# The distribution of eggs per host in a herbivorous insect – intersection of oviposition, dispersal and population dynamics

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**Summary**

**1.** The dynamics of parasitic organisms depend critically upon the frequency distribution of parasite individuals per host. However, the processes giving rise to this frequency distribution have rarely been modelled and tested for organisms with complex host selection behaviour.

**2.** In this study *Microrhopala vittata*, a chrysomelid beetle, was used to investigate how oviposition behaviour, movement and density of host plants interact in shaping the frequency distribution of egg clusters per host in the field.

**3.** Enclosures were stocked with two different host species and different beetle densities and various stochastic process models were fitted to egg cluster count data obtained from these enclosures. The different models were derived considering different scenarios, in particular whether or not plant density limits oviposition rate, whether or not ovipositing females actively seek out the most attractive plant within their perception radius and whether a female's oviposition rate is determined by plant intrinsic factors, the plant's egg cluster load or the surrounding beetle density.

**4.** The model parameters fitted to cage data were used to describe the frequency distribution of egg cluster counts obtained in a release experiment in the field. A total of 220 beetle pairs were released at five locations in a field where this beetle was not observed previously. Each release point was at a border between the two host species.

**5.** One model predicted for the preferred host species the egg cluster count frequencies in the field from parameters estimated in the cages. This model assumed that egg clusters present on a plant increased subsequent oviposition on this plant. All other models could not describe the distribution of egg cluster counts for either of the two host species.

**6.** The results suggest that females seek out attractive hosts actively and the attractiveness of a plant increases with its egg cluster load. This behaviour creates a frequency distribution of egg clusters per host that depends only on beetle density but not on plant density. This conclusion has important implications for modelling insect–plant interactions.

*Key-words*: Chrysomelidae, dispersal, egg count distribution, oviposition behaviour, stochastic processes.

## Introduction

The dynamics of organisms with parasitic lifestyle depend critically on the frequency distribution of par-

asite individuals per host (e.g. Anderson & May 1978; May & Anderson 1978; Hassell, Southwood & Reader 1987; Hassell *et al*. 1991). Knowledge of the frequency distribution of local densities is often necessary for predicting the change in global densities of locally interacting species for a simple reason (Chesson 1996, 1998): if the change of a species' density is determined by local interactions, it is a function of local densities. In this case the overall change in density is calculated

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by applying the function for the change in density to local densities and averaging the resulting values over all local densities. The common practice of applying the function for the change in density to the global (i.e. the mean) density is equivalent to exchanging the order between applying a function and taking the mean. However, the order of these two operations cannot be exchanged for a non-linear function. The proper procedure, namely averaging the values of the function for change in density over the local densities, requires information about the distribution of densities at the local scale of interaction.

This situation applies not only to parasites but also to many herbivorous insects which undergo an immobile larval stage, during which larvae interact on the scale of a host plant. To model the dynamics of these species, one has to understand the processes shaping the distribution of egg counts per host plant. This distribution is a result of potentially complex interactions of movement and oviposition behaviour of females as well as the distribution of hosts. Because of their complexity, these processes have usually been investigated in isolation for herbivorous insects.

There is much research on oviposition choice by females in insects (for review see Mayhew 1997), its implications for community dynamics (e.g. Hassell 1978; Hassell *et al*. 1991; Hanski & Singer 2001) as well as for the evolution of host specialization (Futuyma 1983; Jaenike 1990; Mayhew 1997). Distributional patterns of insects resulting from the interaction of insect movement and host plant distribution have been studied extensively (e.g. Root & Kareiva 1984; Kareiva 1985). However, little is known about how movement, oviposition behaviour and host density interact in shaping the distribution of egg counts per host for herbivorous insects.

This study investigated whether cage observations of oviposition can predict the frequency distribution of egg clusters per plant in the field for *Microrhopala vittata* Fabricius, a chrysomelid beetle, and two of its goldenrod host species, *Solidago altissima* L. and *S. rugosa* Miller. Results from cage experiments were used to build a mathematical description of the oviposition process. The model was tested against patterns in the field. The goal of this approach was to develop empirically grounded models for dynamics of populations with non-linear localized interactions.

## Methods

### STUDY ORGANISM

*M. vittata* is a chrysomelid beetle which, in Connecticut, USA, occurs on three goldenrod species, *S. altissima*, *S. juncea* Aiton and *S. rugosa*. *S. rugosa*, although the most common of these three species in the study region, is used only occasionally as a host. *S. juncea* is the least common host in the region and was not investigated in this study.

Adults of *M. vittata* emerge in late April after hibernation and start to mate and oviposit immediately (Cappuccino 1991). The oviposition period lasts until mid-June. Males and females feed and mate multiple times during the oviposition period and females lay multiple clutches (personal observations). Eggs are laid in clusters of two to four eggs on the upper leaves and are covered with excrement (Messina & Root 1980). Only egg clusters were counted in this study. Unpublished data showed no connection between the number of egg clusters per leaf and the number of eggs per egg clusters. The number of egg clusters per leaf is therefore approximately proportional to the number of eggs per leaf.

The larvae are leaf miners that burrow directly into the oviposition leaf after hatching and stay on the same plant until pupation. An increased number of eggs per leaf increases the mine establishment success and therefore the survival to pupation of each individual larva (Damman 1994). Pupation occurs in the study region between mid-July and August (Clark 1983). The adults usually stay on the same plant before they hibernate in the ground. Although *M. vittata* is, in principle, capable of flying, I have not observed any attempt to fly by these beetles during 3 years of close observation.

### MODEL DEVELOPMENT

The aim of this study was to understand how oviposition and movement behaviour of the beetles interact with host density in shaping the distribution of egg cluster counts. A common garden experiment (density experiment) was performed to determine how the egg cluster distribution depends on the density of conspecifics. A release experiment yielded data about the distribution of egg clusters generated in the field when all females start at one point. These experiments will be described in detail in the next section.

As a framework for the interpretation of the experimental results, I will outline a general mathematical formulation of the oviposition process during which adults disperse, oviposit and die. Using this general framework I will derive more specific stochastic models, which were fitted to the data from the density experiment and used to predict patterns from the release experiment.

Let $n(\boldsymbol{x}, t)$ denote the density of ovipositing females and $m(\boldsymbol{x}, t)$ the egg cluster density at the spatial location $\boldsymbol{x} = (x_1, x_2)$ and time $t$. The density of ovipositing females (henceforth referred to as beetle density) changes at any given location over time due to movement, mortality and the termination of oviposition. The model presented here does not describe the change in beetle density but rather for a given trajectory of beetle density, $n(\boldsymbol{x}, t)$, the change in egg cluster density $m(\boldsymbol{x}, t)$, which is given by the ordinary differential equation:

$$\frac{\partial m}{\partial t} = n \cdot \phi(m, n, p) \tag{1}$$

where $\phi(m, n, p)$ denotes the rate of oviposition per female as function of egg cluster density $m$, beetle density $n$, and plant density $p$. Time dependency of oviposition is captured in $n(x, t)$, the density of ovipositing females. At any point in time this approach considers only the current beetle density and cannot incorporate any effect an individual's history of host encounter could have on its oviposition rate. Cage experiments showed that the number of egg clusters laid per plant by this beetle did not depend on whether hosts were encountered simultaneously or separately (zu Dohna 2003), and therefore justify this simplification.

In the case that eqn 1 is an adequate description of the oviposition process, one has to determine the form of the oviposition rate $\phi(m, n, p)$. This was performed by assuming different alternative forms for $\phi(m, n, p)$ from a priori information and by assessing which is consistent with the results from the density and release experiment.

Preliminary behavioural observations of *M. vittata* showed that females spend much time in the understorey, occasionally climb plants and oviposit on a fraction of the plants they climb. The oviposition decision of a female is likely to depend on the number of egg clusters found on an individual plant, as that is also the scale of larval interaction (Damman 1994). An individual plant should therefore be the unit for describing the oviposition process and $m(x, t)$, the number of egg clusters at location $x$ and time $t$ of eqn 1, should accordingly be understood as egg cluster density on an individual plant at location $x$ and time $t$.

Furthermore, it is useful to distinguish between a female's decision to climb a plant and to oviposit once a plant has been climbed (Singer 1982) and to introduce accordingly $f$, the fraction of females encountering a particular plant which decide to climb this plant (rather than any other plant within their perception radius). The rate of oviposition in eqn 1, $\phi(m, n, p)$, is now given by $f$, the fraction of females climbing the plant, $\times c$, the rate of plant climbing, $\times \phi(m, n)$, the rate of oviposition of a female once it climbed the plant as function of the number of egg clusters on this plant $m$, and beetle density $n$, i.e. $\phi(m, n, p) = c \times \phi(m, n) \times f(p)$.

If females choose plants randomly, all plants within a female's perception radius will be climbed with equal probability. In that case there are two simple alternatives for how the fraction of females climbing a particular plant could depend on plant density, according to the following argument, which is treated more formally in Appendix I: at low plant densities every plant encountered by a beetle is the only one within its perception radius and plant density has no influence on the fraction of beetles climbing a certain plant, hence $\partial m/\partial t = cn(t)\phi(m, n)$. At high plant densities, however, every beetle encounters several plants simultaneously and the probability of a plant being climbed is inversely related to plant density and hence $\partial m/\partial t = [cn(t)/p]\phi(m, n)$. These two scenarios will be grouped under the heading of 'passive plant selection scenarios' and will be referred to as scenarios (Ia) and (Ib), respectively.

In the alternative scenario of 'active plant selection' the probability of a plant being chosen depends on how attractive the plant is to an ovipositing female relative to the neighbouring plants. To simplify this situation a female was assumed to only select the most attractive plant within its perception radius. The attractiveness of a plant could depend on plant intrinsic characteristics or its egg cluster load. How to distinguish these alternatives is described at the end of this section and in Appendix II.

Because of increasing larval survival with increasing number of eggs per leaf (Damman 1994), it was assumed that the attractiveness of a plant increases with its egg load. This assumption led to the following scenario when plant variation is ignored: when no plant has egg clusters, all plants are equal and the rate of oviposition a plant experiences for its first egg cluster is the same as in passive plant selection. As soon as a plant receives an egg cluster it will always be preferred over its neighbours without egg clusters and the oviposition this plant experiences becomes independent of surrounding plant density. Hence there are two alternatives of how egg cluster density on a plant might change over time:

$$\frac{\partial m}{\partial t} = \frac{n(t)}{p} \cdot c \cdot \phi(m, n) \quad \text{for passive plant selection at high plant densities (scenario (Ia))} \quad (2a)$$

for passive plant selection at high plant densities [scenario (Ia)]; and

$$\frac{\partial m}{\partial t} = n(t) \cdot c \cdot \phi(m, n) \quad \text{for passive plant selection at low plant densities or active plant selection after the first egg cluster (scenario (Ib) or (II))} \quad (2b)$$

for passive plant selection at low plant densities or active plant selection after the first egg cluster [scenario (Ib) or (II)].

According to the model described so far, two plants experiencing the same beetle density over time should have the same egg cluster density. This cannot be true in reality, as beetles and egg clusters come in discrete units. Take, for example, a female in a cage with two plants. After moving around and visiting both plants the same number of times the female decides to climb one plant and oviposits. This plant has then a higher egg cluster load even though it experienced the same beetle density. This difference is likely to become exacerbated over time, as the egg cluster might lead to increased attractiveness of the plant.

The model could still describe the change of average egg cluster density per plant but this is not sufficient, as explained in the Introduction. What is needed instead is a model that produces for a plant's given trajectory of beetle density $n(t)$, a probability distribution of egg cluster counts rather than a single egg cluster count value. This was achieved by modelling eqns 2a or 2b as stochastic processes.

**Table 1.** Overview of experiments

| Experiment | Design | Purpose | Questions addressed |
|---|---|---|---|
| Density experiment | Small enclosures stocked with *S. altissima* or *S. rugosa* and one, four, seven, or 10 beetle pairs | 0 Estimate parameters ($\gamma_0$ and $\gamma_1$, $\lambda_0$ and $\lambda_1$ or $\alpha$ and $\beta$) for known beetle densities | Which model can fit cage data? |
| | Each combination of host species and beetle density was replicated five times | 1 Establish a piecewise linear function relating egg cluster density to beetle stocking density to reconstruct cumulative beetle densities from egg cluster densities in release experiment | |
| Release experiment | Five release points in the field, two received 60 beetle pairs, two 40, and one 20. All points were at the border between *S. altissima* and *S. rugosa* | Create patterns of varying beetle density in a situation where beetles are free to move, able to avoid the less preferred host and where beetle densities can be reconstructed | Which model can fit field data using parameters estimated in cages? |

Details of the stochastic process formulation are described in Appendix II. Three models were fitted to the three scenarios described above. The three models differ in whether a female's propensity to oviposit [$c \times \phi(n, m)$ in eqns 2a and 2b] depends on surrounding adult density ['adult interaction model', $c\varphi(n) = \gamma_0 + \gamma_1 n$], a plant's egg cluster load ['egg-load model', $c \times \varphi(m) = \lambda_0 + \lambda_1 m$], or plant intrinsic traits ['plant-trait model', $c \times \varphi(m) = \lambda$, where $\lambda$ follows a distribution with parameters $\alpha$ and $\beta$]. All three models were fitted to both scenarios of passive plant selection [scenario (Ia) and (Ib)], but only the egg-load and the plant-trait models were fitted to the scenario of active plant selection (scenario II) because these models allow variation among individual plants.

The adult interaction model led to a Poisson distribution of the number of egg clusters per plant and the other two models to a negative binomial. In each case the frequency distribution of egg cluster counts per plant depends on two parameters ($\gamma_0$ and $\gamma_1$, $\lambda_0$ and $\lambda_1$ or $\alpha$ and $\beta$) and the integral of beetle density over the oviposition period [referred to henceforth as cumulative beetle density and denoted by $N(t)$]. The frequency distribution of the adult interaction model depends in addition on the integral of the squared beetle density.

Where the cumulative beetle density was manipulated experimentally, the parameters were fitted to the egg cluster count data obtained in the density experiment. In a second step the egg-load and plant-trait model was tested for whether the parameters from the density experiment could describe the distribution of egg clusters in the release experiment. An overview of the two experiments, which will be described in detail below, is presented in Table 1.

### DENSITY EXPERIMENT

Small enclosures (pots with 15 cm radius, covered with 80 cm high aluminium screening) containing two stems of either the preferred host *S. altissima* or the less-preferred host *S. rugosa* were stocked with one, four, seven or 10 beetle pairs on 24 of May 2002. The enclosures were placed on benches outside at the Yale Myers research forest, approximately 15 km from the location

for the release experiment (see next section). The plants were collected from the same field where the release experiment was performed.

Beetles were collected from three different fields 2 days prior to stocking and distributed equally across treatments. Each combination of host species and beetle density was replicated five times. At the end of the oviposition season the number of egg clusters was counted for each individual stem. Because the oviposition season covers most of the plant-growing season many cages had more stems at the end of the experiment than at the beginning (3·3 on average). Egg cluster counts were made on all plants that reached a height above 15 cm at the end of the oviposition season.

An unrealistic feature of the egg-load and the adult interaction model is that the number of egg clusters laid per individual female is not bounded, but increases with beetle density. The main problem of this 'unboundedness' of the number of egg clusters laid per individual is that for high beetle densities the probabilities for realistic egg cluster counts are drawn to artificially low numbers because of non-zero probabilities for unrealistically high egg cluster counts.

To account for this problem, the egg cluster count probabilities for all models were truncated above the maximum number of egg clusters that could be laid in a cage within the observation period. The highest observed egg cluster count in the single-pair cages was used as an estimate for the maximum number of egg clusters a single female could lay in that time. In cages with multiple females the maximum number of egg clusters was accordingly the maximum of a single female multiplied by the number of females per cage. These adjusted probabilities, which sum to one at the maximum and are zero above it, fulfil only approximately the equation used to derive the original frequency distribution (see Appendix II).

The parameters of each frequency distribution ($\gamma_0$ and $\gamma_1$, $\lambda_0$ and $\lambda_1$ or $\alpha$ and $\beta$) were estimated for each plant species by maximizing the likelihood function for the observed egg cluster counts (Rice 1995). The stocking densities of female beetles [per plant for scenario (Ia) and per area for scenario (Ib) and (II)] were used as values for the cumulative beetle densities as stocking

density and cumulative beetle density are proportional if mortality is not density-dependent. The integral of squared beetle density is proportional to the squared stocking density. Systematic model deviations with changing stocking densities would provide evidence for density-dependent mortality or oviposition rate. The zero count data were excluded to estimate parameter values for the scenario of active host selection (scenario (II)).

The maximization routine in *Mathematica* was used to determine the parameter values maximizing the likelihood function when no analytical solution could be obtained. The contours of the likelihood function were plotted in the plane spanned by the two parameters to ensure global maxima. For each parameter estimate the fitted and observed egg cluster count frequencies were compared for all stocking densities using a $\chi^2$ test. Models were compared using the Akaike information criterion (AIC) (Burnham & Anderson 2002).

In addition, piecewise linear curves relating egg cluster densities to beetle densities were constructed by interpolating among mean egg cluster densities for the four stocking densities. These curves were used to reconstruct cumulative beetle densities from observed egg cluster densities in the release experiment, as described in the section 'Predicting egg cluster distribution'.

### RELEASE EXPERIMENT

A release experiment was performed in an abandoned agricultural field in North-eastern Connecticut to create patterns of continuously varying beetle densities. On 16 May 2002, 220 pairs of *M. vittata* were released in an old field (Pomfret, Connecticut) in which this species had not been recorded previously. Five release points at the border between stands of two goldenrod species, *S. altissima* and *S. rugosa* were chosen. The third host species, *S. juncea*, did not occur in the field. Three additional release points in a different field were discarded after it was discovered that beetles were present in this field before the experiment. A fourth release point was not used, because the border between the two plant species moved during the growing season.

Of the five release points used in the analysis, two received 60 beetle pairs, two 40 and one 20. After 61 days, egg clusters were counted and the distance to the release point was recorded for each egg cluster in a $2 \times 2$ m area around each release point.

To describe the change in egg cluster density with distance from the release points, the measured distances between egg clusters and release points were assigned to six different radius classes of 25 cm width (Fig. 1).

### PREDICTING EGG CLUSTER DISTRIBUTION

In a last step, it was investigated which combination of two models and three oviposition scenarios can predict
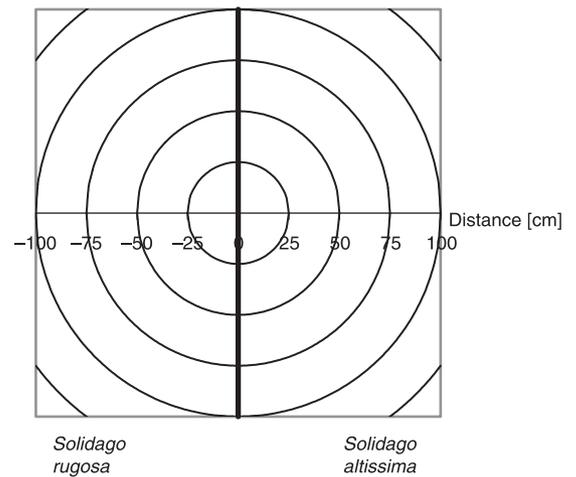
**Fig. 1.** Diagram of a release point: the vertical line indicates the border between the two plant species. The circles show the borders between the distance classes of 25 cm width.

the frequency distribution of egg cluster counts per plant for the release experiment. The frequency distributions of egg cluster counts per plant for the egg-load and the plant-trait model contain two parameters ($\lambda_0$ and $\lambda_1$ or $\alpha$ and $\beta$) and the cumulative beetle density. The question was, therefore, whether the parameter estimates from the density experiment allowed a correct prediction of the frequency distribution for the release experiment, once the variation in cumulative beetle density in the release experiment was known. This approach could not be used for the adult interaction model as its frequency distribution is also a function of the integral of the squared beetle density, which could not be reconstructed.

The underlying pattern of cumulative beetle density was reconstructed from egg cluster counts. First it was assumed that the cumulative beetle density of a given location was determined by the host species growing at the location, its distance from the release point and the number of beetles released. This assumption allows beetle dispersal behaviour and mortality to vary temporally and spatially between but not within a host species. There were three different values for the number of released beetle pairs (60, 40 and 20) and six distance classes, resulting in 18 possible values of beetle density for each host species.

For each of these 18 density classes the cumulative beetle density was estimated from the egg cluster counts using the curves relating stocking density (which is proportional to cumulative beetle density) to egg cluster density in the density experiment. For scenario (Ia) (see 'Model development' section) the number of beetles per plant was estimated from the mean number of egg clusters per plant; for scenario (Ib) the number of beetles per area was estimated from the number of egg clusters per plant; and for scenario (II) the number of beetles per area from the number of egg clusters per area.

Similarly, three different ways were used to calculate the expected count frequencies for a given pattern of beetle densities. The expected number of plants per egg cluster count is given by the product of the egg cluster count probability × the total number of plants potentially receiving egg clusters. Both components of this product were estimated differently under the different scenarios

For all scenarios the basic principle for calculating the egg cluster count probabilities was based on the law of total probability (Rice 1995):

$$P(X = x) = \sum_y P(X = x \mid Y = y)P(Y = y) \qquad (3)$$

where $X$ denotes the number of egg clusters per plant and $Y$ the cumulative beetle density. $P(X = x)$ is the probability of observing $x$ egg clusters per plant in the release experiment, $P(X = x \mid Y = y)$ is the probability of observing $x$ egg clusters per plant given the cumulative beetle density $y$ (estimated in the density experiment) and $P(Y = y)$ indicates the relative frequency at which the cumulative beetle density $y$ is observed in the release experiment.

For scenarios (Ia) and (Ib) $P(Y = y)$ was given by the relative number of plants in the according density class and for scenario (II) by the relative area. The different ways of estimating the parameters of $P(X = x \mid Y = y)$ were described in the section for the density experiments.
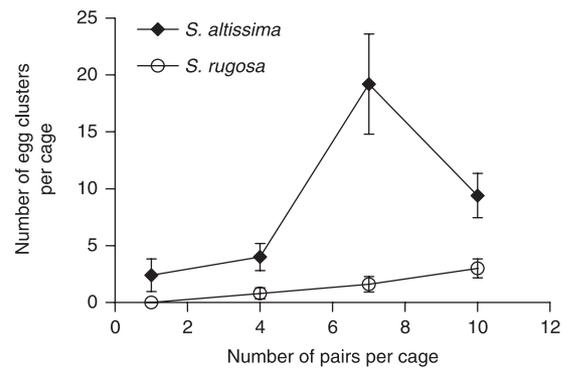
The predicted count frequencies were obtained by multiplying probabilities of eqn 3 with the total number of plants which could potentially receive egg clusters. For scenarios (Ia) and (Ib) this was simply the total number of plants surveyed around the release points. For scenario (II) this number was determined in the following way: the estimated parameter values obtained by ignoring zero counts were used to estimate for each host plant the number of plants with zero counts and therefore the total number of plants that could have received egg clusters in the density experiment. This number was multiplied by the ratio of total area surveyed around the release points over the total cage area in the density experiment to estimate the total number of plants that could have received egg clusters in the release experiment.

For all scenarios and both host species the expected and observed egg cluster count frequencies were compared by calculating a $\chi^2$-value for goodness of fit. Because the egg cluster counts per plant are not independent, this is only a qualitative assessment of the fit of the frequency distribution.

## Results

### DENSITY EXPERIMENT

The change in number of egg clusters per cage with increasing density for *S. altissima* did not conform entirely to the assumptions of the different models (Fig. 2). For *S. altissima* the number of egg clusters laid

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**Fig. 2.** Mean and SE of number of egg clusters laid per cage in common garden enclosures on *S. altissima* (◆) and *S. rugosa* (○) vs. number of beetle pairs per cage. Cages were stocked with one, four, seven or 10 pairs each. The linear interpolations between mean egg cluster densities were used to reconstruct beetle densities in the release experiment.

per female dropped for the highest beetle density, suggesting interference among beetles at high densities. This interference is in contrast to the models that assumed no interference among adults. Because this interference appears to be less evident in the three lower density treatments on *S. altissima*, only they were used to estimate the parameters of the frequency distributions for *S. altissima*. For *S. rugosa* there was no evidence for such interference (Fig. 2). No egg clusters were laid on this plant in the cages stocked with one pair.

When beetle density was measured per plant (scenario Ia) no model could reproduce the egg cluster count data for either of the two plant species (all *P*-values $\leq 0.0001$, Table 2). When beetle density was measured per area (scenarios Ib and II) two models, the plant-trait model (with parameters α and β) and the egg-load model (with parameters $\lambda_0$ and $\lambda_1$), were able to reproduce the egg cluster count data for *S. altissima*. This was true for both, a fit based on including and excluding the zero counts (Fig. 3a–c, all *P*-values = 0.13, $\chi^2$ test, see Table 2 for parameter and *P*-values). The adult interaction model could not fit the cage data for *S. altissima* (*P*-value = 0.003, $\chi^2$ test, Table 2). The AIC of the adult interaction model differed by more than 30 from any of the other models providing 'essentially no empirical support' for the adult interaction model according to the classification of Burnham & Anderson (2002).

For *S. rugosa* all models except for the plant-trait model in scenario (II) could fit the cage data (Fig. 3d–f, *P*-values = 0.17, $\chi^2$ test, Table 2). For both species, all estimates for $\lambda_1$ were positive, indicating that the egg clusters present on a plant increased the subsequent propensity to oviposit.

### RELEASE EXPERIMENT

In the release experiment, 217 egg clusters were found on *S. altissima* and 41 on *S. rugosa*. The plant density

**Table 2.** Results of model fitting and testing. The degrees of freedom ( d.f.) of the $\chi^2$ tests were given by the number of bins with expected counts $= 5$ minus the number of estimated parameters minus 1

| Scenario | Model* | S. altissima Parameter values (in cm² and for α, $\gamma_1$ in cm⁴) | P-value, d.f. ($\chi^2$ test) Cage data | P-value, d.f. ($\chi^2$ test) Field data | S. rugosa Parameter values (in cm² and for α, $\gamma_1$ in cm⁴) | P-value, d.f. ($\chi^2$ test) Cage data | P-value, d.f. ($\chi^2$ test) Field data |
|---|---|---|---|---|---|---|---|
| Ia | AI | $\gamma_0 = 0.34$** | $< 0.0001$ d.f. $= 1$ | – | $\gamma_0 = 0.09$*** | $< 0.0001$ d.f. $= 1$ | – |
| | PT | $\alpha = 1.35$ $\beta = 4.25$ | $< 0.0001$ d.f. $= 1$ | $< 0.0001$ d.f. $= 1$ | $\alpha = 0.24$ $\beta = 2.95$ | $< 0.0001$ d.f. $= 1$ | $< 0.0001$ d.f. $= 10$ |
| | EL | $\lambda_0 = 0.33$ $\lambda_1 = 0.025$ | $< 0.0001$ d.f. $= 1$ | $< 0.0001$ d.f. $= 1$ | $\lambda_0 = 0.08$ $\lambda_1 = 0.12$ | $0.0001$ d.f. $= 1$ | $< 0.0001$ d.f. $= 2$ |
| Ib | AI | $\gamma_0 = 287.6$ $\gamma_1 = 3.07 \cdot 10^4$ | $0.004$ d.f. $= 2$ | – | $\gamma_1 = 6600$** | $0.17$ d.f. $= 1$ | – |
| | PT | $\alpha = 1.46 \cdot 10^4$ $\beta = 26$ | $0.13$ d.f. $= 1$ | $< 0.0001$ d.f. $= 1$ | $\alpha = 1.21 \cdot 10^4$ $\beta = 168.1$ | $0.25$ d.f. $= 1$ | $< 0.0001$ d.f. $= 3$ |
| | EL | $\lambda_0 = 170.7$ $\lambda_1 = 257.8$ | $0.43$ d.f. $= 1$ | $< 0.0001$ d.f. $= 2$ | $\lambda_0 = 59.4$ $\lambda_1 = 20.0$ | $0.15$ d.f. $= 1$ | $< 0.0001$ d.f. $= 1$ |
| II | PT | $\alpha = 1.21 \cdot 10^4$ $\beta = 18.0$ | $0.10$ d.f. $= 1$ | $< 0.0001$ d.f. $= 11$ | $\alpha = 3.40 \cdot 10^7$ $\beta = 3.03 \cdot 10^5$ | $0.04$ d.f. $= 1$ | $< 0.0001$ d.f. $= 1$ |
| | EL | $\lambda_0 = 226.8$ $\lambda_1 = 221.0$ | $0.24$ d.f. $= 1$ | $0.07$ d.f. $= 5$ | $\lambda_0 = 33.3$ $\lambda_1 = 59.7$ | $0.23$ d.f. $= 1$ | $< 0.0001$ d.f. $= 1$ |

*AI = adult-interaction model; PT = plant-trait model; EL = egg-load model. **Parameters were estimated under the constraint $\gamma_0, \gamma_1 \geq 0$. ***Estimation procedure did not converge when both $\gamma_0$ and $\gamma_1$ were estimated.
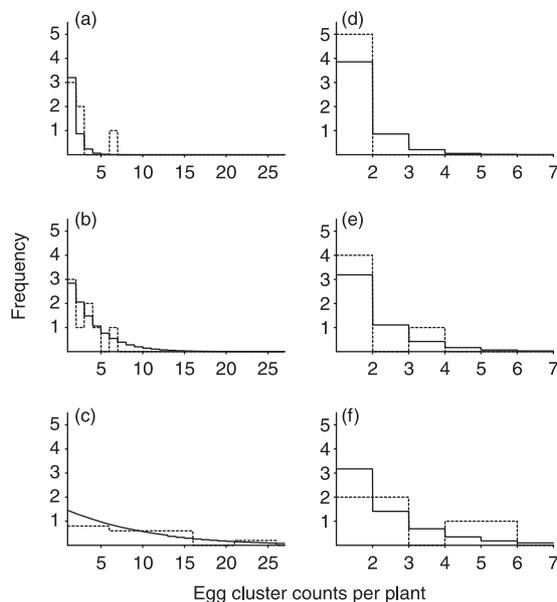


**Fig. 3.** Fitted (solid line) and observed (dashed line) frequencies of egg cluster counts per plant from the common garden enclosures at different densities. (a–c): Counts on *S. altissima* at densities of one, four and seven pairs per cage, respectively. (d–f): Counts on *S. rugosa* at densities of four, seven and 10 pairs per cage, respectively. Note that the scale of the *x*-axis differs between the plots for *S. altissima* and *S. rugosa*. The fitted count frequencies were obtained from fitting eqn II4 to the data using assumptions of scenario (II) (see text). There is no significant deviation between expected and observed frequencies (*P*-value = 0·24 for *S. altissima* and *P*-value = 0·23 for *S. rugosa*, $\chi^2$ test, d.f. = 1, see Table 2).
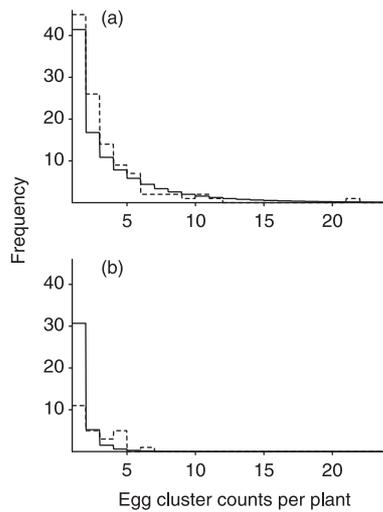
cies in the density experiment). Only in one case could the parameters estimated from the cage describe the frequency distribution of egg clusters in the release experiment, namely when the egg-load model was used to predict egg cluster counts on *S. altissima* in the scenario of active plant selection (*P* = 0·07, $\chi^2$ test, Table 2, Fig. 4a). The same model and scenario yielded the best prediction for *S. rugosa*; however it did not produce a satisfactory fit (*P* < 0·0001, $\chi^2$ test, Table 2, Fig. 4b).

## Discussion

A cage experiment and a release experiment in the field were performed to elucidate for a chrysomelid beetle how its oviposition behaviour and movement interact in shaping the distribution of its egg clusters on two of its hosts. In the cage experiment, parameters for several alternative stochastic models of the oviposition process were fitted to frequency distributions of egg cluster counts per plant. These parameters were then applied to predict the frequency distribution of egg clusters in the field experiment. No model fitted both cage and field data for the less-preferred host. Only one model fitted both data for the preferred host and allowed conclusions about the oviposition process on this host species.

The only model fitting the data assumed that egg clusters increase the attractiveness of a plant and that females choose the most attractive plant within their perception radius. Models assuming that oviposition was driven by plant characteristics or beetle density failed to describe the patterns of egg cluster distribution. Hence, the attractiveness of a plant to ovipositing

varied among the different release points between 32 m⁻² and 163 m⁻² for *S. altissima* and between 108 m⁻² and 201 m⁻² for *S. rugosa* (compared to 36 m² for both spe-

**Fig. 4.** Predicted (solid line) and observed (dashed line) frequencies of egg cluster counts per plant in the release experiment for *S. altissima* (a) and *S. rugosa* (b). The count frequencies were predicted based on parameter estimates in cage experiments for the egg cluster interaction model under the scenario of active host selection (see text). The concordance between prediction and observation is better for *S. altissima* ($P = 0.07$, $\chi^2$ test, d.f. = 5) than for *S. rugosa* ($P < 0.0001$, $\chi^2$ test, d.f. = 1).

females is determined more strongly by egg clusters present on a plant than by plant characteristics. Furthermore, a female's propensity to oviposit does not seem to be influenced by the surrounding beetle density. The data do not reveal, however, whether ovipositing females use the number of egg clusters on a plant as cue or rely on proximate cues such as pheromones released by ovipositing females.

There was evidence for negative interference among adults in high density cages but a model based on no interference was able to predict field data, suggesting that adults avoid interference when they are free to move. Finally, the number of egg clusters laid per area appeared to be independent of plant density for the observed range of plant densities, presumably because females oviposit on the most attractive plant within their perception radius.

The last aspect of the oviposition behaviour is potentially important for community dynamics. The missing feedback of plant density on change in beetle density corresponds to a recipient-controlled system, which tends to be unstable (Chen & Cohen 2001). This lack of feedback could be a reason for the observed occasional build-ups of high density of *M. vittata* (Carson & Root 2000) and for the absence of strong competitive effects from other insect herbivores (Root & Cappuccino 1992).

The positive effect of egg cluster density on the propensity to oviposit bears the potential for outbreaks driven by inverse density dependence (Berryman 1987). Outbreaks driven by endogenous dynamics are consistent with results by Cappuccino (1991), who compared *M. vittata* populations at different stages of

an outbreak and did not find evidence that outbreaks of *M. vittata* were caused by exogenous factors.

The stochastic process model described in this paper might not only be interesting because of the insights it provided on the oviposition process of *M. vittata*. The mathematical formulation in eqn (II4) provides a general direction for understanding the population dynamics of organisms which undergo a sedentary life stage at discrete point locations (e.g. individual hosts) followed by dispersal in continuous space.

The frequency distribution of local counts plays a central role in many population dynamics models (e.g. Anderson & May 1978; May & Anderson 1978; Chesson 1996). These models describe the dynamics of the mean population density assuming the type of frequency distribution (e.g. negative binomial) to be fixed. This assumption would not be adequate for the situation investigated in this study.

In this study a given cumulative beetle density generated a negative binomial distribution of egg cluster counts per plant. For a beetle population whose density varies in space the overall frequency distribution of egg cluster counts is a mixture of negative binomials and is not itself a negative binomial. The population-level frequency distribution has to come from a wider class of distributions with at least one additional parameter describing the variation of beetle density in space.

In this case a population dynamics model has to combine the population-level frequency distribution with an equation for larval density dependence and a model for the dynamics of beetle density in continuous space, such as the moment equation model used by Bolker & Pacala (1997). The construction of such a model will be left for a future study.

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## Appendix I: The role of plant density

The interaction of plant and beetle density for the oviposition process is derived below, assuming that plants are randomly (Poisson) distributed in space. The oviposition rate a plant experiences is equal to the propensity of an individual beetle to oviposit the number of beetles encountering the plant × the probability of a beetle choosing this plant. The probability of a plant being chosen by a beetle is $1/(k+1)$, where $k$ denotes the number of additional plants within the beetle's perception radius.

Because the positions of the plants are independent of each other, $k$ follows a Poisson distribution with parameter $q$, the average number of plants per perception area. The fraction of beetles encountering a plant which decide to climb, $f$, is equal to the average probability of a beetle picking the focal plant and is therefore:

$$f = \sum_{k=0}^{\infty} \frac{1}{(k+1)} \frac{q^k}{k!} e^{-q} = \frac{1}{q} \sum_{k=0}^{\infty} \frac{q^{k+1}}{(k+1)!} e^{-q} = \frac{1}{q}(1 - e^{-q})$$

For small $q$, $e^{-q}$ can be approximated by $1-q$ and $f$ becomes unity. For large $q$, $1 - e^{-q}$ can be approximated by one and $f$ becomes $1/q$.

## Appendix II: Oviposition as stochastic process

The approach used here to derive a stochastic equivalent to eqns 2a or 2b is often referred to as 'continuous time Markov chains' (Chiang 1980). In this formulation the right-hand side of eqn 2 does not describe the increase in the number of eggs, but rather how the probability for another oviposition event increases with the increasing time window. In other words, the probability of an oviposition event on a plant with egg load $m$ in the short time interval $[t, t + \Delta t]$ is given by:

$$P(\text{oviposition within } [t, t + \Delta t]) = \lambda(m, n, t)\Delta t + o(\Delta t) \quad \text{(eqn II.1)}$$

where the first term is the linear approximation of how this probability increases with increasing time window $\Delta t$. The second term denotes higher order terms of $\Delta t$.

Corresponding to the three models described in the text $\lambda(m, n, t)$, equals $n(t)[\gamma_0 + \gamma_1 n(t)]$ (adult interaction model), $n(t)(\lambda_0 + \lambda_1 m)$ (egg-load model) or $n(t)\lambda$, where $\lambda$ varies among plants (plant-trait model). The first case is an example of a time-dependent Poisson process (Chiang 1980) and the probability of observing $m$ egg clusters per plant at time $t$, $p_m(t)$, follows a Poisson distribution with parameter:

$$\Lambda(t) = \gamma_0 \int_0^t n(\tau)d\tau + \gamma_1 \int_0^t n(\tau)^2 d\tau.$$

Incorporating the variation of plant quality leads to a weighted time-dependent Poisson process (Chiang 1980) with parameter $\Lambda(t) = \lambda \int_0^t n(\tau)d\tau = \lambda N(t)$, where $N(t)$ denotes the integral of the beetle density from 0 to $t$. $\Lambda(t)$ was assumed to follow a gamma distribution with mean proportional to $N(t)$ and variance independent of $N(t)$, as the variance depends only on the distribution plant characteristics. The two parameters of the gamma distribution were therefore $\alpha \times N(t)^2$ and $\beta \cdot N(t)$. In that case the distribution of $p_m(t)$ follows a negative binomial with mean $\alpha/\beta \times N(t)$ (Chiang 1980).

Because the egg interaction model does not relate to any well-known process I will derive here the frequency distribution of egg cluster counts per plant resulting from this model. The first step is to derive an ordinary differential equation (ODE) for $p_m(t)$, the probability of observing $m$ egg clusters at time $t$. The procedure for deriving this ODE is described in most textbooks about stochastic processes (e.g. Chiang 1980). For the egg interaction model this ODE is given by:

$$\frac{dp_m(t)}{dt} = -n(t)(\lambda_0 + \lambda_1 m)p_m(t) + n(t)(\lambda_0 + \lambda_1(m-1))p_{m-1}(t) \quad \text{(eqn II.2)}$$

This equation can be converted into a partial differential equation (PDE) and solved using the probability generating function:

$$G_X(s; t) = \sum_{m=0}^{\infty} p_m(t)s^m$$

Differentiating under the summation sign and using eqn II2 one obtains:

$$\frac{\partial G_X(s; t)}{\partial t} = \sum_{m=0}^{\infty} \left[\frac{d}{dt} p_m(t)\right] s^m$$

$$= \sum_{m=0}^{\infty} [-n(t)(\lambda_0 + \lambda_1 m)p_m(t) + n(t)(\lambda_0 + \lambda_1(m-1))p_{m-1}(t)]s^m$$

$$= -n(t)\lambda_0 \sum_{m=0}^{\infty} p_m(t)s^m - n(t)\lambda_1 s \sum_{m=0}^{\infty} mp_m(t)s^{m-1} + n(t)\lambda_0 s \sum_{m=0}^{\infty} p_{m-1}(t)s^{m-1} + n(t)\lambda_1 s^2 \sum_{m=0}^{\infty} (m-1)p_{m-1}(t)s^{m-2}$$

Using the fact that $p_{-1}(t) = 0$ and that $[\partial G_X(s; t)]/\partial s = \sum_{m=0}^{\infty} mp_m(t)s^{m-1}$, one obtains the following PDE for the probability generating function:

$$\frac{\partial G_X(s; t)}{\partial t} = -n(t)\lambda_0(1 - s)G_X(s; t) - n(t)\lambda_1 s(1 - s)\frac{\partial G_X(s; t)}{\partial s} \quad \text{(eqn II.3)}$$

### SOLVING THE PDE FOR THE PROBABILITY GENERATING FUNCTION

Equation II3 can be solved using the method of characteristics (e.g. Hungerbuehler 1997), which yields three ODEs for the parametric representation of eqn II3. Calling the parameter $y$ these three ODEs are:

$$\frac{dt}{dy} = 1, \quad \text{with solution} \quad t(y) = y + c_1$$

$$\frac{ds}{dy} = n(t)\lambda_1 s(1 - s), \quad \text{with solution } s(y) = c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] \Big/ \left(c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] - 1\right)$$

$$\frac{dG}{dy} = -n(t)\lambda_0(1 - s)G = -\frac{ds}{dy}\frac{\lambda_0}{\lambda_1 s}G, \quad \text{with solution}$$

$$G(y) = Cs^{-\lambda_0/\lambda_1} = c_3 \left[c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] \Big/ \left(c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] - 1\right)\right]^{-\lambda_0/\lambda_1}.$$

The solution of the second equation was obtained using the fact from the first solution that $(d/dy)\int_0^{y+c_1} n(\tau)d\tau = n(t)(dt/dy) = n(t)$.

The solution of the third equation was obtained by substituting the solution for $s(y)$.

The general characteristic curve is therefore given by the parametric curve:

$$\gamma(y) = \begin{pmatrix} s(y) \\ t(y) \\ G(y) \end{pmatrix} = \begin{pmatrix} c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] \Big/ \left(c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] - 1\right) \\ y + c_1 \\ c_3\left[c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] \Big/ \left(c_2 \exp\left[\lambda_1 \int_0^{y+c_1} n(\tau)d\tau\right] - 1\right)\right]^{-\lambda_0/\lambda_1} \end{pmatrix}$$

To find the solution for the PDE the initial condition $G_X(s; 0) = s^0 = 1$ was used to establish a relationship between the three constants $c_1$, $c_2$ and $c_3$ represented by the parameter $r$:

$$\gamma_r(0) = \begin{pmatrix} c_2/(c_2 - 1) \\ c_1 \\ c_3\left(\dfrac{c_2 - 1}{c_2}\right)^{\lambda_0/\lambda_1} \end{pmatrix} = \begin{pmatrix} r \\ 0 \\ 1 \end{pmatrix}$$

$$\Rightarrow c_1 = 0, \quad c_2 = r/(r - 1), \quad c_3 = r^{\lambda_0/\lambda_1}$$

Substituting this relationship into the original equation and solving for *r* as function of *s* and *t* gives:

$$s = \frac{\frac{r}{r-1}A(t)}{\frac{r}{r-1}A(t)-1} \Leftrightarrow r = s/(A(t)(1-s)+s), \text{ where } A(t) = \exp\left[\lambda_1\int_0^t n(\tau)d\tau\right]$$

Substituting the solution for *r* into the equation for *G* yields the solution for the PDE:

$$G_X(s;t) = \left(\frac{s}{r}\right)^{-\lambda_0/\lambda_1} = \left(\exp\left[\lambda_1\int_0^t n(\tau)d\tau\right](1-s)+s\right)^{-\lambda_0/\lambda_1}$$

which is the probability generating function for a negative binomial with parameters $\lambda_0/\lambda_1$ and $\exp[\lambda_1\int_0^t n(\tau)d\tau]$ (Chiang 1980). The probabilities $p_m(t)$ can be obtained from $G_X(s;t)$ using the relationship:

$$p_m(t) = \frac{1}{m!}\frac{\partial^m G}{\partial s^m}\bigg|_{s=0} = \exp\left[-\lambda_0\int_0^t n(\tau)d\tau\right]\cdot\left(\frac{\exp\left[\lambda_1\int_0^t n(\tau)d\tau\right]-1}{\lambda_1\exp\left[\lambda_1\int_0^t n(\tau)d\tau\right]}\right)^m\prod_{i=0}^{m-1}\frac{\lambda_0+i\lambda_1}{i+1}$$

$$= \exp\left[-\lambda_0\int_0^t n(\tau)d\tau\right]\frac{1}{\lambda_1^m}\left(1-\exp\left[-\lambda_1\int_0^t n(\tau)d\tau\right]\right)^m\prod_{i=0}^{m-1}\frac{\lambda_0+i\lambda_1}{i+1} \qquad\text{(eqn II.4)}$$

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