 × 12 × 8 cm) with a gossamer-covered opening for proper aeration at one end and a slit for the enclosed leaflet at the other end. The opening was sealed around the stem of the leaflet with a piece of foam to prevent the escape of insects tested.

Predatory insects were caught by sweeping the lower crown of heavily infested horse chestnut trees with a butterfly net in Viennese parks. They were placed singly in the leaf cages and kept there for five days or until they died. The mines on the enclosed leaflets were checked daily for signs of predation and leaflets were replaced when the majority of the mines had been preyed.

Leaf cage experiments were conducted with three adult individuals of the ladybeetle *Calvia decemguttata* L. (Coleoptera, Coccinellidae), three adults and three larvae of lacewings (*Chrysoperla* sp., Neuroptera, Chrysopidae), three adult earwigs (*Forficula* sp., Dermaptera, Forficulidae) and the bushcrickets *Phaneroptera* sp. (three adults) and *Meconema meridionale* Costa (four adults, both Saltatoria, Tettigoniidae).

2.2.3 Field experiment with a predacious bushcricket

Eight potted *A. hippocastanum* seedlings (height 1 m) were infested with high loads of *C. ohridella* in May 2004, resulting in an average infestation level of approximately 80 mines per leaf. After the emergence of L1 leafminers (L = larval stage) they were transferred to a park in Vienna ('Türkenschanzpark'). On May 24, *M. meridionale* individuals were placed singly on four randomly chosen seedlings (one individual per tree) whereas the other four trees were used as control. Seedlings were placed at a minimum distance of at least 5 m to one another and to other horse chestnuts in the park, respectively. Every third day, the presence of *M. meridionale* on the treated trees was checked and new bushcrickets were released when necessary. The bushcrickets were caught with a butterfly net by sweeping other *A. hippocastanum* trees. Control trees were checked at the same dates and *M. meridionale* specimens, which were occasionally found, were removed (five cases in total). After July 1, mines were examined under a dissecting microscope. We discriminated 'alive' (moving larvae or pupae within intact mines), 'dead' (dead or paralyzed larvae and pupae regardless of mortality reasons) and 'preyed' (only mines, where the surface has obviously been damaged by insect mandibles and no larvae

or pupae were present). Data were analysed by comparing mean percentages of alive, dead and preyed leafminers with the treatment (*M. meridionale* released vs. removed) as the grouping variable.

Throughout the text, results were given as mean \pm standard deviation (SD).

2.2.4 Field experiments with predatory ants

The ant species *Liometopum microcephalum* Panzer (Hymenoptera, Formicidae) is well known for its outstanding aggressive predatory behaviour (EMERY, 1891; WIEST, 1967; LUDSCHER, 1979). With its large colonies and its exceptionally strong mandibles it is capable of entirely dominating a colonized tree. This allows allocating observed effects to this ant species with high certainty (EMERY, 1891; WIEST, 1967; STEINER and SCHLICK-STEINER, 2002). Thus, we chose an *L. microcephalum* colony nesting in an *A. hippocastanum* tree of the Laxenburg castle park in Lower Austria for further investigations.

In a first phase, single clipped mines containing late larval instars or pupae of *C. ohridella* were placed in the middle of an ant trail close to the ants' nest in three variants (undamaged, upper epidermis of mine removed and upper epidermis and cocoon opened, $n = 10$ mines for each variant). This trial was conducted on a sunny day with high ant activity in June 2003. The fate of the leafminers was followed for 10 min or until the larvae were preyed and carried away.

In July 2003, at the end of the second generation of *C. ohridella*, large parts of the crown (3–15 m height) of the horse chestnut tree with the *L. microcephalum* colony were checked visually for 30 min for evidence of predation using a lift truck. Additionally, leaves of this tree and of an ant-free control tree were collected. 200 leaflets were chosen randomly from each tree and the total number of *C. ohridella* mines and the number of mines opened by predators counted. Results were given as mean \pm standard deviation (SD).

3 Exclusion of Avian Predators and Wandering Arthropods

The impact of birds and wandering arthropods on a population of *C. ohridella* was investigated in a selective exclusion experiment. In addition, prey density-dependent predation was examined.

The study was conducted in a completely randomized three-factorial block design. The three factors were 'avian predators' (access vs. exclusion), 'wandering arthropods' (access vs. exclusion) and 'exclusion period' (four levels: first generation, second generation, first and second generation of *C. ohridella* and no exclusion). The experiment was conducted at the site 'Vierfeld', an avenue of about 70 *A. hippocastanum* trees in the city of Bern. The avenue was divided into eight blocks, each of which consisted of two to three neighbouring trees. In each block we selected 16 larger branches (basal diameter > 10 cm) of the lower crown to which we randomly assigned the 16 treatments.

The exclusion barriers for the predators of *C. ohridella*'s first generation were fixed at the beginning of June 2001, when the first stages of *C. ohridella* (eggs to L2) were present. Wanderers were excluded by a glue ring around the branch basis (tree tanglefoot pest barriers, ©Tanglefoot Company, Grand Rapids,

MI, USA), whereas birds were prevented from predation by the protection of branches with bird nets (mesh size 1.5 cm). At the end of July when the first larval stages of the second generation were present we removed the exclusion barriers for the first generation of *C. ohridella* and set up the exclusion of predators on the second generation. Mid September, at the end of the second generation we investigated the effect of predator exclusion on predation rates of *C. ohridella* and estimated defoliation at the level of trees examined and branches treated. The rate (=percentage) of defoliation caused by feeding miners of *C. ohridella* was assessed visually at both levels (GILBERT and GRÉGOIRE, 2003). In addition, 20 leaves were collected randomly from each branch treated and the total number of mines in each leaf sample was counted and mines were classified as either attacked by birds (see fig. 1), damaged otherwise or undamaged. Predation rates of *C. ohridella* were calculated as the number of mines attacked by birds or mines damaged otherwise divided by the total number of mines.

The arcsine-transformed predation rates were treated as the response variable whereas the block, avian predators, wandering arthropods and exclusion periods were treated as nominal factors. The experiment was analysed by generalized linear models. The means of the four levels of exclusion period were pair-wise

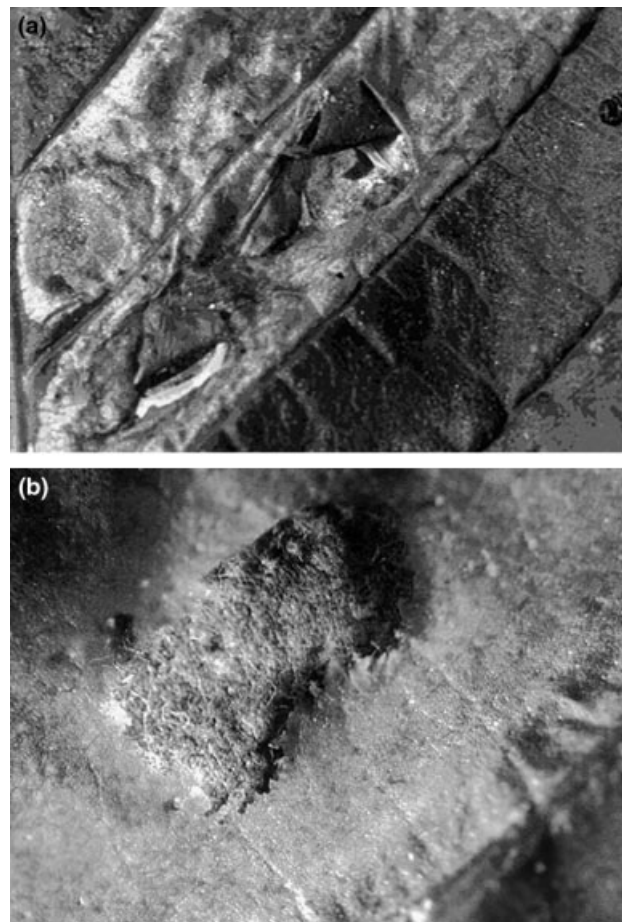


Fig. 1. *C. ohridella* mines opened by (a) tits and (b) an insect predator

compared by Fisher's Least Significant Difference (LSD) *post-hoc* tests. To investigate density-dependent effects of the *C. ohridella* population on bird predation, the relation between arcsine-transformed bird predation rates and arcsine-transformed defoliation of the experimental trees or branches treated were analysed by multiple linear regression in all treatments where no bird nets were set up. The fulfilment of the model assumptions was checked by visual inspection of the residual's distribution for every statistical test conducted.

4 Results

4.1 Field observations of predators

Two different types of mines attacked were identified during the entire study. The first type, in which the upper epidermis of the mine above the pupal cocoon was entirely damaged (fig. 1a), was observed to be caused by birds. Out of 20 bird species that were present in *A. hippocastanum* trees in Bern (appendix 1) only blue tits, *Parus caeruleus*, great tits, *Parus major* and marsh tits, *Parus palustris*, preyed on mines of *C. ohridella*. They were observed in horse-chestnut trees over the whole season preying upon all three leafminer generations. Tits were observed preying over 13% of the period monitored. Blue tits were most frequently observed preying on mines (72%), followed by great tits (25%) and marsh tits (3%). Tits mainly opened mines containing late-instar larvae or pupae.

The other type of mine damage by predators was characterized by irregularly shaped holes on one side of the leaf only, mainly on the upper leaf surface. We supposed that the margins of the epidermis around these holes were fringed as a result of insect mandible action (fig. 1b), which was later confirmed in exposure experiments (see below). Despite the regular occurrence of the second type of mine damage, insects were never observed to prey on *C. ohridella* in the field

Appendix 1. Bird species observed in *A. hippocastanum* trees in the city of Bern, Switzerland, from May to October 2001

Wood pigeon (<i>Columba palumbus</i>)
Turtle dove (<i>Streptopelia turtur</i>)
Black redstart (<i>Phoenicurus ochruros</i>)
Blackbird (<i>Turdus merula</i>)
Common chiffchaff (<i>Phylloscopus collybita</i>)
Firecrest (<i>Regulus ignicapillus</i>)
Spotted flycatcher (<i>Muscicapa striata</i>)
Pied flycatcher (<i>Ficedula hypoleuca</i>)
Great tit (<i>P. major</i>)
Blue tit (<i>P. caeruleus</i>)
Coal tit (<i>Parus ater</i>)
Marsh tit (<i>P. palustris</i>)
European nuthatch (<i>Sitta europaea</i>)
Short-toed treecreeper (<i>Certhia brachydactyla</i>)
Carrion crow (<i>Corvus corone</i>)
Eurasian jay (<i>Garrulus glandarius</i>)
Common starling (<i>Sturnus vulgaris</i>)
House sparrow (<i>Passer domesticus</i>)
Greenfinch (<i>Carduelis chloris</i>)
Common chaffinch (<i>Fringilla coelebs</i>)

Appendix 2. Taxonomic groups of arthropods caught with knockdown samples from *A. hippocastanum* trees in Vienna (2 sites), Enns, A; Zagreb (2 sites), Samobor, HR; Trieste (2 sites), Brixen, I; Bratislava, SK

Taxonomic group	Genera or species with outstanding abundance
Ensifera	<i>Phaneroptera</i> sp., <i>M. meridionale</i>
Dermoptera	<i>Forficula</i> sp.
Psocoptera	
Heteroptera	
Cicadina	
Aphidina	
Thysanoptera	
Neuroptera	<i>Chrysoperla</i> sp.
Mecoptera	
Lepidoptera	<i>C. ohridella</i>
Nematocera	
Brachycera	
Ichneumonidae	
Braconidae	
Chalcidoidea	<i>C. ohridella</i> parasitoids
Platygastroidea	
Formicidae	
Vespidae	
Coleoptera	<i>C. decemguttata</i> , <i>Adalia bipunctata</i>
Araneae	
Acari	<i>E. finlandicus</i>

except for one lacewing larva which tried to open the mine of a late-instar leafminer. Nevertheless, visual observations conducted in Bern as well as knock down samples unveiled the presence of many potential predators such as lacewings (Neuroptera), long-horned grasshoppers (Ensifera), earwigs (Dermoptera), bugs (Hemiptera), ants (Formicidae), wasps (Vespidae) and ladybirds (Coccinellidae) (appendix 2). The ladybird *C. decemguttata* was the most abundant beetle and *Phaneroptera* sp. and *M. meridionale* were the most abundant bushcrickets. Earwigs (*Forficula* sp.) as well as adults and larvae of lacewings (*Chrysoperla* sp.) occurred regularly in low numbers.

Besides insects, spiders and mites were observed in numbers. The most abundant predatory mite found on horse chestnut trees was *E. finlandicus*.

4.2 Exposure of *Cameraria ohridella* to potential insect predators

4.2.1 Egg predation test with a predatory mite

None of the five *E. finlandicus* specimens tested fed on eggs of *C. ohridella*. Although the mites were actively searching for prey, they did not stop when approaching a leafminer egg and not a single attempt to consume an egg was observed. All mites died of starvation and leafminer eggs completed development.

4.2.2 Leaf cage experiments under semi field conditions

All three individuals of the ladybird *C. decemguttata* as well as all lacewing adults and larvae died inside the leaf cages without damaging a single mine. All *C. ohridella* larvae inside the enclosed leaves completed development.

Whereas two earwigs did not try to open the mines and died without having killed a single leafminer, the third individual managed to open three out of 34 mines, two larvae were eaten. The third leafminer larva escaped from the direct attack, but desiccated later. All larvae in undamaged mines completed development.

The three bushcrickets *Phaneroptera* sp. started to feed on horse chestnut leaf tissue and left only the area around the major leaf veins undamaged. In the process they accidentally ate some leafminer larvae. However, the majority of the larvae on the damaged leaflets fell out of their mines and died on the bottom of the leaf cages without further being harmed by the bushcrickets. Due to the destruction of the leaves none of the leafminers finished development.

In contrast, the four *M. meridionale* specimens showed distinct searching behaviour, were able to

locate the larvae in the mines and ripped them out of the leaves. In rare cases, larvae escaped to hidden parts of the mine and survived the attack. However, due to desiccation none of these leafminers survived inside the opened mine. On average, *M. meridionale* ate up to two thirds of all larvae from a single leaflet within one day (fig. 2).

4.2.3 Field experiment with a predacious bushcricket

Predation rates on trees where *M. meridionale* was present were more than twice as high as on control trees (8.3 ± 2.9 vs. $3.3 \pm 1.8\%$). The differences were significant (*t*-test: $t = -4.588$, d.f. = 6, $P = 0.004$) and the survival of the moths was significantly decreased on treated trees (*t*-test: $t = 3.263$, d.f. = 6, $P = 0.017$). $42.0 \pm 8.8\%$ of all leafminers survived on the control trees but only $18.6 \pm 9.2\%$ were alive on the treated trees. The number of moths, which emerged prior to the date of analysis was distinctly lower on treated trees ($3.6 \pm 2.5\%$) than on control trees ($10.5 \pm 4.7\%$), yet statistical significance could not be proved (*t*-test: $t = 2.180$, d.f. = 6, $P = 0.072$). Leafminer mortality caused by other factors than insect predation was higher on treated trees ($73.1 \pm 11.7\%$) than on the control trees ($54.7 \pm 8.7\%$), but differences were not statistically relevant (Mann–Whitney-test: $z = -0.577$, $P = 0.564$).

A detailed analysis of the results revealed that the impact of predation was negligible in very small larvae (L1 and L2) and in spinning stages and pupae, whereas L3 and L4 leafminers suffered heavy attack (fig. 3a). Consequently, more alive leafminers in a late developmental stage were found in the control (fig. 3b).

4.2.4 Field experiments with predatory ants

Liometopum microcephalum workers reacted in different ways towards the three variants of mines placed on their trails. Leafminers inside undamaged mines remained undetected. The ants detected leafminers inside mines, from which the upper epidermis had been removed in several cases. Nevertheless, ants never

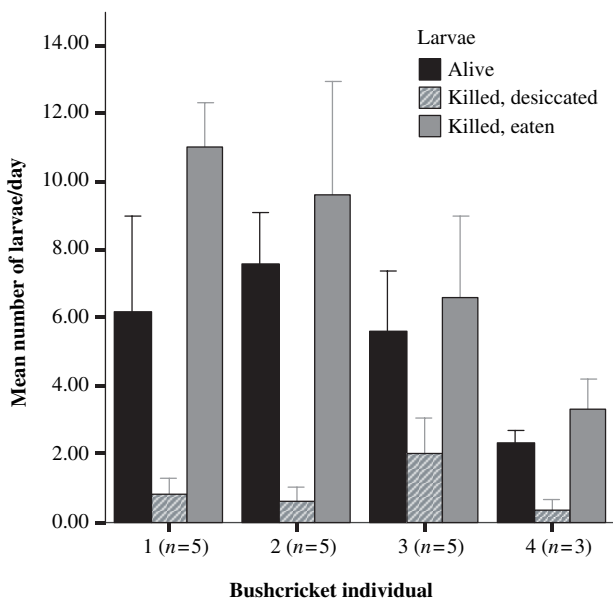


Fig. 2. Predation of the four bushcrickets *M. meridionale* on *C. ohridella* larvae in the leaf cages. *N* in brackets = number of days an individual was tested, error bars = 1 SE

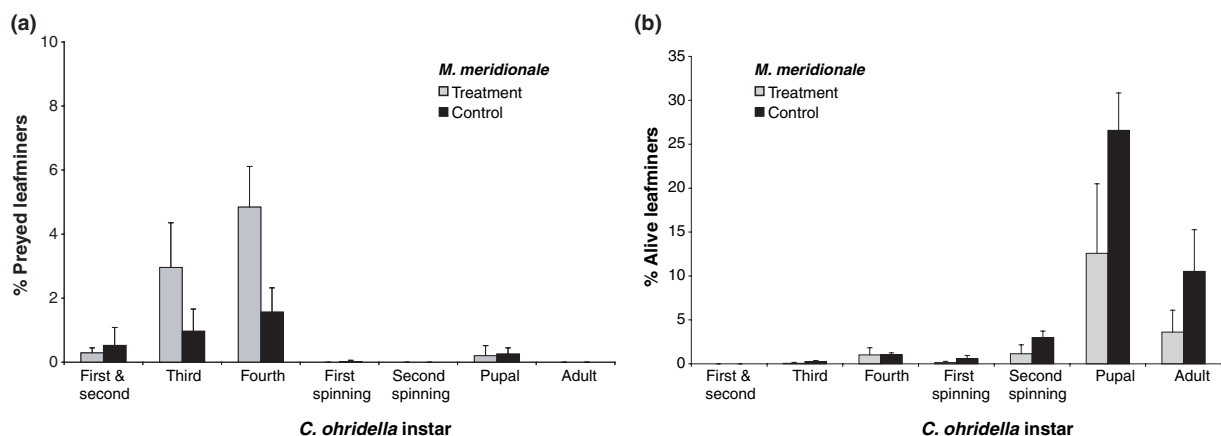


Fig. 3. Proportion of *C. ohridella* mine instars preyed by insect predators (a) and alive (b) in the *M. meridionale* field experiment. Error bars = 1 SE

succeeded in cutting through the silky cocoon tissue. In contrast, leafminers from mines with opened epidermis and cocoon surface always were immediately attacked, pulled out of the cocoon and carried away.

The lift truck examination of the *A. hippocastanum* tree containing an ant colony revealed no evidence of leafminer predation by ants. *L. microcephalum* workers were observed foraging on branches but never on leaves. A comparison of the leaf samples showed considerable differences between the two trees. On the ant-tree, an average of 11.5 ± 5.6 mines of *C. ohridella* were found per leaf, 1.5 ± 1.3 of these mines were found empty due to previous attacks by arthropod predators. Fewer mines per leaf were found on the ant-free tree (7.6 ± 4.0) and a higher number of these were empty (3.7 ± 2.2). Differences between the two trees were highly significant, both for the total number of mines per leaf (Cochran–Cox approximated *t*-test, $t = 7.929$, d.f. = 362, $P < 0.0001$) and for the number of mines per leaf opened by arthropod predators ($t = -11.965$, d.f. = 322, $P < 0.0001$). The significance of our findings is tempered by sample size, but as a tendency, infestation by *C. ohridella* seems to be higher and predation on *C. ohridella* by arthropods lower in the presence of *L. microcephalum*.

4.3 Exclusion of avian predators and wandering arthropods

Leaf defoliation was between 3 and 30% on trees examined and ranged from 2 to 50% on the branch level. In total, 6731 (5.8%) of 116 837 mines counted were attacked by birds, another 1830 mines (1.6%) were classified as damaged otherwise. Hence, birds were responsible for 78.6% of the opened mines. Moreover, the exclusion of birds by nets and the period of exclusion had a significant impact on avian predation rates (table 1). Avian predation was mainly registered in the second generation of *C. ohridella*.

Table 1. Impact of exclusion measures on avian predation and damaged mines of the first two generations of *C. ohridella*

Source of variance	d.f.	Predation rate by birds		Rate of mines damaged otherwise	
		SSQ III	P	SSQ III	P
Block	7	0.702	<0.001	0.315	<0.001
Exclusion period (EP)	3	0.036	0.018	0.032	0.012
Avian predators (AP)	1	0.022	0.013	<0.001	0.941
Wandering arthropods (WP)	1	0.001	0.526	<0.001	0.753
EP × AP	3	0.025	0.076	0.009	0.381
EP × WP	3	0.004	0.755	0.002	0.899
AP × WP	1	0.003	0.327	<0.001	0.661
EP × AP × WP	3	0.008	0.529	0.002	0.896
Error	105	0.365		0.296	

The proportions were arcsine-transformed prior to analysis. SSQ III: sums of squares, type 3.
 $R^2 = 0.687$ respective 0.550 .

However, mines attacked by birds were also found in treatments where avian predators were excluded from branches by nets; this fraction was considered as background noise (probably caused by the uncertain differentiation of mines attacked by birds and of decomposed mines where leafminers emerged). Thus, we estimated an effective predation rate of about 2–3% (fig. 4, treatments where avian predators had access to branches in first and second generation minus treatments where birds were excluded from branches over both generations). However, neither the exclusion measures by nets nor glue rings significantly reduced the proportion of mines damaged otherwise. We measured a significant impact of the exclusion period on the rate of mines damaged otherwise (table 1). The rate of mines damaged otherwise on branches where wanderers were excluded in the first generation (0.014 ± 0.010 SD) was significantly lower than on branches where wandering arthropods were excluded in the second generation (0.025 ± 0.023 SD, Fisher's LSD: $P = 0.012$) or over both generations (0.029 ± 0.027 SD, LSD: $P = 0.002$), but only tentatively lower than on control branches (0.026 ± 0.038 SD, LSD: $P = 0.076$). This circumstance is hardly explicable and might be a statistical artefact of the unequal variances.

The investigation of density-dependent processes in avian predation showed that bird predation rates were positively correlated with defoliation at the branch level, but negatively at the tree level. A higher predation attributed to birds was found to be correlated with higher defoliation at the branch level and low defoliation at the tree level (table 2).

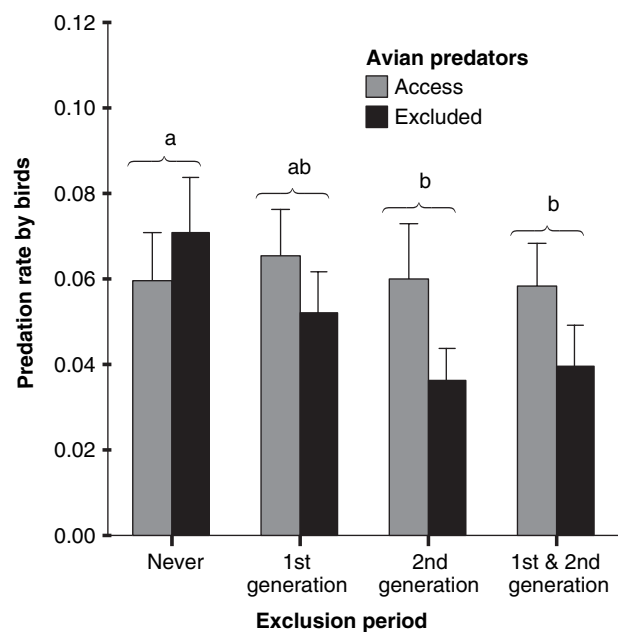


Fig. 4. Rate of attacked mines of *C. ohridella* by birds over the exclusion period. The four different exclusion periods were pair-wise compared by Fisher's Least Significant Difference (LSD) means separation test; exclusion periods with different letters are significantly different ($P < 0.05$). Error bars = 1 SE

Table 2. Multiple linear regression on the dependence of the predation rate by birds upon the defoliation of trees and branches; only treatments where no enclosure measures were set up were considered for analysis

Independent variable	Coefficient	Standard error (SE)	t-value	P
Constant	0.288	0.034	8.382	<0.001
Defoliation of tree	-0.521	0.175	-2.972	0.004
Defoliation of branch	0.399	0.147	2.710	0.008

All variables were arcsine-transformed prior to analysis.
Residual SE: 0.094 on 77 d.f., Multiple $R^2 = 0.103$, $F_{2,77} = 4.434$, $P = 0.015$.

5 Discussion

In general, leaf mining confers some protection against predator attack and it is supposed that mining larvae suffer much less from predation than exposed phytophagous larvae (ASKEW and SHAW, 1974). Therefore, parasitoids are considered as the most important natural enemies of leafminers. However, in the case of *C. ohridella*, parasitism is ineffective in reducing leafminer densities (GRABENWEGER, 2003; HEITLAND et al., 2003), which raises the question of the relevance of predators for population control.

The most exposed stage during a leafminer's development is undoubtedly the egg on the leaf surface. In fact, egg mortality in *C. ohridella* can be as high as 30% (GIRARDOZ et al., 2004) and at least part of this mortality might be caused by predators. However, the omnivorous predatory mite *E. finlandicus*, which occurs on various tree species including horse chestnuts (KROPCZYNSKA, 1970; SCHAUSBERGER, 1992; SCHAUSBERGER, personal communication), is probably no egg predator of *C. ohridella* since all specimens tested did not feed on a single egg, but rather died of starvation. Mites were never observed to interrupt prey searching when approaching leafminer eggs. It is therefore assumed that *E. finlandicus* is not able to detect the eggs of *C. ohridella* on horse chestnut leaves.

Despite one *Cameraria carnea* larva attacking a mine during observations in Bern, insects were never observed in the field preying upon mines, although their feeding traces were present at many sites investigated. In the case of the southern oak bush-cricket, *M. meridionale*, the reason was due to its nocturnal activity (TRÖGER, 1986). Thus, only the exposure experiment could reveal its distinct feeding of *C. ohridella* larvae. Although *M. meridionale* is well known for preying on aphids and other small tree-inhabiting insects (INGRISCH, 1976; DETZEL, 1998; TRÖGER, 1986), it seems to be extremely efficient at locating and preying on leafminer larvae. In our field experiment we probably even underestimated the impact of the bushcrickets for two reasons. First, the tested trees were frequently colonized by the highly mobile bushcrickets from the surrounding vegetation and some *M. meridionale* preyed on control leafminers before they could be removed. Second, some larvae escaped the direct predator attack but may have desiccated

without the protective mine-microhabitat later on. These cases were indistinguishable from 'dead' leafminers during analysis of the leaves.

Whereas there is doubt that the cocoon built by the spinning instars confers protection against parasitoids our results show that the cocoon successfully prevents leafminers from being preyed by insect predators. Spinning instars have neither been preyed on treated nor on control trees (fig. 3a) and *M. meridionale* obviously avoided to attack the cocoons. Leafminers hitherto have not been recorded as prey of *M. meridionale* or any other bushcricket. Since *M. meridionale* lives in tree species, which are often inhabited by other leafminers than *C. ohridella* (*Quercus* spp., *Betula* spp., DETZEL, 1998) we suspect it to prey on mining insects in general.

Besides *M. meridionale*, only ants consumed larvae of *C. ohridella* in our exposure experiments. Yet, *L. microcephalum* workers either seem not to be able to recognize this potential prey inside intact mines or fail in cutting through the silky tissue of the cocoon like the above-mentioned bushcricket. Correspondingly, on the tree with the ant colony, we did not observe increased, but even decreased predation rates on *C. ohridella*. Cautious interpretations are demanded by our small sample size, but we hypothesize, that the ants' presence may have caused this decrease in predation rates, most probably via a reduction in the number of other predators of *C. ohridella*. A similar effect was shown by JAMES et al. (1999). This may even have caused the stronger *C. ohridella* infestation of the ant tree. Our results are in contrast to an observed successful preying on *C. ohridella* by the ant *Crematogaster scutellaris* (RADEGHIERI, 2004), an increased survival of the larval stages of an oak leafminer due to the exclusion of ants (FAETH, 1980) and the traditional use of ants as pest control agents in various cultures (e.g. VAN MELE and CUC, 2000 and references therein).

In the course of this study it was impossible to test all potential predators found on *A. hippocastanum* trees. A quantitative assessment of the predator complex of an insect is methodologically demanding and therefore rarely described in literature (but see BACHER and LUDER, 2005). The simple identification of predation traces will always be related with uncertainty and consequently faultiness. There is evidence that several sac-spider species of the families Clubionidae, Anyphaenidae and Corinnidae are able to pierce holes into mines and prey on leafminer larvae, as observed on the citrus leafminer (AMALIN et al., 2001). Other potential predators of *C. ohridella* might be wasps and bugs. For example, workers of *Vespa crabro* have been observed foraging on infested horse chestnut leaves in Bulgaria (R. TOMOV, personal communication) and Hemiptera could pierce through the mine surface and suck on the larvae, a behaviour which is e.g. described for the mirid bug *Macrolophus caliginosus* on agromyzid leafminers (ARNO et al., 2003).

Our study indicated that birds might be more efficient predators of *C. ohridella* than most arthropods. Tits were frequently observed attacking *C. ohridella*, which corresponds with observations of ZEGULA et al. (2002). Although predation of birds was

significant, predation rates were too low to have an immediate impact on leafminer populations. However, due to the sampling of leaves at the end of the second leafminer generation, where the fraction of mines of the first leafminer generation was under 10% we almost certainly underestimated the impact of birds in the first *C. ohridella* generation. Other investigations indicated a predation rate of birds in the first leafminer generation of about 4% (Kehrli and Bacher, unpublished data). Overall, predation rates of birds seem to be of the same order of magnitude as published parasitism rates (HEITLAND et al., 2003; GRABENWEGER, 2003).

The investigation of density-dependent effects of the *C. ohridella* population on bird predation showed controversial results. Birds seemed to prefer searching for mines on trees that were only moderately defoliated by *C. ohridella*, but foraged on branches with higher mine density. Our data do not allow drawing any conclusions on density-dependent processes of avian predation in general and further research is needed to clarify this point. However, experiments in other pest systems suggest that at low prey population densities birds along with other enemies can keep prey abundances low (HOLMES et al., 1979; HOLMES, 1990; GUNNARSSON, 1996; TANHUANPÄÄ et al., 2001), which eventually can reduce plant damage (ALTEGRIM, 1989; MARQUIS and WHELAN, 1994; GREENBERG et al., 2000) and yield loss (MOLES and VISSER, 2002). We suspect that antagonists of *C. ohridella* fail to regulate this new prey/host due to its large reproductive potential (FREISE, 2001). Control of pest populations by natural enemies will ultimately depend on the recruitment of the *C. ohridella* relative to its antagonists (BERRYMAN, 1999). Thus, every effort should be made to keep *C. ohridella* populations in spring as low as possible by additional control measures like the consequent removal of leaf litter over the winter (DESCHKA, 1993; GRABENWEGER, 2001; GILBERT et al., 2003; KEHRLI and BACHER, 2003, 2004; PAVAN et al., 2003) and conservation of native parasitoids (KEHRLI et al., 2005).

Conservation or augmentation of native predators may contribute to an integrated control strategy against *C. ohridella*. However, our study demonstrated that only few of the predacious species that occur on *A. hippocastanum* trees actually include *C. ohridella* in their diet. Thus the mere presence of a generalist predator does not indicate a trophic relationship to the prey (SCHENK and BACHER, 2002). Out of all predacious arthropods tested, only *M. meridionale* was found accounting for a measurable impact on leafminer populations. However, its biocontrol value is questionable due to its generally low population densities on trees (INGRISCH and KÖHLER, 1998) and its polyphagous feeding behaviour. In addition, an artificial augmentation of *M. meridionale* may not be advisable because the bushcricket itself is slowly expanding its area from the South to the North of Europe (KALTENBACH, 1970; DETZEL, 1998; SCHLUMPRECHT and WAEBER, 2003) and may have an unforeseen ecological impact in the newly invaded regions. With the exception of the above-mentioned bushcricket, the whole class of arthropod predators seems to be of

minor importance compared to birds. The augmentation of tit densities might be more promising. First, we found indications that tits might show positive density dependent predation on *C. ohridella* larvae and second their high learning capability will presumably allow them to adapt faster to this new prey than predaceous arthropods and parasitoids. The conservation of tits, for example by providing additional nesting boxes or attraction by suet, could therefore be one component of an integrated control strategy against the horse chestnut leafminer in urban areas.

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