

Geometrical Games between a Host and a Parasitoid

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ABSTRACT: Avoiding detection by parasitoids is nearly impossible for most leafminers in their visually striking mines, and they often suffer from a high mortality rate by a great variety of parasitoid species. The leafminer-parasitoid interaction bears a strong resemblance to the princess-monster game developed in game theory, in which a "monster" (parasitoid) selects an optimal search strategy to capture the "princess" (leafminer), while the princess selects an optimal strategy to hide from the monster. This article attempts to illustrate and to quantify the additional complexity that occurs when the princess can modify the arena in which the monster searches. Feeding activity of the leafminer *Phyllonorycter mallela* creates feeding windows, which are spots on the mine. Its main parasitoid *Sympiesis sericeicornis* is able to insert its ovipositor only through these feeding windows. Parasitism risk depends both on the leafminer-feeding pattern, which determines the structure of the arena in which the parasitoid searches, and on the position of the leafminer within the mine. The adaptive value of observed patterns of mine development and leafminer behavior is evaluated by comparing them to predictions from a simulation model of random patterns and leafminer positions. The leafminer creates a heterogeneous environment by leaving a central area of uneaten tissue. This area acts as a protecting shield and greatly diminishes the risk of parasitism. Hence, by controlling the structure of the arena in which the princess-monster game is played, the leafminer defines some of the rules of the game.

Keywords: leafminer, risk of predation, feeding behavior, game theory, parasitoid, evasive behavior.

Predation risk is a major selection force determining the morphology, behavior, and life-history traits of prey (Vermeij 1982; Stearns 1992; Dill and Fraser 1996). On the part of the prey, the selective choice of a defense strategy

depends both on an estimation of the risk of predation and on the cost of possible defense mechanisms. The risk of predation increases during the sequence "detection-attack-fight-consumption" (Abrams 1986; Endler 1991; Malcom 1992). One may, therefore, expect prey species to have developed a whole battery of defense mechanisms in order to stop these interactions as soon as possible (Endler 1991).

Foraging can make an individual an easy target. Selection should be particularly strong in order to avoid detection while foraging and, thus, thwart predators early in the attack sequence. Theoretical and empirical studies have shown that foragers balance energy gains with predation risk when making behavioral decisions such as the timing of activities, the choice of patches and microhabitats, and locomotion distances (Millinski and Heller 1978; Werner et al. 1983; Lima et al. 1985; Abrahams and Dill 1989).

Among herbivorous insects, leafmining is a particularly risky foraging style. As a group, leafminers suffer from a high mortality rate, mainly due to parasitoids, which is often 80% or more (Hawkins et al. 1997). Parasitoids often detect deformation of leaves due to the mining activity while in flight (Sugimoto 1977; Casas 1989). It is, therefore, particularly difficult to escape detection, and so defenses must be mounted against direct attacks. For example, the tentiform leafminers of the genus *Phyllonorycter* (Lepidoptera: Gracillariidae) use the large volume of their mines to escape parasitoids (Meyhöfer et al. 1997).

The behavioral interaction between the apple tentiform leafminer *Phyllonorycter mallela* and one of its main parasitoids *Sympiesis sericeicornis* Nees (Hymenoptera: Eulophidae) has been studied in detail and can be summarized as follows (Meyhöfer et al. 1994, 1997; Bacher et al. 1996, 1997). Tissue-feeding larvae consume parenchyma tissue and the epidermis while leaving the cuticula intact, thereby creating visible spots or feeding windows on the lamina of the leaf (fig. 1). Larvae are either eating or resting when a parasitoid walks on their mine. When the parasitoid encounters a feeding window, it violently inserts its ovipositor. This insertion causes high-frequency vibrations that are perceived by the host, which in response stops feeding. Repeated insertions trigger the host to alternate between resting and moving and sometimes wriggling.

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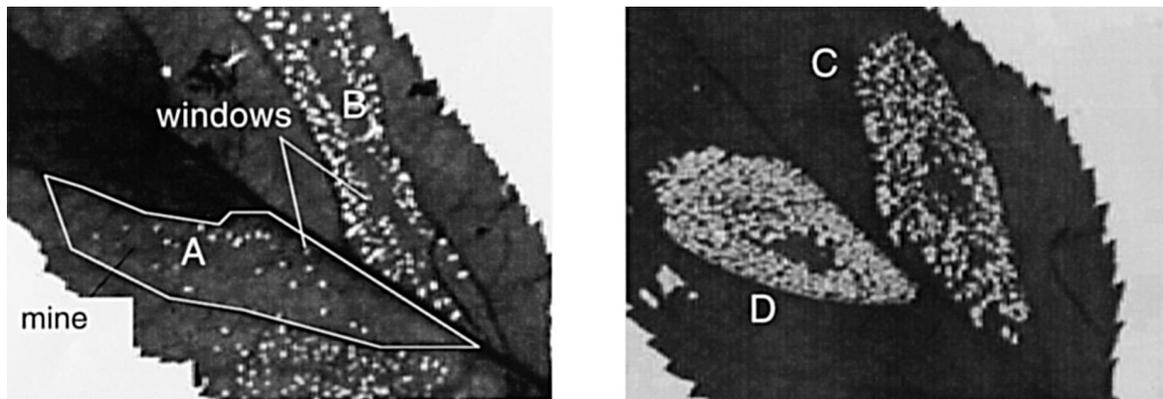


Figure 1: Different stages in the development of a mine. The outline of the mine (A) is in white. The white spots are feeding windows; the uneaten surface is in black. Mines A, B, C, and D have 6%, 50%, 65%, and 80% of surface eaten, respectively. The first three larval instars eat the spongy mesophyll tissue, constructing a more or less circular blotch mine. In the fourth and fifth instars, however, feeding is extended to the palisade tissue, and a layer of silk is spun over the lower mine surface. Contraction of the silk pulls the lower epidermis into folds and enlarges the cavity of a mine, giving it its characteristic tentiform appearance. The fully grown *Phyllonorycter* larva pupates inside its mine.

This hide-and-seek game can last up to 20 min and 200 unsuccessful attacks. Successful evasive behavior probably accounts for some of the cases (~15% of the time; Casas 1989) in which parasitoids abandon leaves containing unparasitized leafminers in the field.

The leafminer-parasitoid interaction described above is similar to the princess-monster game developed in search theory (Fitzgerald 1979; Lalley and Robbins 1988). The optimal strategies developed by the monster and the princess are to minimize and to maximize, respectively, the time to capture. Many parameters need to be taken into account, among others, the costs of searching and hiding and the geometry of the arena in which the game is played. The princess's strategy is to minimize the information available to the monster about her location in the arena by moving very quickly to different points chosen at random. Lalley and Robbins (1988) defined the monster's strategy as a set of trajectories that would lead to a uniform distribution of visited points over the arena. These points are chosen at random, thereby minimizing the information available to the princess about the threat of immediate attack.

In both the theoretical model and in the biological system, capture is certain to occur if the game runs long enough. Hence, the only chance of survival for the host is when the time of capture exceeds the parasitoid giving-up time. The giving-up time is determined by several factors internal to the parasitoid (such as egg load and past experience) and external (such as the quality of other hosts; Godfray 1994). For the host, freezing and waiting is not a good strategy, as the parasitoid uses a pseudosystematic search and covers most of the surface during a searching

bout (Casas 1988; Meyhöfer et al. 1997). Hence, the larva has to move. Where it should move can only be understood by investigating the pattern of potential hiding spots and how this pattern changes with leafminer feeding.

The interaction between the leafminer and its parasitoid is more complex than the pure princess-monster game because the arena is structured by the mining activity. This article attempts to illustrate and to quantify the additional complexity when the princess-monster game is played. Given the number of factors determining the risk of parasitism, we focus here on the geometrical aspects of the interaction: the mine construction by *P. malella* and its use in terms of risk of parasitism by *S. sericeicornis*. In this leafminer system, the host can be parasitized only when it lies under or is adjacent to a feeding window. Therefore, the distribution of the feeding windows and the location of the host are important factors in determining the risk of parasitism. Furthermore, during a parasitoid's searching bout on a leaf, the larva changes behavior and location only after perceiving the first insertion of the ovipositor. As leafminers can be killed during the first insertion of the ovipositor, we analyze the position of the larva and the window pattern in the absence of parasitoid in order to determine the strategy of larvae to avoid parasitism (see Meyhöfer et al. 1997). The focus of this article is on the spatial distribution of larvae and windows, so we do not consider the added component of the sequential movement of the larvae. Thus, we focus here on the influence of the geometry of the arena on the princess-monster game rather than on the dynamical aspects of the pursuit. First, we quantify the actual pattern of mine development and

the location of the larva in the mine from observation. The adaptive value of the observed pattern of mine development and larval behavior is then evaluated by comparing it to a simulation model of random mine development and larval behavior.

Material and Methods

Description of the System

Phyllonorycter mallela (species group *blancardella*) is a polyvoltine leafmining microlepidopteran. A detailed description of the biology of a closely related host species *Phyllonorycter blancardella* is given in Pottinger and LeRoux (1971). The larval development is divided into five instars. The first three larval instars are sap feeders. They set the outline of the mine and, therefore, the total surface available to later stages.

Feeding by instars four and five creates "feeding windows" in the upper epidermis of leaves. A young fourth instar larva (L_4) creates a new feeding window every time it eats. Later, enlarged windows are created as a result of the superposition of feeding events. Windows start merging when about 20% of the leaf epidermis has been removed, leading to a decline in the number of windows. Most, and sometimes all, of the tissue is eaten up at the end of the larval development. The percentage of epidermal tissue eaten is a convenient measure of the development of the pattern of feeding windows, as the total area of a mine fluctuates from leaf to leaf and mine to mine.

Sympiesis sericeicornis is a bivoltine polyphagous ectoparasitoid attacking leafminers from several insect orders in deciduous trees. *Sympiesis sericeicornis* is one of the most important species attacking *Phyllonorycter* species on apple trees (Askew and Shaw 1974). It oviposits on tissue-feeding larvae as well as on pupae. It does not search for sap feeders but may use them for host feeding after fortuitous encounters (Casas 1989).

Behavioral Analysis of the Parasitoid

We conducted observations of *S. sericeicornis* foraging for *Phyllonorycter* larvae in mines in apple leaves using a video system (recorder: Panasonic AG-7355, camera: Panasonic WV-BL600 equipped with Computar 18-108/205 lens). Only mines with L_4 and L_5 larval instars (tissue feeders) were used for the observations and the leaves contained only a single mine. Each leaf was cut off the plant and the stem was placed in a small glass filled with water inside a glass observation box (17 cm × 11 cm × 10 cm). The lower epidermis of the mined area was replaced by a clear piece of plastic attached to the leaf with Pritt-strick glue. A mirror placed under the leaf allowed us to record both

sides of the leaf on the same video frame. The leaves were prepared 4 h before the beginning of the observation. Preliminary experiments indicated that this experimental setup did not alter the behavior of the leafminers.

Only experienced female parasitoids were used for the observations to avoid learning. Females were kept individually in containers with unmined seedlings for 4 h before the beginning of the experiment in order to increase the likelihood of oviposition. After being introduced into the observation box, the parasitoid reached the mined leaf within a few minutes.

The parasitoid inserted the ovipositor several times while tracking the larva inside its mine. We distinguished insertions when the distance between the host and the parasitoid was within the reach of the ovipositor (the ovipositor length being approximately half the length of the parasitoid body) and insertions when the host was further away. Only the former are considered as potential attacks. We recorded the width and length of the larvae, its position, and the percentage of the larva's body under feeding windows at the start of the observations.

The behavioral observations started when the parasitoid began to walk on the mine and ended with the departure from the mine. Thirty-five sequences of 35 different mines and 35 different wasps were recorded. All observation resulted in true oviposition.

Mine Development

To determine the development of feeding windows over the course of mine construction, 11 mines were continuously recorded over 2 d using a digital (CCD) video camera (DALSA CA-D1). Therefore, for each of the 11 mines, every feeding event was recorded (location and time) during a period of 2 d. The mines on the first day generally had only a few windows.

Mines were lighted from below to increase contrast. All images were analyzed using NIH Image (version 1.61, National Institutes of Health). Those recorded during the behavioral observations were first drawn on a transparency by hand and then digitized using a scanner. Those obtained with the digital camera were imported directly. Each image was partitioned into the mine and the background on the basis of gray levels. The surface of all intact tissues was recorded. The eaten area is the total surface of the feeding windows. The total area of the mine is the sum of both surfaces.

Modeling Mine Development

Here, we develop a model that simulates the development of mines by randomly constructing windows. The resulting predicted pattern will serve as a null hypothesis to deter-

mine whether observed patterns of mine development offer significantly better protection of the leafminer from parasitoid attack.

To simulate random mine construction, we used the area of the mine, the choice of the location of individual feeding events, and the superposition of feeding windows. We assumed that each successive feeding event created identical circular windows. Their radii are given by the observed distribution. The location of each window was determined by randomly selecting a point on the leaf surface as the center of the feeding window. Epidermal tissue from the simulated leaf was then removed. As the simulations proceeded, new windows often overlapped previous ones, resulting in less tissue removed. If a new window was added to an area that was previously completely covered by windows, the new window was discarded and was not considered in the total number of windows making up the mine.

We compared the predicted patterns from the random feeding model with observed patterns of one single mine recorded over 2 d. We focused on two periods of mine development, early (between windows 8 and 23) and late (between windows 51 and 64). As the starting point of the simulations, we used the observed locations of windows 8 and 51. To determine whether the observed pattern of mine development differed from those produced by the simulation model, we used Monte Carlo techniques. We simulated mine construction 99 times, allowing us to detect differences at the conservative significance level of $P = .05$, using the rank of the observed statistic within the simulated values (see Ripley 1981; Diggle 1983; Cressie 1991). Every simulation required the repeated handling matrices of 17,000 pixels. Furthermore, we carried out an additional analysis on 10 additional mines to corroborate the results obtained with the Monte Carlo tests. These tests are described in the "Results" section. We used two statistics to quantify patterns of mine development: the spatiotemporal correlation of two successive feeding events and the distance between a feeding event and the mine border.

Development over the Lifetime of a Mine

To investigate the development of mines over their entire lifetime, we created random feeding patterns by running the random feeding model as described above for 20 simulated mines from 0% to 67% consumed tissues. Feeding patterns were analyzed after 20, 100, and 200 events and every 200 events thereafter. Simulations were finished once 1,800 feeding events were simulated, which corresponded to roughly 67% of consumption. To characterize the development of the pattern, we used the area of the largest

connected piece of uneaten tissue relative to the total area of uneaten tissue.

Space Use of the Leafminers within Mines

To investigate the position of the host relative to the spatio-temporal pattern of window creation, we used a simulation model to determine whether observed larval leafminer position offered significantly better protection from parasitoid attack than random locations within the mines. We simulated and compared three situations: random larval positions on random window patterns, random larval positions on observed window patterns, and observed larval positions on observed window patterns. Differences in the risk of parasitism between the first and second cases are due to the spatiotemporal feeding pattern itself. Differences between the second and third cases are due to the location of the larva given the observed mine structure.

To simulate random patterns, the development of 20 mines was simulated exactly as above. For each mine, the pattern was stored at 20, 100, and 200 feeding events and every 200 events thereafter, up to 1,800 events. For testing the random larval positions on observed window patterns, we used the 35 observed window patterns recorded during the parasitoid observations as imported images. To test the observed positions of larva on the observed windows patterns, we used the 35 mines and their respective larval positions at the start of the parasitoid observations.

Larvae were simulated as rectangles, using observed widths and lengths. Thus, the relative sizes of the larva and pattern were kept as observed for each mine and larva. The latter was not allowed to grow between events. The first point of the rectangle was chosen at random from the surface of the simulated leaf, and then the orientation of the rectangle was selected at random. The portion of the larva exposed under the feeding windows was then calculated. One hundred larvae were placed at random on every mine pattern, and the mean percentage of larva's body exposed was calculated. This mean was for a given mine with a given number of feeding events (i.e., 20, 100, and 200, up to 1,800). A global mean for a given number of feeding event was obtained by averaging over the 20 simulated mines.

Results

Behavioral Analysis of the Parasitoid

We conducted analysis observations of the parasitoid's attack behavior on the surface of the leaf. The parasitoid inserted the ovipositor several times while tracking the larva inside the mine. Ovipositor insertions were done almost exclusively in the feeding windows (homogeneity

test on 30 females at $\alpha = 0.05$, followed by a χ^2 test on a total of 435 insertions in windows and 13 insertions in unidentified locations, $\chi^2 = 377$, $P = .001$).

To determine the effect of mine area on the leafminer's risk of attack, we measured the time between the parasitoid's arrival and the first potential parasitism event. We concentrated on the time of the first potential parasitism event because the risk of parasitism after the first event is difficult to interpret due to the agitated movement of the host and the reactions of the parasitoid.

The larger the size of the eaten area, the shorter the time between arrival on the mine and the first potential attack (fig. 2A; $\ln(y) = 5.7 - 0.03x$, $t = -4.98$, $df = 34$, $P < .001$ for the slope). The same results applied to the number of ovipositor insertions from arrival on the mine and first potential hit (fig. 2B; $\ln(y) = 2.7 - 0.01x$, $t = -2.13$, $df = 34$, $P = .04$ for the slope).

Mine Development

Two statistics were used for testing in order to find out if the geometry of real mines differ from these predicted by the random simulation model. These statistics were applied on patterns in 11 mines (see "Material and Methods"). For the first statistic, we calculated the distance between the center of two successive feeding windows. This statistic gave an indication of the spatial correlation between successive windows. For each of the 99 simulations, the mean value of distances between the center of two successive windows was calculated for early and late mine development (15 and 13 events, respectively). The rank of the observed mean distance was well within the distribution of simulated ones for both early and late development (early: $\bar{X} = 16.7$ mm, rank 59; late: $\bar{X} = 14.1$ mm, rank 28). Thus, there was no spatial correlation between successive feeding windows.

The second statistic was the distance between the center of the window and the nearest point on the border of the mine. This statistic captures the apparent concentration of unfed tissues in the center of the mine (fig. 1). The observed mean distances to the mine's border were markedly different from those predicted by the random model. For early development, the observed mean distance (4.6 mm) was greater than any distance predicted by the model ($P < .05$ using ranks). Therefore, feeding events were concentrated in the interior region of the mine. The difference between observed and predicted distances was reversed later in the mine development. The observed mean distance (1.45 mm) was shorter than all but two of those predicted by the model ($P < .05$ using ranks). The mean distance decreased threefold over 2 d, and feeding events were located at the periphery of the mine in the second day. Overall, the pure random model was clearly rejected.

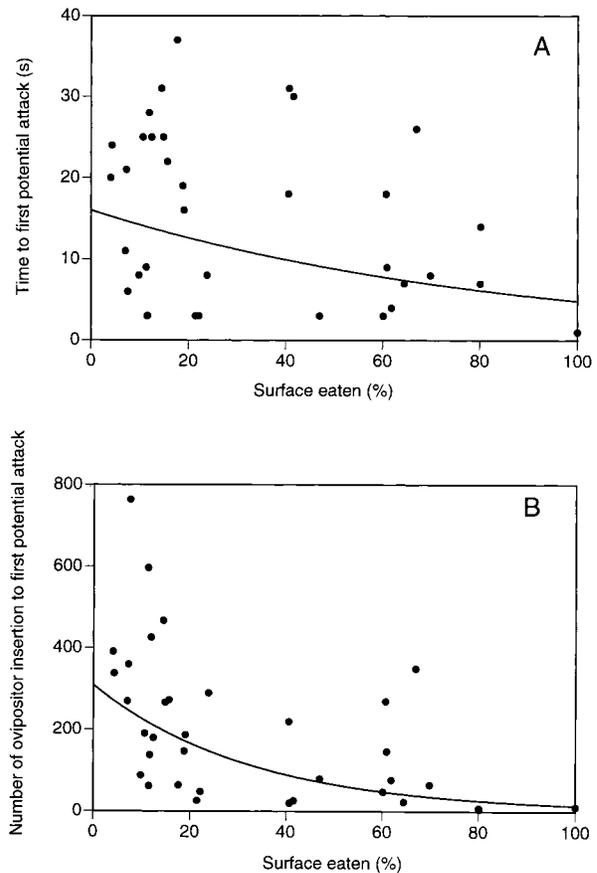


Figure 2: A, Time spent (in seconds). B, Number of insertions far from the host by the parasitoid from arrival on the mine to the first insertion of the ovipositor near the larva as a function of the surface eaten. The increase of the size of the surface eaten diminishes both the time spent to locate the larva by the parasitoid and the number of oviposition until the first attack.

These Monte Carlo tests were performed on early and late development of a single mine due to the huge computational burden involved. In order to check whether the observed patterns were representative of the population of patterns, the other 10 mines (see "Material and Methods") were analyzed using the simpler procedure. We first tested to find out whether the distribution of distances between feeding events on the two patterns from the mine analyzed in full was different from those calculated on the other 10 mines. We pooled the data of the 10 mines, each one being continuously recorded over a 2-d period (the early and the late development). We checked for homogeneity between early patterns (Kruskal-Wallis test: $\chi^2 = 8.81$, $df = 9$, $P = .45$) and late patterns (Kruskal-Wallis test: $\chi^2 = 16.27$, $df = 9$, $P = .06$). The single mine was not different from the 10-mines population either early (Kol-

gomorov-Smirnov test: $n_1 = 14$, $n_2 = 118$, $K_s = 0.33$, $P = .0973$) or late (Kolgomorov-Smirnov test: $n_1 = 13$, $n_2 = 132$, $K_s = 0.27$, $P = .36$).

We then tested to see whether the distribution of distances between the feeding events and the border of the mine were different for the single versus the pool of 10 mines. For this purpose we first filtered out the compounding effect of the total area of the mine, which differs from mine to mine. We used the difference between the mean distance to the border on the first day and the mean distance to the border on the second day. The value for the mine analyzed in full was well within the distribution of the 10-mines population (mean for the single mine: 1.45 mm, rank 7). Thus, we concluded that the single mine was not a particular case, and we can, thus, safely extend the conclusions from the Monte Carlo analysis to the population of mines in general.

To summarize, mines are not produced by the successive random location of windows. Larvae start producing small windows from the middle and then move outward, leaving the center of the mine intact. As a result, the real mines showed a large portion of tissue left intact in one piece during most of the mine's lifetime (fig. 3), while the simulated ones consisted of many small windows spread throughout the mine.

Space Use of Leafminers within Mines

To investigate the use of the mine by the leafminer, we simulated and compared three situations: random larval positions on random window patterns (fig. 4A), random larval positions on observed patterns (fig. 4B), and ob-

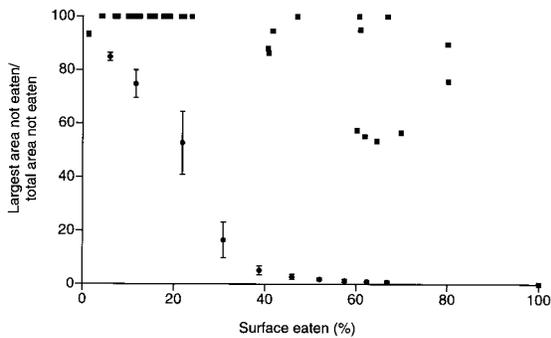


Figure 3: Percentage of uneaten tissues making up the largest connected island as a function of the surface eaten. *Squares:* observed mines; *Dots:* random patterns. Mines are not produced by the successive random location of windows. Larvae start producing small windows from the middle and then move outward, leaving the center of the mine intact. As a result, the real mines show a large portion of tissue left intact in one piece during most of the mine's lifetime, while the simulated ones consisted of many small windows spread throughout the mine.

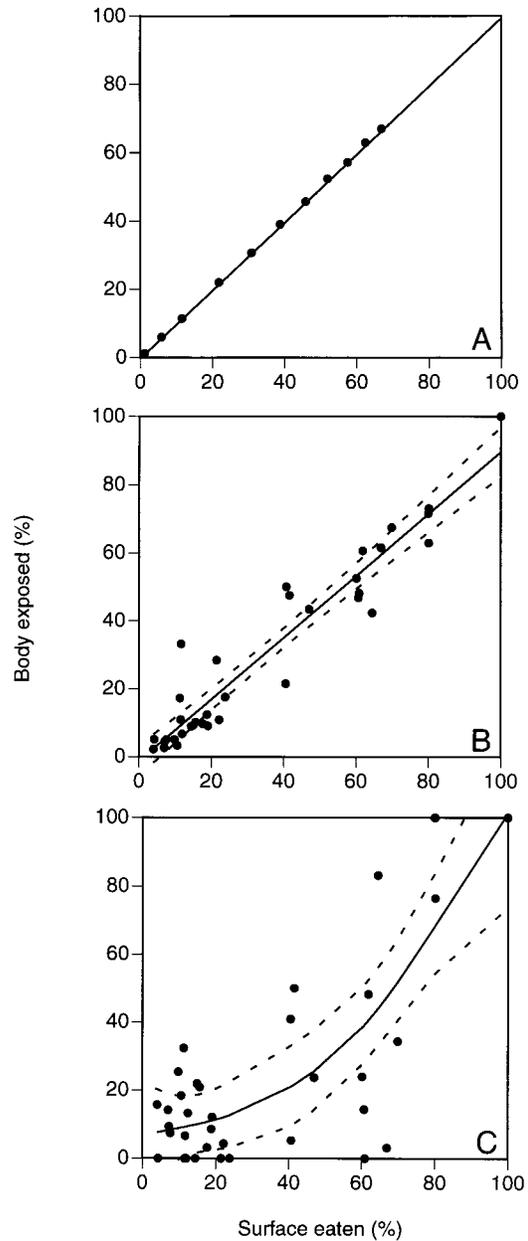


Figure 4: Proportion of body exposed (percentage under the feeding windows) as function of the surface eaten, window pattern, and larval position. *A*, Random simulations of larval position on random windows patterns. *B*, Random simulations of larval position on observed windows patterns. *C*, Observed larval positions on observed windows patterns. This analysis distinguishes between the effects of building a pattern against parasitism and the use of it. The use of space within the mine is as important as the construction itself. The spline algorithm, with B-splines as basis functions, uses cross validation. The upper and lower variability bands correspond approximately to 95% confidence intervals.

served larval positions on observed patterns during an attack (fig. 4C). Hence, our analyses distinguished between the effects of building a pattern against parasitism and the use of it.

We define parasitism risk as the portion of the larva exposed under feeding windows (fig. 4). Parasitism risk was highest when the larva was randomly located on a random window pattern (fig. 4A). In comparison, randomly located larvae in an observed mine reduced parasitism risk only marginally, as the larva did not preferentially use the central piece of uneaten tissue (fig. 4B). A much larger decrease in parasitism risk occurred when larvae occupied the observed positions in mines with observed patterns of windows because, in this case, larvae were preferentially under cover (fig. 4C). To test these results statistically, we carried out an analysis using spline regression (Hastie and Tishirbani 1990; Bowman and Azlani 1997). If one considers the region between 20% and 80%, which is the only region in which the larva can adopt different strategies, the difference between expected values given by the random position model and observed values is important (up to 20%).

A consideration of the variances in the risk of parasitism highlights other aspects of the different strategies. The difference in risk for a larva positioned at random on a random window pattern (fig. 5A) and on an observed window pattern (fig. 5B) was due to the much wider range of possibilities offered by the observed window pattern. When the uneaten surface was large, the larva could hide totally under both the random and the observed patterns. However, when 20% of the surface was eaten, the larva had no place to hide completely when the windows were randomly placed in the mine. In contrast, there were still places to hide under the observed pattern even when over 60% of the mine was covered by windows.

Discussion

We know very little about the behavioral defenses by which hosts avoid parasitism (Malcom 1992; Gross 1993; Hochberg 1997). As these authors stress, all that we do know is a qualitative nature. This strongly contrasts with the vigorous research programs focused on the defenses against parasitoids in the last step of the interaction, such as encapsulation (Carton and Nappi 1997; Kraaijeveld and Godfray 1997; Kraaijeveld et al. 1998). However, if encapsulation is under strong selection pressure, the defensive strategies earlier in parasitoid-host interaction should be under an even stronger pressure. Our study documents a host-behavioral pattern—constructing mines with protected refuges—which greatly reduces the risk of parasitism and, therefore, is likely to be the product of strong natural selection.

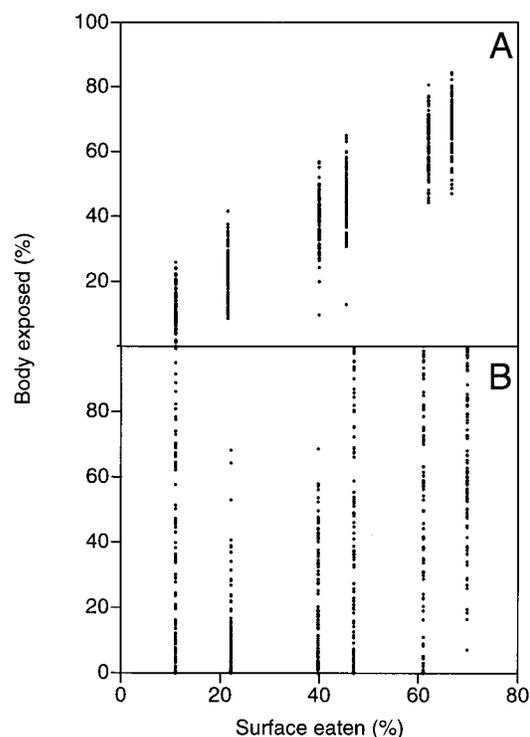


Figure 5: Percentage of exposed body as function of the surface eaten for random positions of the larva on random windows patterns (A) and observed window patterns (B). Observed patterns increase both the probabilities of hiding and of being hit.

Building and Using a Tentiform Mine

During feeding, the construction of windows is unavoidable, and these feeding windows increase the risk of parasitism for two reasons. First, strong visual contrast with uneaten tissue as well as locally produced semiochemicals may give cues to parasitoids about the location of the larva. Second, feeding windows are the locations through which *Sympiesis* inserts its ovipositor. These risks can be mitigated by two behaviors of the host. First, a feeding event lasts only a few minutes, after which the larva moves away to a next feeding spot or rests. Therefore, fresh feeding windows do not necessarily contain larvae, which the parasitoid can attack. Second, the lack of spatial correlation between locations of consecutive feeding windows minimizes the information given away to the parasitoid. If a parasitoid finds a window created very recently, the next one may be located at any distance on the mine surface. With up to 250 windows on a mine, locating the host is not an easy task!

If leafminer larva produced a random pattern of windows in a mine, there would be no particular place to hide. Instead, the larvae leave a central area of the mine

free of feeding windows, and then they use this as a protected refuge against parasitism. A marked decrease in the risk of parasitism is observed, and we, therefore, conclude that the larva is aware of its position relative to the mine's geometry. If we consider the variance of the risk, it shows clearly that a random location on an observed pattern is a self-defeating strategy; a larva can be fully at risk when the eaten surface is as low as 10%. Hence, exploiting the created pattern to its full benefit is of utmost importance. In conclusion, the use of space within the mine is as important as the construction itself in determining the risk of parasitism.

Princess-Monster Games in a Heterogeneous Environment

In the princess-monster game theory, the homogeneity of the arena is a key element. For the princess, it implies that there is no refuge in which to hide. Thus, with all positions being equally at risk, the princess chooses the nearest location at random, thereby minimizing the information given away to the monster. The same applies to the monster who moves at random in order to give as little information as possible to the princess.

Phyllonorycter malella creates a highly heterogeneous environment by designing the arena through the nonrandom location of feeding windows over the mine surface. Using the created heterogeneity to rest preferentially under cover further reduces the risk of parasitism. Thus, both the heterogeneity of the arena and the nonrandom position of the host concur to produce a nonuniform distribution of resting positions. This distribution is set irrespective of the location and behavior of the parasitoid. However, the host's use of preferential places to hide could favor preferential search by the parasitoid. Thus, a full analysis of the princess-monster game would require consideration of the position of both the host and the parasitoid. Information is also required as to the positions of both protagonists relative to the feeding pattern. Further studies should focus first on the choice of the feeding window by the parasitoid. Then, using parasitoid with known egg load, it should be possible to distinguish the relative contribution of the mine construction, the use of the habitat by the host, and the giving-up time of the parasitoid to the risk of parasitism.

Many other prey-predator and host-parasitoid interactions are characterized by a strong geometrical component coupled with probabilistic rules. Among host-parasitoid systems, comparative study of feeding strategies could give clues as to the genesis of the surprisingly high diversity of mine forms (Hering 1951). For example, our results indicate that leafminers creating linear and serpentine mines would be particularly under risk, as their movements are extremely limited. This is supported by the work

of Sugimoto (1977), who showed that the parasitoid *Kratochviliana* sp. attacking the serpentine leafminer *Phytomyza ranunculi* uses the increasing width of the mine constructed by the growing larva to move in the right direction along the mine to find the larva. The counterstrategies of the host may be the numerous self-crossings typical of this type of mine, since self-crossing makes the parasitoid likely to lose the direction of the mine (Kato 1985). Among prey-predator systems, prey escaping predators by fleeing under cover (Blumstein 1998) or hiding in crevices (Cooper et al. 1999) are good examples of other princess-monster games in heterogeneous environments. The approach taken here can be extended easily to these situations and also enables quantitative ranking of predation risks given by different escape strategies.

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