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Cameraria ohridella (Lepidoptera: Gracillariidae) Oviposition Preferences for Leaf Part and Sun Exposure

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Abstract: The horse-chestnut leaf miner has achieved the most spectacular invasion successes in Europe, which still holds many secrets and unsolved questions. The oviposition is especially important for insects whose larvae have very limited mobility. Therefore, this study aimed to test whether oviposition is conditioned by lighting and if the placement of the egg on the leaf determines the success. A sample of 200 horse-chestnut leaves was used, half from the sunny and the other from the shaded part of the crown, the eggs and mines were counted, and the location of the eggs on the leaves was determined. Three locations were distinguished: midrib, lateral vein and lamina. In total, just over 3,000 eggs were detected, with most eggs and mines found on sunlit leaves, on the lamina. As many as 90% of the eggs hatch into larvae inside the leaves, which initiate the development of mines. The most beneficial leaf part to lay eggs is near the midrib, but this place is chosen the least often. The question of why most eggs are laid on sunny leaves, even though the success and performance of the leaf miner is lower, remains unanswered.

Key words: *Aesculus hippocastanum* L., herbivore, horse-chestnut leaf miner, invasive insect, light conditions, plant-insect interactions

Introduction

The horse-chestnut leaf miner *Cameraria ohridella* Deschka & Dimic, 1986 (Lepidoptera: Gracillariidae), is a species that has spread in an extremely spectacular way throughout practically the entire European continent in just thirty years (Šefrová & Laštůvka 2001, Gilbert et al. 2004). Described in the Balkans in the mid-1980s (Deschka & Dimić 1986), in the first decade of the 21st century it was already found in Sweden, Lithuania, the British Isles and Ukraine (Augustin et al. 2009). Molecular studies based on herbarium materials confirmed the presence of the leaf miner in the Balkans at least a hundred years earlier (Lees et al. 2011). However, it had not previously shown such a tendency to expand. Many factors have been cited as contributing to this success: high fertility, multivoltinism, low pressure from natural enemies (Girardoz et al. 2007), high level of leaf acceptance (low selectivity) of females prior to egg-laying (Beguinot 2009), the occurrence of diapausing pupae in each generation (Samek

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2003), the widespread distribution of the main host – the horse chestnut tree *Aesculus hippocastanum* L. near roads and accidental spread through road transport (Šefrová & Laštůvka 2001). Natural populations of the chestnut tree occur only in a small area of the Balkan Peninsula and are in many cases limited to a few individuals (Thomas et al. 2019). However, since the seventeenth century, the horse-chestnut tree has been widely planted throughout almost all of Europe, as an ornamental park and avenue tree, and in forests as food for game (Bellini & Nin 2005). It copes well in all habitat conditions (in cities, along roads or in parks as a solitary species) and usually lives to the age of 150-200 years, and sometimes even more (Thomas et al. 2019). Even the mass occurrence of the leaf miner, which causes premature leaf fall, fortunately does not cause significant damage to the trees, only their thickness (Jagiełło et al. 2019c) or fruiting (Thalmann et al. 2003) is reduced. In the natural conditions in the Balkans, the leaf miner is not as abundant as outside the natural habitat of the horse chestnut tree (Kindl et al. 2002, Lees et al. 2011, Walas et al. 2018). Its maximum density, depending on the place of gradation, can reach the values: 48.9 mines per leaf (Percival et al. 2012), 80 mines per leaf (Grabenweger et al. 2005), 84.2 mines per leaf (Mesic et al. 2012), 106.5 mines per leaf (Ferracini & Alma 2008) or in terms of surface area 0.02mines/cm^2 (D'Costa et al. 2014), 0.2 mines/cm^2 (Jagiełło et al. 2019c). Such high densities result in high competition for food resources, especially in subsequent generations of the year.

The selection of a site for laying eggs for each folivore is a three-step process. The first step is to choose the host plant, the second is to choose the appropriate organ, in the case of the leaf miner it is a leaf, and to choose the appropriate location on the leaf. The site where the egg is laid is particularly important in endophytic species such as gallmakers or leaf miners whose larvae are unable to move to different leaves (Faeth 1990). In the case of the horse-chestnut leaf miner, which is a monophagous insect (Deschka 1993), the problem of host plant selection is well recognized. The only species in Europe that ensures safe development of larvae is *A. hippocastanum*, which is native to the Balkan Penisula and also grows as an urban tree, widely cultivated in parks and along streets. In the case of botanical gardens and arboreta, leaf miner eggs have also been found on the leaves of other species of the genus *Aesculus* (D'Costa et al. 2013), and also small numbers of them on the leaves of trees growing near chestnut trees, mainly on *Acer pseudoplatanus* L. (Péré et al. 2010) or *A. saccharinum* L. (Sinchuk et al. 2023). In most cases, the young larvae were unable to produce a mine, and even if they succeeded, the larvae quickly died (Péré et al. 2010) or they were smaller and had reduced fecundity (Walczak et al. 2017).

In the case of the horse-chestnut leaf miner, it seems that females, when faced with competition for food resources, tend to disperse the offspring survival risk rather than optimize the location of egg laying (Jagiełło et al. 2019b) which can also be evidenced by laying eggs on plants other than the main host plant. Thus, it can be safely stated that the issue of host plant selection by female leaf miners is quite well understood.

Jagiełło et al. (2019a) reported that under controlled conditions *A. hippocastanum* leaves that have grown in the shade provided better food for the developing horse-chestnut leaf miner larvae. The pupae gained greater weight and utilized food better, as evidenced by a higher food utilization rate. However, our preliminary observations in natural conditions and research of Bogoutdinova et al. (2023) indicated higher mine densities in the sunlight parts of the chestnut tree crowns. These observations and studies do not answer the question of whether conditions for mine development are more favorable in sunny places or whether more eggs are actually laid. This can only be achieved by counting the eggs laid by the female. The third step in selecting a place to lay eggs, i.e. the location on the leaf, has not yet been studied at all so far in the case of the horse-chestnut leaf miner.

The aim of the presented study was to determine whether oviposition on the leaf blade depends on leaf lighting and which site on the leaf is preferred by females. It was assumed that the preferred sites will be occupied first and there we will observe more mines in relation to the number of eggs laid. It was hypothesized that regardless of lighting, the proportions of eggs in individual sites on the leaf blade are similar.

Materials and methods

Material collecting

The research was conducted on a field alley near Kórnik, Poland (N 52° 14' 53.4, E 17° 7' 14.7) where there are several dozen horse chestnut trees about 40 years old. The trees grow on both sides of the road and their crowns touch, causing significant shading. The degree of light reduction on the inner side of the alley was confirmed on a cloudy day by the simultaneous measurements of photosynthetic active radiation (PAR). Inside the avenue PAR was 28,9 μmol of photons m^{-2} s^{-1} (SD = 11,1) and within

a nearby open area 461,1 μmol of photons m^{-2} s^{-1} (SD = 26,5). The Line Quantum Sensors (Apogee Inc.) were used to measure PAR.

Ten *A. hippocastanum* trees were selected for the study and 20 leaves were taken from each tree (10 from the sunlight and 10 from the shaded part). The leaves for analysis were collected from a height of 1.5-2.5 m in the first days of June 2016, when only mines and eggs of the first generation were present on the leaves. The middle leaflet from each compound leaf was taken for further analyses (eggs counting, leaf area measurement, etc.). The collected material was transported to the laboratory for detailed inspections and surface measurements. Using binoculars, we analyzed the placement of eggs and mines on the leaf blade and classified them into three categories: at the midrib, at the lateral vein, and on the lamina.

SLA measurement

The fresh middle leaflets from leaves were measured and analyzed using WinFoliaPro 2012 software (Regent Inc.). Then leaves were dried at 65°C for 3 days and weighed to calculate specific leaf area (SLA–leaf area/leaf dry mass). Because part of the leaf was already damaged by the horse chestnut leaf miner, SLA analysis was performed again for the undamaged parts of the leaves cut with a single hole punch. The results of correlation were very consistent (r^2 = 0.83; $p < 0.0001$).

Statistical analyses

Pearson correlation was used to assess the association between leaf area or SLA and number of eggs. Mixed-model analysis of variance followed by Tukey HSD test was used to determine the significance of the effect of light and position on the leaf (fixed factors) on the number of eggs and mine formation efficiency. Mine proportion data were transformed using the Bliss formula prior to analysis. Tree and leaf were treated as random factors. The Shapiro–Wilk test was conducted to test for normality and Levene's test to test for homogeneity of variance. The analysis was performed using JMP Pro 16.1.0 (SAS Institute Inc., Cary, NC, USA).

Results

A total of 3042 *Cameraria ohridella* eggs were found on two hundred collected leaves, the vast majority (2025 mines + 281 eggs) were found on the sunlight part of the tree crown. The rest (660 mines + 76 eggs) were in the shaded part. A maximum of 83 eggs were found on one leaf, and only one leaf had no eggs at all. The average number of eggs laid on a leaflet in the sunlit part is 23.1 eggs/leaflet, and in the shaded part it is 7.4 (Tab. 1). The leaf area from the sunlight and shaded parts of the crown did not differ significantly ($p = 0.3077$), but significant differences were found in the specific leaf area (SLA) ($F_{1,8.89} = 317.1$; $p < 0.0001$), which means that the sun-exposed leaves were thicker. The lack of differences in the size of the leaflet surface between the sunlit and shaded parts of the crown resulted in a significantly ($F_{1,8.99} = 102.5$; $p < 0.0001$) higher egg density on the sunlit leaves (Tab. 1). In the case of the sunlight part of the crown, the number of eggs was positively correlated with the leaf area ($r^2 = 0.499$; $p < 0.0001$) and negatively with the leaf SLA ($r^2 = 0.206$; $p < 0.0001$), whereas in the case of leaves in the shade, no such dependencies were found.

The analysis of egg distribution on the leaf showed a significant interaction (Tab. 2) between light condition and oviposition site (Fig. 1). The light treatments differed only in the number of eggs per lamina, where there were more of them in the sunlight part, while at the midrib and at the lateral veins the differences between the light treatments were small.

The vast majority of eggs (over 88%) developed mines. The reasons for the failure or delay of the remaining eggs to develop were not determined, but the proportion of mines to all eggs laid was shown to be similar on leaves from the sunlit and shaded parts ($F_{1,9.02}=1.0029$; $p=0.3427$). The development of the mine was assumed to be an indication that the female has selected a favorable site for oviposition. This is expressed as the ratio of the number of developed mines to all eggs laid. This ratio depended on both lighting and oviposition site, and there was also a significant interaction between these factors (Tab. 3). The highest mine development efficiency was demonstrated by oviposit at midrib, in both lighting treatments it was over 96% (Tab. 4), but there were the fewest eggs, only about 30 in each of the lighting treatments. When oviposition occurred near the lateral veins, mines developed the least frequently, but still, in both light variants, it was over 84%.

Discussion

The results of our study on the female's choice of a leaf on which to lay eggs confirm the results of Bogoutdinova et al. (2023), i.e. significantly more eggs were found on leaves from the sunlit part of the crown. This result is surprising, because the most frequently observed relationship in plant-insect interactions is greater damage to shaded leaves than

Table 1. Mean (SD) *Aesculus hippocastanum* leaflets area (cm^2), specific leaf area (SLA), mean number *Cameraria ohridella* eggs per leaflet and eggs density (No. eggs/cm^2) at shade and sunlight part of tree crown

Treatment	Mean leaflet area (cm^2)	SLA (cm^2/g)	Mean number eggs (incl. mines) per leaflet	Egg density (No. eggs/cm^2)
Shade	64,2 (17,7)	347,3 (60,7)	7,4 (4,1)	0,12 (0,07)
Sunlight	70,1 (29,0)	190,6 (56,9)	23,1 (16,6)	0.32 (0,14)

Table 2. Anova results for number of eggs oviposit at horse-chestnut leaves

Fixed factors	df	df (Error)	F	*p*
Light conditions (Lc)	1	9	40,66	0,0001
Oviposition place (Op)	2	18	85,34	<0,0001
Lc*Op	2	549	75,68	<0,0001
Random factors		**Variance components ratio**	**% variability**	**Wald *p***
Tree (T)		0,0129	1,22	0,66
T*Lc		0,0394	3,71	0,25
Leaflet (L)		0,0007	0,06	0,95
L*Op		0,0081	0,77	0,68
Residual			94,2	

df – degrees of freedom; df (Error) – degrees of freedom for error; F – ANOVA F coefficient; *p* – p-value.

Table 3. Anova results of mines proportion at horse-chestnut leaves

Fixed factors	df	df (Error)	F	*p*
Light conditions (Lc)	1	12,72	4,90	0,0458
Oviposition place (Op)	2	25,36	5,15	0,0133
Lc*Op	2	377,8	3,23	0,0405
Random factors		**Variance components ratio**	**% variability**	**Wald *p***
Tree (T)		-0,0253	0,00	0,4925
T*Lc		0,0804	7,39	0,1976
Leaflet (L)		0,0075	0,69	0,4891
L*Op		-0,0261	0,00	0,0400
Residual			91,92	

df – degrees of freedom; df (Error) – degrees of freedom for error; F – ANOVA F coefficient; *p* – p-value.

Table 4. Effectiveness of mine deployment

Light conditions	Oviposition place	Number of eggs	Number of mines	% of mines
Shade	Lamina	243	224	92,18
Shade	Lateral vein	466	410	87,98
Shade	Midrib	27	26	96,30
Total		**763**	**660**	
Sunlight	Lamina	1732	1540	88,91
Sunlight	Lateral vein	543	457	84,16
Sunlight	Midrib	31	28	90,32
Total		**2306**	**2025**	

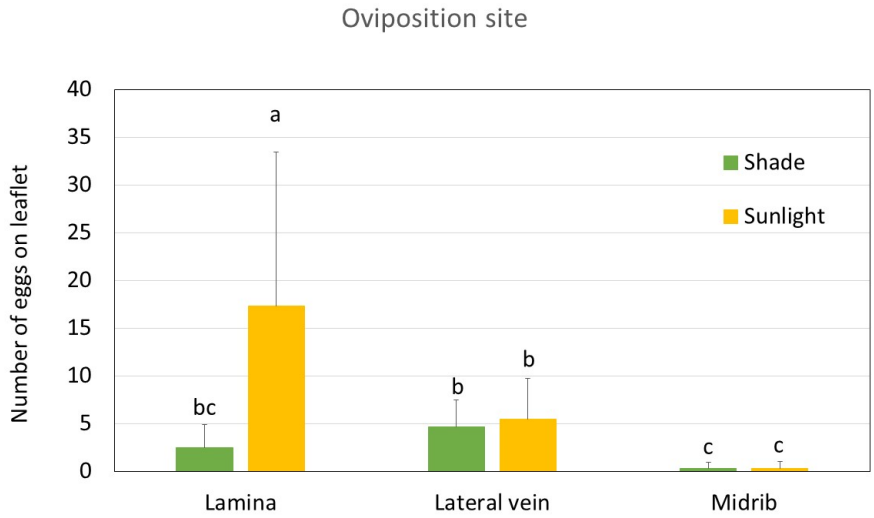

Fig. 1. Mean number of Cameraria ohridella eggs on the part of the horse chestnut leaves from sunny and shaded parts of the crown. Means with the same letter are not significantly different between treatments at the same time ($p < 0.05$ ANOVA followed by Tukey HSD test). The vertical lines represent ±1 standard deviations of the mean.

to sunlit ones (Roberts & Paul 2006, Karolewski et al. 2013). The subtle, but highly species-dependent, effect of shading on the density and mortality of mining insects was pointed out by Bultman and Faeth (1988). In the case of another *Cameraria* species feeding on *Quercus emoryi* Torr., significantly more mines were found on leaves from the shade (Faeth 1991). However, this is not an absolute relationship, as there are known species of insects that occur more frequently on sun-exposed leaves, an example of which is *Altica brevicollis* Foudras on the leaves of hazel *Corylus avellana* L. (Łukowski et al. 2015). The common preference of folivores for shaded leaves is most likely related, on the one hand, to the lower content of defensive substances in them (Hemming & Lindroth 1999, Henriksson et al. 2003), and on the other with a higher nitrogen content (Fortin & Mauffette 2002). The horse-chestnut leaf miner does not fit into these common trends and is less likely to inhabit shaded leaves, even though it grows larger there and utilizes food better (Jagiełło et al. 2018, Jagiełło et al. 2019a). It remains an open question why the leaf miner prefers to inhabit sunlit leaves. This may be due to the limited impact of oviposition-deterring pheromones. Such compounds have not yet been described in *C. ohridella*, but they occur in another mining insect, *Agromyza frontella* (Rondani) (Diptera) (McNickle & Evans 2018) and in several Lepidoptera species (Schoonhoven 1990). Higher temperatures can cause disruptions in pheromone communication (Sentis et al. 2015, Boullis et al. 2016), which may result in increased egg density per leaf surface.

The second theoretical factor, contributing to the increased number of eggs on sunlit leaves, is their greater abundance of food. Leaves exposed to sunlight have a greater thickness, which is documented by lower SLA values, which means that there is more food for developing larvae per unit area. However, leaf tissues exposed to the sun have more phenolic compounds, less nitrogen and water, and therefore constitute lower quality food (Karolewski et al. 2013, Uyi 2020). We do not know whether females, when choosing sun exposed leaves, do not pay attention to the quality of the food, but are guided only by its availability. However, previous studies have shown that although the female has the ability to recognize volatile substances released by the leaves (Johne et al. 2006), she does not avoid leaves showing symptoms of pathogen damage, but rather tries to maximize the chance of offspring by dispersing eggs over the available surface (Jagiełło et al. 2019b).

A separate issue is the third stage of selection, i.e. the location on the leaf where the egg was placed. In the case of the horse-chestnut leaf miner, they are found only on the upper (adaxial) leaf surface (Weryszko-Chmielewska & Haratym 2012). Eggs are laid near the veins (Jagiełło et al. 2019b) at the three distinguished locations on the leaf (midrib, lateral vein, lamina), the most frequently inhabited are the veins of higher orders, i.e. those at lamina, but only in the sunny part of the crown. It is interesting that the number of eggs at the midrib (approx. 30) and lateral veins (approx. 500) is similar in both lighting treatments. There are probably two reasons for oviposition near the veins. The first is related to

the improved camouflage on the veins, as opposed to the leaf blade. Egg size varied, with the average egg length and width being 416 x 300 μm (Weryszko-Chmielewska & Haratym 2012). They are almost transparent in the initial stage and camouflage better on the veins, which may protect them from predation (Guerra-Grenier 2019). The second reason is due to the fact that the early larval instars are sap-feeding (Šefrová & Skuhravý 2000, D'Costa et al. 2013) and young larvae can take this food directly from the veins. If we assume that mine formation is a manifestation of selecting an appropriate site for oviposition, then the best site is near the midrib (mine formation efficiency over 90% in both lighting treatments), but the question remains why only slightly over 20% of the midribs were inhabited and in only a few cases were several eggs found on one midrib. The lowest mine formation efficiency was observed with oviposition at the lateral veins and intermediate with eggs laid on the lamina, and these trends were similar both on the sunny and shaded parts of the crown.

Conclusion

Significantly more eggs of the horse chestnut leaf miner were found on sunlit leaves than on shaded ones. This predominance of sunlit leaves is due to the greater number of eggs laid on the lamina, as their numbers near the midrib and lateral veins were similar. Based on the ratio of eggs to mines, the midrib appears to be the most favorable site for egg-laying, as in both lighting conditions, over 90% of the eggs hatched into larvae that successfully developed mines. The reason for the preference for the lamina of sunlit leaves remains unknown, and the disruption of oviposition-marking pheromone communication by higher temperatures remains a hypothesis.

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