

## Research Article

# Would Mothers Relax Their Degree of Selectivity for Supports Suitable for Egg-Laying When the Local Density of Conspecific Females Increases? A Case Study with Three Common Lepidopteran Leaf Miners

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Selecting suitable supports for egg-laying, among host species and host individuals, as well as between leaves of various qualities within a preferred host, is a major component of prehatching maternal care in herbivore insects. This feature is especially important for those species having a tightly concealed larval stage, such as leaf miners. Yet, increasing density of neighbouring conspecific females may possibly induce ovipositing mothers to relax their degree of selectivity, so as to distribute their eggs more evenly among host leaves and reduce the risk of future scramble competition between larvae within a same leaf. We test this hypothetical prediction for three common leaf-mining moths: *Phyllonorycter maestingella*, *Phyllonorycter esperella*, and *Tischeria ekebladella*. The prediction was supported by none of the three tested species. This suggests that, in these tiny insect species, mothers are either unable to account for the local density of neighbouring conspecific females and/or they have no effective motivation to react accordingly. In addition, this also suggests that host individuals differing by the average quality of their leaves yet exert no differentiated attractivity towards mothers at a distance. In turn, this emphasizes the role of contingent factors in the patterns of spatial distribution of insects' densities.

## 1. Introduction

Prehatching maternal care is common place among herbivore insects since, usually, the larval stage is hardly mobile and the diet of larvae is often limited to a rather narrow range of host plants [1, 2]. Accordingly, ovipositing mothers ordinarily share the entire and double responsibility of (i) making available the best resource for offspring by *selecting appropriately the supports to be egg-laid* and (ii) preventing the risk of scramble competition within the brood by *limiting the size of egg clutch*. This stands all the more strictly for those insects with larval stage tightly concealed within a narrow part of the host plant, such as *mine-forming* insects [3].

For mothers, in leaf-mining species, the selection of supports to be egg-laid consists not only in reaching the proper host species but, further on, by selecting the most appropriate host individuals and, eventually, the more promising

subsets of host leaves that will thus satisfy at best the minimum requirements of mothers after careful probing. The later selective choice is often decisive since leaf quality may vary at least as much within individual hosts than between them [4–9].

In quantitative term, let “ $\alpha$ ” be the proportion of host leaves that, being probed, would positively answer the level of quality required by egg-laying mothers, that is, the “leaf-acceptance ratio.” Then, whether being accepted, the positively probed leaf is egg-laid. Let “ $n_c$ ” be the size of the deposited egg clutch (or, hereafter, the number of monooccupied mines resulting from the hatching of a clutch of eggs: the “mines-clutch size”).

Such a “prehatching maternal care”, involving constraining limitations upon both the leaf-acceptance ratio “ $\alpha$ ” and the clutch-size “ $n_c$ ,” is real mother investment since both limitations contribute to slow down the progress of

oviposition, which, in turn, may become a serious constraint upon mothers, in a context of limited time expenditure [10].

Moreover, the cooccurrence of conspecific ovipositing females in the immediate vicinity may likely exerts a supplementary constraint on mothers, as far as this cooccurrence is acknowledged by them [11, 12]. In order to prevent the increased risk of future scramble competition between larvae, mothers may then be induced to decrease further (if possible) the clutch-size " $n_c$ " and also somewhat relax the severity of leaf-selection (increasing the leaf-acceptance " $\alpha$ ").

Such supplementary tuning of mothers' behaviour, as an answer to the hypothetical perception of the concurrence from conspecific females, may have obvious implications in terms of density-dependent source of regulation of insects' populations.

At first, it should be noticed that, most often, the densities of leaf miners, in field conditions, are low enough for the risk of scramble competition being quite limited [13–15]. However, in yet nonexceptional circumstances, the proportion of host leaves supporting more than one mine may become significant and the resulting cooccurrence has been reported detrimental for the development and survival of progeny [14, 16].

Now, the cooccurrence of conspecifics can be mediated several ways, in particular via the frequencies of mother's encounters with either previously deposited eggs or with other conspecific mothers also present within the host canopy (without prejudice, in addition, of possible indirect mediations by the host plant or by shared natural enemies: [17]).

In tiny insects such as leaf miners, it is commonly considered that mother would generally *not* recognise previous egg deposits [9, 13–15, 18–25]. Yet, this point, that is, the insensitivity of mothers to conspecifics' eggs density, was positively rechecked for each sample considered in this study, by controlling the variance to the mean ratio to be always  $>1$ .

This, however, does not rule out the second alternative, that is, mothers' sensitivity to the local density of conspecifics. Although being unable to recognise the presence of minute eggs deposits on leaves, mothers might, yet, be able to more easily recognise the presence of conspecific females in their neighbourhood and might be sensitive to their relative density in the patch of host leaves. Thus, when mothers' densities are not too low, the perception of conspecifics seems not unlikely *a priori* and the possible resulting reaction of mothers, in terms of reducing either their degree of selectivity among host leaves or their clutch size (or both) ought to be considered and tested.

We address this issue, considering three moth species (*Phyllonorycter maestingella*, *Phyllonorycter esperella*, and *Tischeria ekebladella*) mining, respectively, three major European host-tree species (beech, hornbeam, and oak, resp.). For each moth species, several sites (from 6 to 22) were selected in consideration of their relatively high (while noneruptive) average numbers of mines per leaf, the latter varying in a range sufficiently large to test efficiently for the possible influence of the density of neighbouring conspecific females. As the average value of clutch size in leaf-mining insects is ordinarily close to unity; this parameter offers only a tenuous

opportunity for further reduction under the hypothetical influence of neighbouring conspecifics. Therefore, we focus specifically upon the possible positive answer of the leaf-acceptance ratio " $\alpha$ " to the local density of conspecific females. The rationale behind such an answer is that increasing the leaf-acceptance ratio would proportionally reduce the average eggs' density per leaf, so that mothers may be induced to relax the severity of leaf selection prior to egg laying as a response to increasing density of conspecific females around. In the same perspective, we test whether local density of mothers correlate, with average habitat quality or not.

## 2. Methods

*2.1. Estimation of the Quantitative Traits of Egg-Laying Behaviour:  $\alpha$ ,  $n_c$ , and  $\mu$ .* The proportion of host leaves actually accepted by mothers and then egg-laid is rather easily checked in the field. Yet, this ratio has evidently no univocal significance in terms of mothers' behaviour since it depends not only upon the degree of selectivity of mothers but also upon their unknown local density and, accordingly, may not at all serve as a surrogate for estimating the behaviourally relevant ratio of leaf-acceptance " $\alpha$ ." While " $\alpha$ " is virtually impossible to record, at least under field conditions, it may be estimated indirectly, using an appropriate inferential method, the "Melba" procedure.

In short (see [26, 27] Béguinot 2011, 2012 for details), this procedure relates the hard-to-observe parameters  $\alpha$  and  $n_c$  to the easily field-recorded distribution  $\Pi(\eta)$  of the numbers of leaves according to the number  $\eta$  of either eggs or mines they support. Briefly, the procedure is based on the fact that, thanks to acceptable simplifying assumptions (see appendices), the distribution  $\Pi(\eta)$  should theoretically answer a specific equation with  $\alpha$  and  $n_c$  as the adaptable parameters. Conversely, the inferred values for  $\alpha$  and  $n_c$  are those that yield the best fit between the recorded distribution  $\Pi(\eta)$  and the corresponding theoretical distributions  $\Pi(\eta)$ , parameterised in terms of  $\alpha$  and  $n_c$ . In turn, the estimated average number  $\mu$  of mothers' probing visits per leaf is derived, dividing the recorded average number of mines per leaf by  $(\alpha \cdot n_c)$ .

The "Melba" procedure is rapid and easy to run and, therefore, reveals particularly appropriate when a large series of samples are to be analysed, as is the case here.

Now, the average local density of mothers within the sampled portion of the host canopy is also a factor very difficult to monitor in the field. Yet, it is likely that increasing (resp., decreasing) the local density of egg-laying mothers would directly result in an increase (resp., decrease) of the average number  $\mu$  of mothers' probing visits received per host leaf. The hypothetical dependence of the leaf-acceptance  $\alpha$  upon the local density of mothers may thus be tested by considering the hypothetical dependence of  $\alpha$  upon  $\mu$ .

*2.2. Field Data.* At first, it should be noticed that the notion of mothers relaxing their degree of selectivity as an answer to an increase of their local density makes all the more sense that this local density of females—and the resulting value

of  $\mu$ —are high. Accordingly, relatively high levels of mining impact were selected for this study (from 0.10 to 0.88 mine per leaf), so that the average number  $\mu$  of mothers' probing visits to host leaves is also high, comprised between 0.1 and 1.5 visits per leaf. This is just below the threshold level for the occurrence of nascent eruptive outbreaks, (i.e., impacts  $>1$  mine/leaf: see [16]). Note that such outbreaks are quite infrequent in the three species considered here and even slightly lower ranges of impacts, say between 1.0 and 0.1 mine per leaf, as is the case here, are not met so commonly. This, indeed, makes the practical difficulty to gather appropriate samples as numerous as desired and to cover a larger range of leaf-mining species, including less common taxa.

Host-trees canopies were sampled in the centre of France, mainly, south Burgundy, from August to November; a total of 34 different stands were sampled, and 14118 leaves were examined, supporting a total of 4502 mines. The repartition of samplings and observations according to leaf-mining species is as follows: *Phyllonorycter maestingella* (Müller, 1764) on *Fagus sylvatica* L.—22 stands, 10146 leaves with 2726 mines; *Phyllonorycter esperella* (Goeze, 1783) on *Carpinus betulus* L.—6 stands, 2473 leaves with 1355 mines; *Tischeria ekebladella* (Bjerkander, 1795) on *Quercus sessiliflora* (Sm.)—6 stands, 1499 leaves with 421 mines.

### 3. Results

The leaf-acceptance ratio  $\alpha$  is plotted, Figure 1, against the average number  $\mu$  of mothers' probing visits per leaf for each of the three studied leaf-mining moths, *Phyllonorycter esperella*, *Phyllonorycter maestingella*, and *Tischeria ekebladella*. At any given level of females' local density, that is, at any corresponding value  $\mu$ , the leaf-acceptance ratio  $\alpha$  shows a relatively large scatter. Yet, aside this dependence of  $\alpha$  upon the average level of foliar quality of each particular host-individual (and may be also aside some intraspecific variability in mothers' requirements [28, 29], the leaf-acceptance ratio shows no more than a weak dependence (if any) upon the density  $\mu$  of mothers' probing visits, and, thus, upon the local density of conspecific egg-laying females in the sampled portion of canopy. For all three species under study,  $r^2$  is near zero: *Phyllonorycter maestingella*:  $r^2 = 0.07$ ,  $n = 22$ ; *Phyllonorycter esperella*:  $r^2 = 0.02$ ,  $n = 6$ ; *Tischeria ekebladella*:  $r^2 = 0.02$ ,  $n = 6$ .

### 4. Discussion

The oviposition pressure, resulting from the local density of conspecific females, may possibly influence the behaviour of egg-laying mothers through (i) the ability of mothers to detect directly the occurrence of previously deposited conspecific eggs or (ii) their capacity to account for the density of neighbouring conspecific females themselves.

The first alternative is generally considered unlikely within most tiny leaf-mining species with very minute eggs, as mentioned above, and this was actually verified in each case in the present study. The second, independent alternative, on the contrary, had to be considered and was tested accordingly (using the average density  $\mu$  of mothers' probing

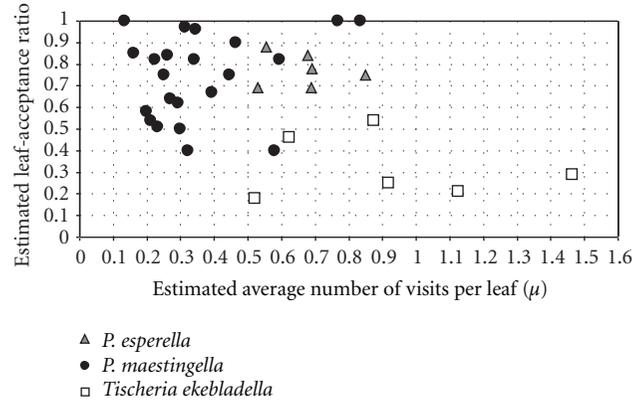


FIGURE 1: The leaf-acceptance ratio  $\alpha$  plotted against the average number of mothers visits per leaf  $\mu$  for three species of leaf-mining moths on woody dicots: *Phyllonorycter esperella*, *Phyllonorycter maestingella*, and *Tischeria ekebladella*.

visits to leaves as a proportional proxy for the local density of conspecific females).

As mentioned above, the leaf acceptance ratio  $\alpha$  answers two causal components, as it depends upon both (i) the insect own degree of selectivity, that is, the threshold level of mothers' requirement regarding the host leaves properties making them acceptable for subsequent egg-laying and (ii) the average quality of displayed host leaves (as viewed "in the eyes of mothers" [30]), that is, the proportion of those host leaves which met the threshold level of mothers' requirement.

The rationale behind a hypothetical relationship between  $\alpha$  and  $\mu$  is thus twofold:

- (i) as already underlined, mothers may increase the proportion  $\alpha$  of acceptable leaves by relaxing their minimum requirement level for host leaf quality. A larger proportion of acceptable leaves would counteract the growing oviposition pressure  $\mu$  due to an increased local density of conspecific females and the related risk of stronger future scramble competition between larvae;
- (ii) reciprocally, one can imagine that a given host individual with a higher average quality of leaves, resulting in a higher ratio of leaf acceptability  $\alpha$ , may hypothetically "attract" more females from a distance and then contribute to increase their local density and the resulting oviposition pressure  $\mu$ .

Now, according to the results of the regression of the leaf-acceptance  $\alpha$  against the density  $\mu$  of mothers' probing visits, taken as a proxy for the related density of neighbouring females (Figure 1), the latter factor  $\mu$  explains only less than 10% of the variance of the leaf-acceptance ratio, respectively, 7%, 2%, and 2% for *Phyllonorycter maestingella*, *Phyllonorycter esperella*, and *Tischeria ekebladella*. As might be expected, the major, remaining part of the variance of the leaf acceptability  $\alpha$ , at given  $\mu$ , is likely resulting from variations of the average quality of leaves between the different sampled host individuals of the same species

[2, 12, 15, 31–35]. In addition, the degree of mothers' requirement for leaf acceptability may also somewhat vary among sampled sites. Yet, this second contribution to the variance of  $\alpha$  is thought to be quite less than that liable to hosts' variability.

Note also that the quasi-independence of the leaf-acceptance  $\alpha$  upon the local density of mothers cannot result from a mutual cancel of the two influences hypothesised above ((i) and (ii)) since both influences would lead to a dependence of  $\alpha$  upon  $\mu$  with the *same* (positive) sign. Accordingly, both hypotheses above reveal inconsistent. This suggests, at least for the three species under study,

- (i) that in such tiny insects, mothers are either unable to account for the local density of their neighbouring conspecifics, or they have no substantial motivation to react accordingly;
- (ii) that if mothers are able to detect their preferred host-plant species at some distance, they yet seem unable to evaluate at a distance the average level of the quality of the foliage, or they show no motivation to take advantage of that. Thus, the hypothesis of a differentiated attractivity on mothers of host individuals according to their average leaf quality is not supported. This, in turn, puts supplementary emphasis upon the arguably predominant role of contingent factors in the often strongly uneven patterns of spatial distribution of insects densities (Tack, personal communication).

Enlarging the range of studied species in these respects would remain desirable since a direct sensitivity and answer of egg-laying mothers to the local density of their conspecifics may not be excluded for some other species, even perhaps for some species among tiny microlepidoptera.

## Appendices

### A. The Three Basic Assumptions Rooting the “Melba” Procedure

The following points are assumed (and, yet, systematically checked for the third point):

- (i) *random* distribution of mothers' *probing* visits among host modules (here host leaves). Of course, this is no longer the case for *efficient* visits, that is, concluded by ovipositions, as soon as not all modules are acceptable, that is,  $\alpha < 1$ . This first assumption is commonly referred to for these kinds of herbivore insects [18, 23, 36–40];
- (ii) *equiprobability* of mothers' probing visits among modules; the differences which may actually exist between the probabilities of visits, for example, in relation to variations of the individual size of modules, are neglected as a first approximation, as far as all these modules belong to the *same type* and represent the same “space module” for the insect, according to the observations of Digweed [24], the

argumentation of Kuczyński and Skoracka [41] and Gripenberg and Roslin [25]. Indeed, such simplifications are commonly used in models, see for example, Kagata and Ohgushi [42] for leaf miners or Kuczyński and Skoracka [41] for leaf gallerers;

- (iii) *those insect species only* are considered, for which mothers *do not* decidedly avoid nor restrict oviposition upon modules already visited and egg-laid previously by themselves or conspecifics [13–15, 18–20, 22–25, 43, 44]. As this third assumption may not always be verified; however, implementing the “Melba” procedure should be discarded when the distribution of the numbers of eggs per acceptable unit has a variance significantly lower than the mean, thus suggesting a trend for some avoidance of cumulative egg deposits on a same module.

### B. Brief Summary of the Rationale of Melba Procedure

According to the two first assumptions above (i.e., random distribution and equiprobability of probing visits among leaves), the distribution of the number of *probing* visits received per host leaf would ideally conform to a Poisson law. Now, among all these probing visits, only those received by *potentially acceptable* leaves, according to mothers' requirements, are concluded by an egg clutch deposit: the reason why, at the difference of the distribution of visits, the distribution of eggs deposits (and associated offspring) within the whole set of sampled leaves is *not* conformed to, and more aggregated than, Poisson.

Conformity to Poisson law of the distribution of egg-deposits is expected *only* within the set of *potentially acceptable* leaves (*on proviso* of the third assumption above being satisfied, since then, mothers *do not avoid* ovipositing upon leaves already previously egg-laid).

Then, let  $\Pi(v)$  be the proportion of leaves that received  $v$  “efficient” visits (each one concluded by an egg clutch deposit), among the *whole set* of  $n_u$  sampled leaves.

For  $v \neq 0$ , that is, leaves having received at least one “efficient” visits, only the acceptable ones are concerned, by definition. Then,  $\Pi(v)$  is given by applying the Poisson law to the set of *potentially acceptable* host leaves *only*, which represent a proportion  $\alpha$  of the whole set of displayed leaves. Accordingly, for  $v \neq 0$ :

$$\Pi(v) = \frac{\alpha \cdot \exp(-\mu) \cdot \mu^v}{v!} \quad (v \neq 0). \quad (\text{B.1})$$

For  $v = 0$ , that is, leaves having received no efficient visit, two contributions are to be considered: all the nonacceptable leaves (proportion  $(1 - \alpha)$ ) and also those acceptable leaves that, by chance, have received no visits:

$$\Pi(v) = 1 - \alpha + \alpha \cdot \exp(-\mu) \quad (\text{for } v = 0), \quad (\text{B.1}')$$

with  $\mu$  as the average number of probing visits received per host leaf ( $\mu$  is, as well, the average number of “efficient” visits received per potentially acceptable leaf).

Now, what may be observed and quoted *a posteriori* in the field is not the number of efficient visits per leaf but their direct material consequences (the “recorded objects”) in terms of the number  $\eta$  per host leaf of either deposited eggs or resulting larvae (or alternatively the number of associated “artefacts” such as mines or galls). Accordingly, the clutch-size  $n_c$  may either apply to *deposited eggs* or the *resulting artefacts*.

If *deposited eggs* are the objects directly recorded in the field, then  $n_c$  corresponds to the usual definition of clutch size: the number of eggs deposited in a single bout.

If *resulting artefacts* (mines, galls, etc.) are now the more easily recorded objects, then  $n_c$  is the average number of these “residual” artefacts resulting from one clutch of eggs; in this case  $n_c$  (the “residual” clutch-size) might be lower than the egg clutch size itself, depending on the ratio of developmental success of eggs.

The number  $\eta$  of eggs or artefacts per leaf is thus  $\eta = \nu \cdot n_c$ , with  $\nu$  as the number of visits received and  $n_c$  being either the “eggs” or the “artefacts” clutch size. The proportion  $\Pi(\eta)$  of host leaves supporting  $\eta$  eggs or artefacts, among the whole sample of  $n_u$  host leaves, is therefore obtained by substituting  $\eta/n_c$  to  $\nu$ , in (B.1) and (B.1)′:

(i) for any full positive values of  $(\eta/n_c)$ , that is, for acceptable leaves visited at least once:

$$\Pi(\eta) = \frac{\alpha \cdot \exp(-\mu) \cdot \mu^{(\eta/n_c)}}{(\eta/n_c)!}, \quad (\text{B.2})$$

(ii) and for  $\eta = 0$ :

$$\Pi(0) = 1 - \alpha + \alpha \cdot \exp(-\mu). \quad (\text{B.2})'$$

The average number  $\mu$  of “efficient” visits per acceptable leaf, is given by

$$\mu = \frac{(n_e/n_c)}{(\alpha \cdot n_u)} = \frac{n_e}{(\alpha \cdot n_c \cdot n_u)}, \quad (\text{B.3})$$

with  $n_e$  as the total number of eggs (or total number of resulting artefacts: mines/galls) within the whole studied sample of  $n_u$  potential host leaves (acceptable or not) (note that considering either eggs or associated artefacts does not modify neither  $(n_e/n_c)$  nor  $\mu$ , since, correspondingly,  $n_c$  is the clutch size applied to either eggs or their resulting artefacts. Therefore, the acceptance ratio  $\alpha$  also remains unchanged since  $\alpha = (n_e/n_c)/(\mu \cdot n_u)$ ).

The estimation of both  $n_c$  and  $\alpha$  is obtained by comparing the field-recorded distribution  $\Pi(\eta)$  (established for either eggs or their resulting artefacts) to the corresponding computed distribution  $\Pi(\eta)$ .

In practice, this estimation is obtained iteratively, seeking for the set of values  $\{n_c \ \& \ \alpha\}$  which leads to the best fit between *field-recorded* and *computed* distributions  $\Pi(\eta)$ . It should remain in mind that, as already mentioned,  $n_c$  corresponds either to the *eggs’* or to the *mines/galls’* clutch-size.

The average number  $\mu$  of egg-laying mothers probing visits per host leaf (and as well the average number of clutch deposits per potentially acceptable leaf) is

$$\mu = \frac{(n_e/n_u)}{(\alpha \cdot n_c)}, \quad (\text{B.4})$$

see (B.3).

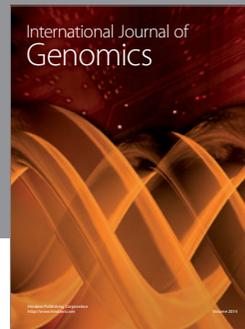
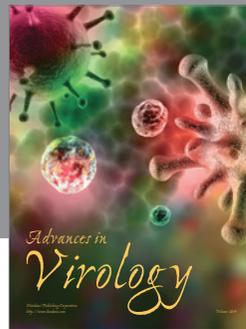
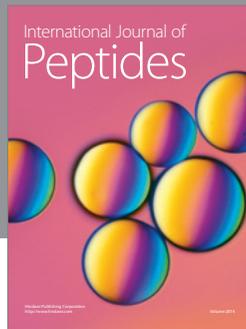
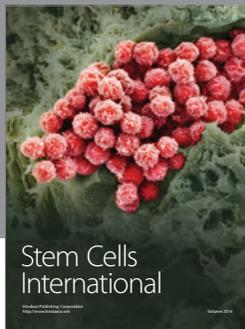
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