

## HABITAT COMPLEXITY, SPATIAL INTERFERENCE, AND “MINIMUM RISK DISTRIBUTION”: A FRAMEWORK FOR POPULATION STABILITY

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**Abstract.** In the past century, the debate over whether or not density-dependent factors regulate populations has generally focused on changes in mean population density, ignoring the spatial variance around the mean as unimportant noise. In an attempt to provide a different framework for understanding population dynamics based on individual fitness, this paper discusses the crucial role of spatial variability itself on the stability of insect populations. The advantages of this method are the following: (1) it is founded on evolutionary principles rather than post hoc assumptions; (2) it erects hypotheses that can be tested; and (3) it links disparate ecological schools, including spatial dynamics, behavioral ecology, preference–performance, and plant apparency into an overall framework. At the core of this framework, habitat complexity governs insect spatial variance, which in turn determines population stability.

First, the “minimum risk distribution” (MRD) is defined as the spatial distribution of individuals that results in the minimum number of premature deaths in a population given the distribution of mortality risk in the habitat (and, therefore, leading to maximized population growth). The greater the divergence of actual spatial patterns of individuals from the MRD, the greater the reduction of population growth and size from high, unstable levels.

Then, based on extensive data from 29 populations of the processionary caterpillar, *Ochrogaster lunifer*, four steps are used to test the effect of habitat interference on population growth rates. (1) The costs (increasing the risk of scramble competition) and benefits (decreasing the risk of inverse density-dependent predation) of egg and larval aggregation are quantified. (2) These costs and benefits, along with the distribution of resources, are used to construct the MRD for each habitat. (3) The MRD is used as a benchmark against which the actual spatial pattern of individuals is compared. The degree of divergence of the actual spatial pattern from the MRD is quantified for each of the 29 habitats. (4) Finally, indices of habitat complexity are used to provide highly accurate predictions of spatial divergence from the MRD, showing that habitat interference reduces population growth rates from high, unstable levels. The reason for the divergence appears to be that high levels of background vegetation (vegetation other than host plants) interfere with female host-searching behavior. This leads to a spatial distribution of egg batches with high mortality risk, and therefore lower population growth.

Knowledge of the MRD in other species should be a highly effective means of predicting trends in population dynamics. Species with high divergence between their actual spatial distribution and their MRD may display relatively stable dynamics at low population levels. In contrast, species with low divergence should experience high levels of intragenerational population growth leading to frequent habitat-wide outbreaks and unstable dynamics in the long term.

Six hypotheses, erected under the framework of spatial interference, are discussed, and future tests are suggested.

**Key words:** aggregation; apparency; habitat heterogeneity; herbivory; ideal free distribution; insects; *Lepidoptera*; *Ochrogaster lunifer*; performance; predation; preference; spatial dynamics.

### INTRODUCTION

Over the past century, many researchers have sought temporal density-dependent factors that act to regulate population size through time (Volterra 1926, Nicholson

1954). However, the relatively simple differential equations that describe regulation, useful though they have been in the development of population ecology, are limited in their scope as they are not linked directly to individual fitness. For example, they often assume (either implicitly or explicitly) high levels of density-independent mortality that maintain low population growth rates, without addressing the evolutionary assumption that selection should act to reduce this mor-

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tality risk for individuals, leading to higher, destabilizing, population growth. Selection may also act to decouple individuals from density-dependent mortality if individuals can increase their fitness in doing so.

It has become increasingly clear that a spatial dimension is essential for understanding population dynamics, both at large, metapopulation scales (Kareiva 1990, Hanski 1991, Lande et al. 1998), and at smaller, within-population scales (Walde and Murdoch 1988, Kareiva 1990, Hassell et al. 1991, Taylor 1993). Recent studies have also shown the importance of spatial interactions across a range of scales (e.g., de Roos et al. 1991, Harrison et al. 1995), and all of this has led some authors to warn of the limitations of traditional differential equations for describing population stability (Donaldson and Nisbet 1999).

Furthermore, by their very nature, ordinary differential equations assume that noise (including spatial variability, demographic stochasticity, and variation in individual fitness) is absent from the system, or at least that existing noise is negligible and can be ignored (May 1973, Donaldson and Nisbet 1999). Yet field ecologists know only too well that significant noise, particularly spatial noise, is often present in natural systems. The potential stabilizing effects of extrinsic spatial noise have also been suggested by studies of host–parasitoid interactions that show how pseudo-interference between parasitoids (a form of noise that is intrinsic to the interaction itself) can lead to stability under particular conditions (see Taylor 1993 for review).

The present paper sets out to demonstrate that extrinsic spatial noise, rather than obscuring the underlying mechanisms of population dynamics, actually contributes directly to population stability by reducing the fitness of many individuals in the system. In particular, the spatial complexity of habitats is shown to interfere with the spatial patterns of herbivores, leading to higher space-dependent mortality, and so reducing fitness in the population. It is postulated that this new approach of focusing on the effect of spatial interference, in particular habitat interference, on the link between individual fitness and population stability will lead to testable hypotheses of population dynamics that are currently lacking in population ecology. Other advantages of this method are that it is founded on evolutionary principles rather than post hoc assumptions, while it links population stability with a number of disparate ecological schools, including spatial dynamics (Walde and Murdoch 1988, Kareiva 1990), behavioral ecology (Kacelnik and Bateson 1996), preference–performance (Thompson 1988, Price 1991), and plant apparency (Rausher 1979), within an overall framework.

Even though it has been more than 20 yr since Southwood (1977) first put forward the habitat templet as a potential unifying theme for the classification of spatio-temporal population and community dynamics, no

framework has ever been developed to quantify the effects of habitat complexity on the spatial patterns of individuals within populations that could be used to link the habitat templet to population stability. Several studies have shown the potential importance of habitat subdivision on herbivore population stability (e.g., Myers 1976, De Jong 1979, Atkinson and Shorrocks 1981, Ives and May 1985). However, such studies invariably regard herbivore spatial patterns within the habitat as being independent of habitat structure itself (see Soberrón 1986 for a rare exception). Thus, aggregated distributions are often assumed to be the result of “cohesive aggregation” (with individuals attracting one another to form aggregations regardless of habitat structure), rather than “adhesive aggregation” (with individuals attracted to particular resources or other features of the habitat; and, thereby, creating an aggregated distribution through a direct link between habitat structure and population spatial pattern).

However, it has been established from extensive studies on host plant preference that “adhesive” forces are common in plant–herbivore systems, with herbivores or their eggs being clustered on high quality hosts (free adhesive aggregation), or hosts that are conspicuous regardless of quality (adhesive aggregation due to interference), with hosts that are obscured by background vegetation receiving many fewer eggs or no eggs at all (e.g., Rausher 1979, Thompson 1988, Floater 1997, Floater and Zalucki 2000). If habitat complexity (with high levels of background vegetation) interferes with the host searching efficiency of herbivores, greater habitat heterogeneity should lead to altered herbivore spatial patterns across plants, which may lead to altered population dynamics (Floater and Zalucki 2000). In simple habitats, herbivores should be better able to aggregate on high quality hosts leading to high population growth, while in complex habitats (with greater structural interference), herbivores may be limited to aggregating on highly conspicuous hosts, leading to lower population growth.

In order to examine the effect of habitat interference on the link between individual fitness and population growth, the concept of the “minimum risk distribution” (MRD) is developed. This is defined as the spatial arrangement of individuals that would result in the minimum number of premature deaths in a population, given the distribution of mortality risk in the habitat (from natural enemies, resource competition, and abiotic factors). The MRD leads to maximum population growth, and high population instability, for any given habitat. The MRD can then be used as a benchmark against which to compare actual spatial patterns of individuals in the field that result from habitat interference. As the actual distribution becomes more dissociated from the MRD, so space-dependent mortality will increase, and population growth will decline away from unstable levels (Fig. 1).

Due to the complexity of linking habitat structure to

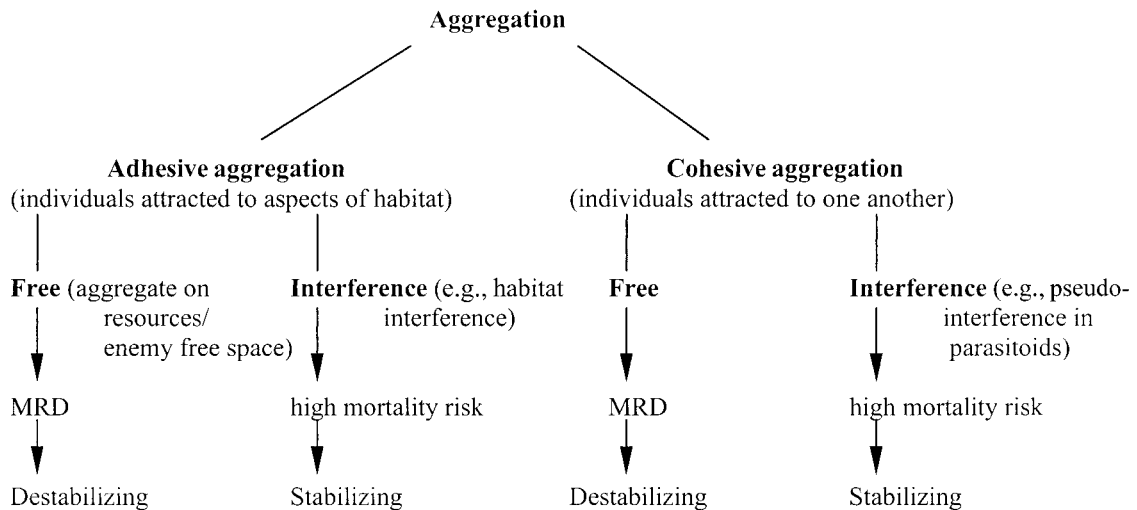


FIG. 1. Classification of different types of spatial aggregation and their hypothesized effects on population stability. Free adhesive aggregation leads to maximized individual fitness (with individuals aggregating in optimal group sizes on high-quality resources); this leads to the minimum risk distribution, MRD, that has a high, destabilizing growth rate. Adhesive aggregation due to interference occurs when background vegetation disrupts herbivores' searching ability leading to over-aggregation on "apparent" resources, reducing individual fitness and increasing stability. Note that an example of interference in cohesive aggregation is the pseudo-interference displayed by parasitoids that leads to the  $CV^2 > 1$  rule (Hassell et al. 1991).

herbivore population stability, the problem was broken down into four steps of analysis. (1) Field surveys and experiments were used to quantify the costs and benefits of aggregation for eggs and larvae of the processionary caterpillar, *Ochrogaster lunifer* Herrich-Schäffer. Potential costs and benefits include the risk of mortality from natural enemies and competition for resources. (2) These costs and benefits were then used to develop individual-based models of egg-laying behavior that led to maximized female fitness; and, therefore, to the "minimum risk distribution" (MRD). (3) The MRD was then used as a benchmark against which the actual spatial pattern of individuals could be compared. The degree of divergence of the actual spatial pattern from the MRD was quantified for each of 29 habitats. (4) Finally, the effect of habitat complexity on population growth and stability was assessed by regressing the degree of divergence from the MRD against various indices of habitat structure. If greater habitat complexity leads to greater interference in herbivore movements and egg laying behavior, we may predict that the resulting spatial patterns of eggs and herbivores will diverge further from the MRD, significantly reducing population growth, and increasing population stability.

#### *The minimum risk distribution, MRD*

The spatial distribution of individuals within a population is crucial to the dynamics of that population, because the degree of aggregation can affect the risk of individual mortality in many different ways. Potential benefits of greater aggregation include reductions in the probability of attack from natural predators

(Chew and Robbins 1984, Damman 1987, Stamp and Bowers 1988, Walde and Murdoch 1988, Lawrence 1990, Itô 1993), facilitated feeding (Long 1953, Ghent 1960, Nakamura 1977, Tsubaki 1981, Cornell et al. 1987), thermoregulation and prevention of desiccation (Seymour 1974, Tsubaki 1981, Porter 1982, Joos et al. 1988, Breuer and Devkota 1990), and division of labor (Hölldobler and Wilson 1990). On the other hand, a more aggregated distribution can lead to potential costs, such as cannibalism, disease, predator attraction, and, perhaps most important, resource depletion (Dethier 1959, Dempster 1971, Walde and Murdoch 1988, Pettitt and Wietlisbach 1992, Dhandapani et al. 1993, Schlegel and Bauer 1994).

The trade-off between these various costs and benefits leads to the "minimum risk distribution" (MRD), the spatial distribution of individuals that results in the minimum number of premature deaths. By definition, the MRD is the spatial distribution that corresponds to optimal population growth given the distribution of mortality risk that exists within the habitat (cf. Sjerps et al. 1993). While the MRD will change with various parameters such as population density and resource distribution, these parameters are readily measurable either directly or indirectly; and the MRD can therefore be predicted for a given set of conditions, and compared to the actual distribution of individuals within the habitat.

Given that a difference exists between the MRD and the actual distribution of individuals under given conditions, the way in which this difference changes quantitatively with habitat conditions (in particular, host characteristics and habitat heterogeneity) can be used

to understand and predict changes in population growth. Thus, factors that reduce the difference will lead to high intragenerational population growth with habitat-wide outbreaks in the long term, while factors that increase the difference, such as habitat heterogeneity interfering with individual movement, may lead to more stable dynamics.

In many cases the MRD may approximate to Fretwell's ideal free distribution, in which individuals are "free" to distribute themselves across resource patches so that each has an equal probability of survival and level of performance (Fretwell and Lucas 1970). However, whereas students of the ideal free distribution have generally focused solely on the effects of resource availability in different patches to assess the ideal distribution for individuals to maximize their fitness (Parker and Sutherland 1986, Lessells 1995, Van der Meer and Ens 1997), the MRD results from the net distributional risk from all risk factors in the environment, including natural enemies and abiotic factors, as well as effects of resource quality and quantity.

The second way in which the MRD differs from the ideal free distribution is the time scale over which these distributions occur. The ideal free distribution predicts movements of individuals between resource patches that may occur continuously, leading to a steady state in time (Van der Meer and Ens 1997). In contrast, the purpose of modeling the MRD is to predict the population consequences of spatial distribution. So while many herbivores in the larval stage are not "free" to move between patches over time, the MRD still predicts maximum population growth in a habitat by minimizing the mortality risk of individuals through an entire generation (or life stage). For example, a mobile female herbivore can influence offspring mortality risk by ovipositing on an appropriate host plant, while the offspring themselves are often unable to move between plants to reduce risk once oviposition has taken place. Consequently, while the ideal free distribution is an evolutionary model of individual behavior on the time scale of individual movement, the MRD should be regarded as a benchmark of spatial distribution that corresponds to the hypothetical maximum growth of a population. In both cases, these distributions result from the evolutionary selective advantages of individual searching behavior.

Even if selection acts on individual movement to reduce spatial mortality risk, the actual spatial pattern of individuals will invariably differ from the minimum risk distribution as time, habitat characteristics, and individual physiology put constraints on individual behavior. The MRD can therefore be used as a comparison with actual spatial patterns in the field to better understand the environmental constraints that limit risk minimization and lead to higher population stability.

#### *The study system*

*Ochrogaster lunifer* is a common univoltine species in coastal areas of southeast Queensland (Floater

1996a). The species is closely related to, and often confused with, the bag-shelter moth, a canopy-nesting species found in inland areas of Australia (Froggatt 1896, Mills 1950, 1951a, b, Common 1990, van Schagen et al. 1992, Floater 1996a, b). The present study confines itself to the ground nesting *O. lunifer*. The larvae feed on several species of *Acacia*, particularly the black wattle, *A. concurrens* Pedley, the most common phyllodinous acacia in the study region. The non-feeding adults emerge in late October, with females ovipositing on the trunk of host trees. Adults have no functional mouthparts, and females survive for a few days. Furthermore, at any particular site adults emerge synchronously, with all egg batches being deposited within several days. Each female lays a single batch of 150–550 eggs in her lifetime, and covers the eggs in a thick mass of white scales shed from her anal tuft. The white scale mass is 25–35 mm in diameter, and consequently egg batches are highly conspicuous on the trunks of host trees. The eggs give rise to a gregarious cohort of processionary caterpillars. The caterpillars, which initiate feeding in the second instar, are central-place foragers (Fitzgerald and Peterson 1988), moving up into the canopy en masse to feed for a few hours each day before returning to the base of the tree. The cohort produces a silk nest around the original scale mass. Larvae molt synchronously within the nest, where the exuviae remain intact; these exuviae can therefore be used to assess larval survival and growth from one instar to the next within the cohort (Floater 1996b). Caterpillars remain gregarious throughout all larval stages (eight instars), with caterpillars derived from different egg batches on the same tree merging to form a single cohort. Amalgamated cohorts may comprise as many as 600 final instar caterpillars. Cohorts can defoliate their hosts, whereupon the larvae leave en masse in search of another tree (Floater 1996c). In May, final instar caterpillars disperse, and undergo prepupal diapause underground until the following spring, when pupation occurs a few weeks before the adults emerge.

The major mortality agents in the egg and early larval stages are the dermestid beetles, *Dermestes ater* De Geer and *Trogoderma apicipenne* Reitter, which are generalist predators. Dermestids commonly destroy an entire batch of eggs or cohort of first instar larvae. To distinguish the survival of batches from the survival of larvae within a batch, the term "batch extinction" is used to describe 100% mortality of eggs or larvae in a batch. Details of natural enemies and comprehensive life tables of *O. lunifer* are given in Floater (1996a), Floater and Zalucki (1999).

#### METHODS

##### *Egg surveys*

Surveys of eggs were conducted at 39 localities in southeast Queensland, Australia, from October to No-



vember in 1993 and 1994 (Floater 1996a). Ten of the localities had less than two egg batches present in either year and only data from the remaining 29 localities are presented here (see Appendix for a description of the 29 sites with code references and the number of trees sampled at each site). *Acacia concurrens* was the dominant host tree at all but three sites (BC23, BC4, and N1) where *A. aulacocarpa* was present. In 1993, the trunk of each tree was searched, and the presence, number, and size of egg batches recorded. Because of the conspicuousness of the egg batches and their location at the base of the tree, all egg batches present on the trees sampled were recorded. The number of eggs per batch ( $y$ ) was estimated from the volume of the scale mass ( $x$ ) by the equation;  $y = 0.08x + 98.007$  ( $r^2 = 0.63$ ,  $P = 0.0004$ ). The calculation of the regression is described in Floater (1997).

#### *Larval development and survival in the field*

In January 1994 (when larvae were entering instar IV), a survey was conducted of larval cohorts remaining on each tree at 18 of the survey sites ("batch extinctions" due to predation by dermestid beetles are common during the egg and early instar stages). The number of extant cohorts remaining on each tree was recorded, and the nest material of each extinct cohort was collected for detailed examination. If present, larval skins were assigned to instars by measuring head capsule width. Previous work has shown that the measurement of head capsule width provides a highly accurate record of larval instar, as well as providing a comparison of larval development among different cohorts (Floater 1996b). The age of the cohort at extinction was defined as the larval stage above that of the last larval molt present; e.g., if the largest molted skins present in the nest material were instar II, the cohort was determined to have gone extinct in instar III. Other evidence present in the nest material of extinct cohorts, and used to produce life tables of cohort survival, included larvae and larval skins of dermestid predators, remains of eggs showing attack by predators or parasitoids, and caterpillar droppings (which demonstrated that feeding had taken place in the second instar before extinction). Previous detailed work had shown conclusively that dermestid predation of eggs and early instar caterpillars led to a characteristic scattering of the scale mass, leading to its eventual disappearance, and both scale scattering and signs of chewing mouthparts used to feed on *O. lunifer* eggs were attributed to dermestid predation (Floater 1996a; G. J. Floater, unpublished data).

In May 1994, after larvae had dispersed from trees to pupate, a further survey of nests was conducted at the 18 localities surveyed in January to monitor the survival of cohorts. At 12 localities, nest material was collected from each tree and examined for larval exuviae to record the survival of individuals within surviving cohorts. Head capsules were removed, counted,

and measured to give an estimate of the number and size of individuals that had been present at the end of the penultimate instar (instar VII). If a cohort had gone extinct between instar IV and the beginning of the final instar, the age of the cohort at extinction was determined. Larvae were adjudged to have emigrated from the tree if an abrupt reduction in the number of larvae from one instar to the next was found in conjunction with defoliation of the tree (Floater 1996c). Nest material appearing at the base of trees that formerly had no eggs was used as evidence of larval immigration from another tree.

In order to examine the relationships between larval survival and larval development, it was not only important to know the number of egg batches originally deposited on each tree, but also the number of these batches surviving to the final instar. Between the first and fourth instars, batches on the same tree tend to remain distinct. In the later larval stages, larvae from different batches combine to form a single nest at the base of the tree. In statistical analyses of larval survival and development, data were grouped into "single-batch" cohorts (these included trees on which one batch was deposited, as well as trees on which multiple batches were deposited but only one survived to instar II), and "multi-batch cohorts" (the combined larvae of two or more batches surviving to instar II).

#### *Manipulating cohort size*

In order to explore effects of cohort size on larval development and survival, two experiments were set up in which the number of larvae per cohort was manipulated.

*Experiment 1: early larval stages.*—Cohorts of first instar larvae were collected from the field in November 1995, and placed along with the scale mass into plastic tubs with damp cotton wool to prevent desiccation. On molting into the second instar, the larvae were removed from the scale mass and separated into seven different group sizes, comprising one, two, three, five, 10, 100, and 200 caterpillars. Twenty replicates were created for group sizes one to five, 10 replicates for group size 10, and five replicates each of group sizes 100 and 200. As a precaution against confounding genetic effects, sibling larvae derived from the same egg batch were allocated to different group sizes, and were not used in more than one replicate of a particular group size.

The experimental cohorts were placed on 100 potted saplings of *A. concurrens* in the greenhouse. A small amount of scales was placed at the base of each plant, and the larvae were released onto the scales. The plant pots were arranged in plastic trays with four pots per tray. During the experiment the trays were kept full of water, which avoided the possibility of disturbing the larvae by watering from above, and restricted access to the plants by ants. The water also prevented larvae from migrating from one plant to another. The exper-

iment ran for 21 days, after which the cohorts were removed, and the larvae counted and weighed.

*Experiment 2: late larval stages.*—Larvae used in this experiment were reared on potted plants of *A. concurrens* in the greenhouse for seven weeks. At the end of this period, the larvae were in the fourth instar. The larvae were then separated into six different group sizes; comprising three, 10, 25, 50, 100, and 150 caterpillars. Ten replicates were created for each group size, except for groups of 150 larvae of which there were six replicates. The experimental cohorts were released on 10 January 1995, at a former sand-mining site that had been replanted with *A. concurrens* by the mining company, Consolidated Rutile Ltd. The trees were three years old at the time of release. Fifty-six trees growing on the edge of the stand next to a sand track were tagged and numbered. All the trees chosen were mature *A. concurrens* of similar height, canopy size, and condition. The 56 experimental cohorts were then randomly assigned to the tagged trees. On 11 May 1995, after all surviving larvae had dispersed from the trees to diapause, the nest material at the base of each tree was collected and placed in a marked plastic bag. In the laboratory, exuviae of all instars were separated from the nest material, and head capsules removed and measured.

#### Statistical analysis

*Analysis of distribution.*—The spatial distribution of egg batches was analyzed in three ways. First, the coefficient of dispersion (CD = variance/mean) of egg batches across trees was calculated for each locality; a coefficient of dispersion greater than unity implies an aggregated distribution. Second, deviance from the Poisson distribution was tested using *G* tests. Third, Taylor's Power Law (Taylor 1961, Southwood 1978),

$$\ln s^2 = a + b \ln m \quad (1)$$

was used to investigate the relationship between the mean number of batches per tree, *m*, and the degree of aggregation. As the variance, *s*<sup>2</sup>, equals the mean (*a* = 0, *b* = 1) in random spatial patterns, a slope greater than unity (*b* > 1) demonstrates that the degree of aggregation increases with the density of egg batches.

*Analysis of survival.*—Logistic regression was used to test the relationship between proportion survival and group size. Proportion survival was logit transformed to linearize the relationship (McCullagh and Nelder 1989, Sokal and Rohlf 1995);

$$\ln(p/q) = \beta_0 + \beta_1 x \quad (2)$$

where  $\ln(p/q)$  is the logit; *p* = proportion survival to a particular stage; *q* = 1 - *p*; *x* = initial group size;  $\beta_0$  and  $\beta_1$  are constants. In analyses of field sampling data, initial group size was defined as the number of eggs deposited per tree. For laboratory and field experiments, initial group size was defined as the number of larvae initially placed on each sapling. Since the

dependent variable in the logistic regressions is binomially distributed, the regression line was fitted iteratively using the maximum-likelihood method.

Logistic regression was used to test spatial density dependence of dermestid predation of egg batches against the initial density of batches. The major mortality agents in the egg and early larval stages are dermestid beetles, which commonly destroy an entire batch of eggs or cohort of first instar larvae. To distinguish the survival of cohorts from the survival of larvae within a cohort, the term "batch extinction" is used to describe 100% egg and/or larval mortality in a cohort. Because egg batches of *O. lunifer* are extremely conspicuous, and deposited at the base of host trees, the exact number of batches at a site can be recorded with ease. Furthermore, the nest that subsequently develops around the batch stores various forms of evidence documenting the cause of batch extinction (e.g., the presence of predator exuviae), and the age of larvae when extinction occurred (from the record of larval exuviae). These aspects of the species' life history provide a high level of precision for spatial density dependence tests.

*Analysis of scramble competition.*—Nicholson (1954) described scramble competition as competition that acts abruptly on all individuals when there is insufficient resource to maintain every individual. This happens because the resource is divided equally among individuals. In the most extreme case of scramble competition, survival is reduced from 100% to 0% instantaneously:

$$\begin{aligned} p &= n_s/n_i = 1 && \text{when } n_i/u \leq d \\ p &= 0 && \text{when } n_i/u > d \end{aligned} \quad (3)$$

where *p* = proportion survival; *n*<sub>i</sub> = initial number of larvae; *n*<sub>s</sub> = number of larvae surviving; *u* = amount of resource (e.g., tree size); *d* = threshold larval density that the resource can support. Eq. 3 was used to predict the larval densities at which resource depletion took place. The equation is appropriate for *O. lunifer*, as 100% mortality of larvae generally occurs abruptly when the primary host is defoliated.

#### Habitat structure and heterogeneity

During the egg surveys in 1993, a record was made of tree size (trunk diameter), and, at 18 sites, plant cover surrounding the tree. Two measures of plant cover were recorded: (1) the number of perennials within 3 m of the host tree (Index I), and (2) the number of directions (0–4 including north, south, east, and west) in which these plants were growing in relation to the host tree (Index II). The mean, standard deviation, and coefficient of variation were then calculated for each host characteristic for each site to give various indices of habitat structure. Details of habitat variables measured and their values can be found in Floater and Zalucki (2000). These indices were then used to predict

TABLE 1. Spatial distribution of egg batches at 29 localities over two years, showing the mean, standard deviation, and coefficient of dispersion (CD = variance/mean) at each locality.

Site	1993					1994				
	No. batches/tree			G	P	No. batches/tree			G	P
	Mean	SD	CD			Mean	SD	CD		
Stradbroke Island										
D1	0.32	0.79	<b>1.95</b>	...	...	0.16	0.87	<b>4.65</b>	...	...
DH1	1.00	1.86	<b>3.46</b>	15.0	***	0.41	0.89	<b>1.94</b>	...	...
G6	0.58	1.15	<b>2.28</b>	8.6	*	0.06	0.24	0.96	...	...
J1	0.36	0.60	0.99	...	...	0.06	0.24	0.96	...	...
J2	0.69	1.09	<b>1.72</b>	2.6	NS	0.44	1.04	<b>2.46</b>	...	...
P1	0.48	1.00	<b>2.06</b>	...	...	0.12	0.44	<b>1.58</b>	...	...
P2	0.52	0.95	<b>1.75</b>	6.1	*	...	...	...	...	...
P3	0.92	1.64	<b>2.92</b>	17.1	***	0.08	0.27	0.94	...	...
TI12	3.36	4.22	<b>5.30</b>	22.6	***	2.43	3.13	<b>4.03</b>	11.8	**
Y1	0.40	0.67	<b>1.13</b>	...	...	...	...	...	...	...
Mainland										
BC23	0.06	0.25	<b>1.04</b>	...	...	0.10	0.31	...	...	...
BC4	2.50	2.96	<b>3.50</b>	14.6	***	4.23	6.09	<b>8.77</b>	16.7	***
BR1	0.56	1.01	<b>1.83</b>	6.9	*	...	...	...	...	...
EK1	0.04	0.20	<b>1.00</b>	...	...	...	...	...	...	...
L123	0.25	0.57	<b>1.30</b>	...	...	0.45	1.17	<b>3.04</b>	...	...
LR1	0.16	0.51	<b>1.62</b>	...	...	...	...	...	...	...
MC12	0.36	0.64	<b>1.14</b>	...	...	...	...	...	...	...
MG3	0.12	0.39	<b>1.24</b>	...	...	0.11	0.30	0.92	...	...
MN1	0.34	0.75	<b>1.65</b>	...	...	0.25	0.65	<b>1.69</b>	...	...
N1	0.22	0.47	0.98	...	...	0.38	0.64	<b>1.06</b>	...	...
TF6	0.12	0.33	0.90	...	...	...	...	...	...	...
TF10	0.12	0.33	0.92	...	...	...	...	...	...	...
TF412	0.22	0.74	<b>2.49</b>	...	...	0.13	0.73	<b>4.09</b>	...	...
TH12	0.18	0.71	<b>2.80</b>	...	...	0.28	0.63	<b>1.42</b>	...	...
TH3	0.15	0.38	0.96	...	...	0.62	0.96	<b>1.50</b>	...	...
TH4	0.20	0.45	<b>1.01</b>	...	...	0.32	0.55	0.95	...	...
TH6	0.10	0.30	0.93	...	...	0.07	0.26	0.97	...	...
WR2	0.04	0.20	<b>1.00</b>	...	...	...	...	...	...	...
WW1	0.64	0.78	0.95	0.6	NS	1.20	1.26	<b>1.32</b>	3.2	NS

Notes: A coefficient of dispersion greater than unity (highlighted with bold type in the table) suggests an aggregate distribution. At localities where batch densities were sufficiently high (see Sokal and Rohlf 1995), G tests were performed to test significant deviation from the Poisson distribution (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.005$ ; NS, not significant).

the divergence of (1) observed spatial distributions from the MRD, and (2) observed survival from that predicted by the MRD.

## RESULTS

### *Clutch size and spatial patterns in the field*

Over both years, clutch size at the 29 localities ranged from 140 to 555 eggs, while the mean clutch size per site ranged from 175 at TH3 in 1993 to 485 at MC12 in 1993. The mean clutch size across all sites (calculated as the mean of the means) was 333.1 in 1993, and 296.5 in 1994.

The distribution of egg batches across trees varied from random to aggregated. Of the 29 localities at which the distribution of egg batches was recorded in 1993, 20 (69%) displayed a coefficient of dispersion (CD = variance/mean) greater than unity, while in 1994, 13 (65%) of 20 localities displayed a CD greater than unity (Table 1). Over both years, twelve surveys had sufficiently high densities of egg batches to conduct goodness-of-fit tests. Nine of these showed a significant deviation from the Poisson distribution at the

5% level. In all cases, this deviation was due to an aggregated spatial distribution of egg batches.

The relationship between  $\ln$  (variance) and  $\ln$  (mean) of egg batches per tree across localities was linear, agreeing with Taylor's Power Law (Fig. 2). The regression equation in 1993 ( $y = 0.89 + 1.38x$ ;  $r^2 = 0.936$ ,  $P < 0.0001$ ) was similar to that in 1994 ( $y = 1.11 + 1.40x$ ;  $r^2 = 0.910$ ,  $P < 0.0001$ ). In both years, the slope was greater than unity ( $b = 1.4$ ), demonstrating that the degree of aggregation increased with the density of egg batches at a locality, and that localities with apparently random spatial patterns were those at which the density of egg batches was low.

Females tended to oviposit on large trees. Out of 21 localities (each with a range of batches per tree), eight showed a significant size difference at the 5% level (ANOVA) between trees with no eggs and trees with one or more batches, while four showed a difference with  $P < 0.0001$ . At all eight of these localities, trees with no eggs were significantly smaller.

### *Predation of eggs and early larval stages*

Of the 627 cohorts surveyed from egg to final larval instar, 496 (79%) failed to survive, with most losses

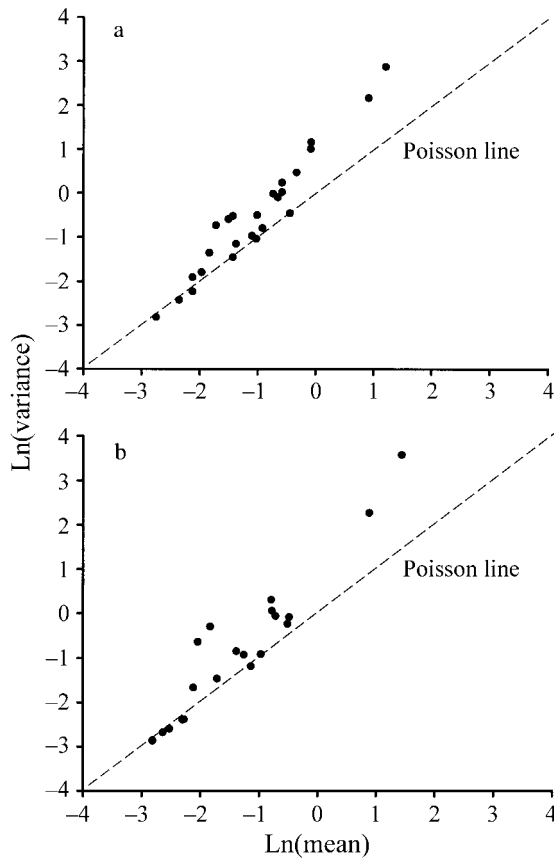


FIG. 2. Variance-mean relationship of egg batches per tree in (a) 1993 and (b) 1994. The solid line represents the predicted relationship for the Poisson distribution (slope  $b = 1$ ).

occurring in the egg, first, and second instar stages. The mortality factor leading to the greatest number of cohort extinctions was dermestid predation (representing 72% of batch extinctions), though the species of dermestid responsible varied from site to site. On North Stradbroke Island, *Dermestes ater* was the dominant predator at all but one locality, while at all localities on the mainland, the most important predator was *Trogoderma apicipenne*.

The spatial distribution of predation across trees with similar batch densities differed significantly from the binomial, indicating that when predation occurred on a tree, there was a higher than expected probability that more than one batch would be destroyed (Table 2). However, this was not due to predators acting in a spatially density-dependent manner; indeed across trees within a site, proportion predation was lowest on those trees with very high batch densities (Table 3). Of the 16 populations tested for spatial density dependence, four showed highly significant inverse density dependence ( $P < 0.005$ ), and twelve showed no significant relationship ( $P > 0.05$ ). Localities with significant inverse density-dependent predation were

TABLE 2. Spatial distribution of egg batch predation across trees.

No. batches per tree	No. batches surviving							$D$	$P$
	0	1	2	3	4	5	6		
Two	30	11	12	...	...	...	...	0.45	<0.01
Two (J2)	4	0	3	...	...	...	...	0.42	<0.15
Three	8	3	4	5	...	...	...	0.37	<0.01
Four	2	0	0	2	0	...	...	0.48	NS
Five	3	2	2	2	1	0	...	0.31	NS
Six	4	0	1	0	1	0	0	0.34	NS

Notes: The distribution of predation was tested against the binomial for trees across all sites with two, three, four batches, and so forth (e.g., trees with three batches were grouped into those with none, one, two, or three surviving batches). The distribution of predation for trees with two batches was also tested for one particular site (locality J2), where the number of trees with two batches was high. The  $D$  value of the Kolmogorov-Smirnov test was used to determine a significant deviation from the binomial distribution.

those with high batch densities and several density classes, where a significant statistical relationship could be detected. At localities where no relationship was found, there was generally an insufficient range of batch densities to detect any sort of relationship. An inverse density-dependent relationship at TH12, where the number of density classes and total number of egg batches were low, was approaching significance ( $P = 0.09$ ). Clutch size had no effect on the probability of batch extinction (logistic regression at site L123:  $\beta_1 = -0.01$ ,  $G$  value = 1.3,  $P = 0.247$ ).

At three of the four localities where the spatial pat-

TABLE 3. Results of logistic regressions showing the effect of the number of egg batches per tree on egg and early larval predation by dermestids at 16 localities.

Locality	Density classes (no.)	Batches (no.)	$\beta_1$	$G$	$P$
TI12	8	94	<b>-0.1</b>	9.4	<b>0.002</b>
BC4	7	65	<b>-0.4</b>	9.4	<b>0.002</b>
DH1	6	42	0.2	3.6	0.059
P3	6	26	<b>-0.9</b>	19.2	<b>&lt;0.0001</b>
G6	5	29	0	0	1
P1	4	24	-0.4	1.1	0.303
D1	4	16	0.7	1.9	0.163
TF412	4	12	-0.5	1.1	0.293
J2	3	36	<b>-1.5</b>	12.7	<b>0.0004</b>
Y1	3	20	0.8	1.5	0.220
L123	3	37	0.6	0.5	0.488
WW1	3	34	0.05	0.003	0.956
TH12	3	17	-1.4	2.9	0.090
MN1	3	15	0.3	0.1	0.684
J1	2	18	0	0	1
MC12	2	9	-1.8	1.2	0.265

Notes: The number of "density classes" is the number of different egg batch densities found on trees at a locality; e.g., at TI12, densities of 1, 2, 3, 5, 6, 7, 8, and 14 batches per tree were present (eight classes in total). A negative slope ( $\beta_1$ ) implies inverse spatial density dependence. Values of  $\beta_1$  significantly different from 0 ( $P < 0.05$ ) are indicated by bold type.



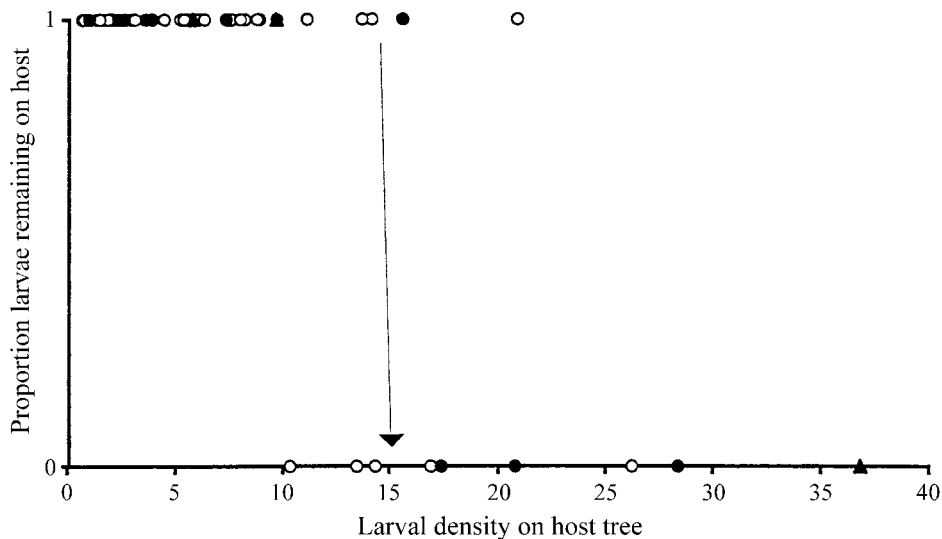


FIG. 3. Scramble competition of *O. lunifer* larvae in cohorts derived from one (open circles), two (solid circles), or three (triangles) egg batches on the same host, showing the effect of larval density (number of eggs/tree size),  $d$ , on the likelihood of emigration from the host. The arrow shows the approximate density of larvae at which scramble competition occurs (when resources are depleted and proportion survival becomes zero).

tern of predation was significantly inversely density dependent, the distribution of predators appeared to be random, with no significant relationship between the presence/absence of predators and batch density (TI12:  $\chi^2 = 1.67$ ; 5 df,  $P = 0.892$ ; BC4:  $\chi^2 = 4.95$ ; 5 df,  $P = 0.422$ ; J2:  $\chi^2 = 1.87$ ; 2 df,  $P = 0.394$ ). This was true at locality J2, where a single predator species was present, as well as for sites with both species. At the fourth locality, P3, the presence of predators was higher on trees with low batch densities ( $\chi^2 = 9.79$ ; 4 df,  $P = 0.044$ ). However, the relationship was only barely significant at the 5% level, and given the number of tests conducted, this result should be regarded with caution. In general, the inverse density-dependent pattern of predation across trees appeared to be due to a random distribution of predators relative to egg batch distribution, combined with predation satiation; trees with different batch densities had an equal probability of receiving predators, but on trees with high batch densities, predators were not able to exploit every batch. Consequently, single batches were most vulnerable to randomly distributed, generalist predators.

#### *Tree carrying capacity and scramble competition*

Of the 75 larval cohorts monitored from instar II to the final instar at 12 localities, 59 were derived from a single egg batch, 13 from two batches, and three from three batches. Twenty-two (29%) of the 75 cohorts went extinct or emigrated before the final instar. These cohorts were excluded from analyses of within-cohort survival; thereby, avoiding confounding effects of early stage batch extinctions (which are generally due to previous predation), and larval emigration (which was analyzed separately). In the remaining 53 cohorts, a

total of 4935 larvae survived to the final instar; mean =  $93.1 \pm 111.2$  SD. The proportion surviving from egg to final instar in these cohorts was  $0.24 (\pm 0.21)$ .

The effects of clutch size, clutch number, and tree size on larval performance were investigated for (a) cohorts sampled at Lytton (the site with the highest number of data), and (b) cohorts across all sites combined. At Lytton, the combined effects of clutch size, clutch number, and tree size on larval survival were highly significant (Table 4a). The same result was found for cohorts across all sites (Table 4b). In both cases, larger tree size, smaller clutch size, and the presence of more than one batch led to increased larval survival.

At Lytton, multiple regression of single-batch cohorts showed that the combined effect of clutch size and tree size on larval development (measured as mean head capsule width for the cohort) was highly significant ( $r^2 = 0.70$ ,  $P = 0.009$ ). Both at Lytton, and across all sites, increased larval size was related to larger tree size and larger clutch size. Tree size had a greater effect on larval development (Lytton:  $P = 0.006$ ; all sites:  $P = 0.0004$ ) than did clutch size (Lytton:  $P = 0.051$ ; all sites:  $P = 0.002$ ). There was no correlation between tree size and clutch size ( $\rho = 0.133$ ,  $P = 0.479$ ). The number of batches on a tree had no effect on larval size (ANCOVA:  $F_{2,51} = 0.69$ ,  $P = 0.504$ ; covariate tree size).

Larval density (initial number of larvae/tree size) had a significant effect on scramble competition (logistic regression:  $G = 24.6$ , df = 1,  $P < 0.0001$ ). Emigrations took place above a threshold density ( $d \approx 15$ ; Eq. 3), corresponding to resource depletion (Fig. 3). Above this threshold, no larvae completed devel-

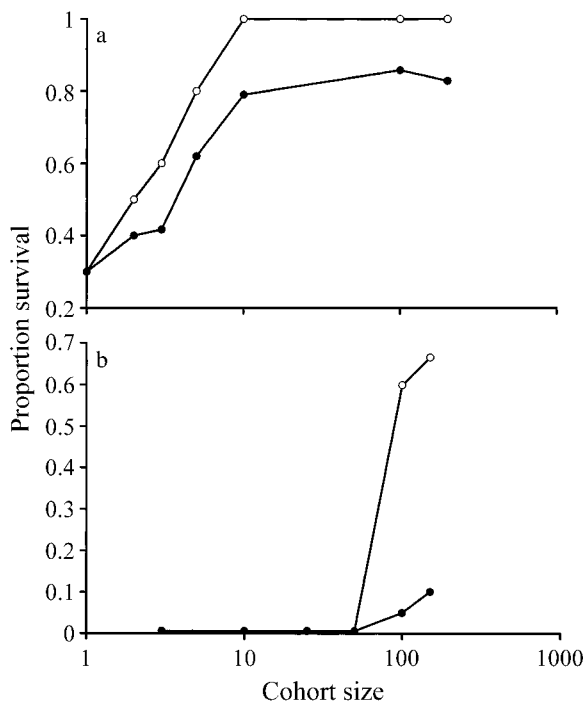


FIG. 4. Effect of larval cohort size on the survival of larvae (solid circles) and entire cohorts (open circles): (a) survival of early stage larvae (instar II–III) in groups of 1, 2, 3, 5, 10, 100, and 200 (log scale); (b) survival of late stage larvae (instar IV–VIII) in groups of 3, 10, 25, 50, 100, and 150 (log scale).

opment on the tree. Only four (7%) of the 59 larval cohorts derived from single batches emigrated before the final instar. In multi-batch cohorts, five (31%) of 16 cohorts emigrated before the final instar, a significantly greater proportion than single-batch cohorts ( $\chi^2 = 7.14$ ; 1 df,  $P = 0.008$ ). Across all sites, a total of nine cohorts emigrated before the final instar. In contrast, only one immigration event was recorded, suggesting that emigration involves a high risk of mortality.

#### Manipulated cohort size: early larval stages

One of the cohorts of 200 larvae defoliated its host plant before the end of the experiment and was excluded from statistical analyses. Successful larval establishment was high on greenhouse plants, with 1279 (79%) of the initial 1620 larvae, and 63 (64%) of the initial 99 cohorts having survivors at the end of the experiment. Larval and cohort survival increased with initial cohort size (Fig. 4a): (1) larval survival;  $\ln(p/q) = 0.006x + 0.62$  ( $G$  value = 54.4; 1 df,  $P < 0.0001$ ), (2) cohort survival;  $\ln(p/q) = 0.22x - 0.18$  ( $G$  value = 23.5; 1 df,  $P < 0.0001$ ). Cohort size had a significant effect on larval development ( $F_{6,56} = 12.98$ ,  $P < 0.0001$ ), with larvae in groups of 200 attaining double the mass of solitary larvae (Fig. 5).

#### Manipulated cohort size: late larval stages

Survival of larvae was extremely low in this experiment, with 144 (5.2%) of the initial 2780 larvae surviving to the final instar (Fig. 4b). The highest percentage survival for a single cohort was 22%. All cohorts of three, 10, 25, and 50 caterpillars went extinct. Within-cohort mortality was high in cohort sizes of 100 (94.7% mortality) and 150 (89.9% mortality). However, the majority of cohorts in these size classes did not go extinct. Out of 10 cohorts with 100 initial larvae, six had survivors (though one of these had the remains of only one individual), while out of six cohorts with 150 initial larvae, four had survivors. Though mortality was high in cohorts of 100 and 150, larval survival was significantly greater than in smaller cohorts (logistic regression:  $\beta_1 = 0.025$ ,  $G = 107.8$ ,  $P < 0.0001$ ).

#### MODELS OF OVIPOSITION PATTERNS

##### Levels of aggregation for maximum female fitness

Two models were constructed to predict oviposition patterns in a habitat that would maximize female fitness. The second of these models approximated to a minimum risk distribution, MRD. Empirical data were used to define the performance of egg clutches on trees as a function of tree size and existing egg load (see Table 4). Females were released sequentially into the model universe, and were able to select the host tree that would maximize clutch performance given the size of the tree and the number of batches already present on the tree (the models were not spatially explicit; females were able to compare the suitability of all trees in the habitat). The subsequent distribution of egg batches predicted for a particular locality (using the same tree sizes and the total number of batches re-

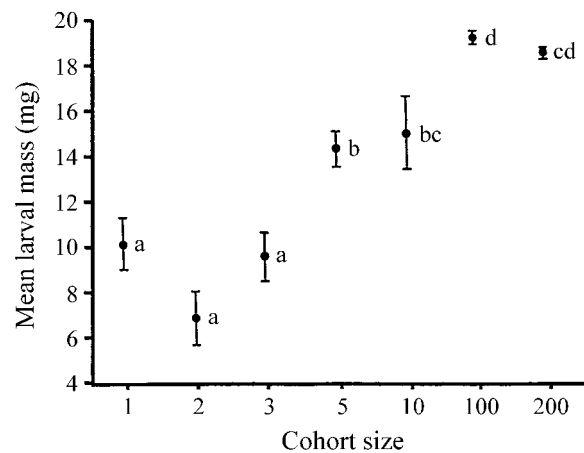


FIG. 5. Effect of larval cohort size on early-stage larval development, measured as mean larval mass ( $\pm 1$  SE) after 21 d from initiation of feeding in instar II. Different letters represent significantly different larval masses, while similar letters represent masses that are not significantly different from one another (Fisher post hoc tests from multiple ANOVA).

TABLE 4. Results of logistic regressions showing the effects of clutch size (number of eggs per batch), tree size, and batch density (number of batches per tree) on survival of individuals from egg to final larval instar at (a) Lytton (L123) and (b) all localities combined.

	a) Lytton			b) All localities		
	$\beta_1$	G value (1 df)	P	$\beta_1$	G value (1 df)	P
Clutch size	-0.003	22.1	<0.0001	-0.002	109	<0.0001
Tree size	1.428	108.4	<0.0001	2.086	778	<0.0001
Number of batches						
1 batch	-3.335	8.8	<0.005	-5.114	1365	<0.0001
>1 batch	-3.094			-3.875		

Notes: Batches that went extinct or emigrated from trees were not included in analyses. Analyses included: (a) 15 trees, 5457 eggs; (b) 42 trees, 17 590 eggs.

corded at that particular locality) was then compared to the batch distribution observed in the field.

Suppose a female deposits a batch, B, on a tree of size  $u$ . The probability that her batch survives depends on the probability that the batch escapes predation in the early stages. Furthermore, the probability of resource depletion (and, therefore, extinction of batch B) in later stages depends on the number of other batches on the tree that escape predation. Let us define the carrying capacity of the tree, integer  $k$  (i.e., the number of batches that the tree can support), in terms of tree size:

$$k = f(u). \tag{4}$$

Let  $p_n$  be the probability that a batch escapes predation if it is deposited on a tree with  $n - 1$  other batches, and let  $m$  be the number of other batches that escape predation. If  $p_n$  is independent for batches on the same tree, the probability,  $S_B$ , of batch B surviving to final instar on a tree of size  $u$  is then

$$S_B = p_n \quad \text{when } n \leq k$$

$$S_B = p_n \{P(m = 0) + P(m = 1) \dots + P(m = k - 1)\}$$

$$= p_n \sum_{r=0}^{k-1} C_r p_n^r (1 - p_n)^{(n-1-r)}$$

$$\text{when } n > k \tag{5}$$

That is, when  $n \leq k$ , the tree is large enough to support all batches on the tree; and, therefore, the probability of batch B surviving is simply the probability of the batch escaping predation ( $p_n$ ). However, if the tree is too small to support all batches,  $n > k$ , batch B will survive only if it itself escapes predation, while a sufficient number of other batches are destroyed, so reducing the number of remaining batches to, or below,  $k$ .

Eq. 5 describes the probability of batch survival as a function of predation and tree size. The proportion of individuals that survive within the clutch is influenced by the presence of other batches on the tree and tree size. As the proportion of larvae surviving in batch B is affected by the presence or absence of other batch-

es on the tree, let  $g(u)$  and  $h(u)$  be the probabilities that a larva in batch B survives on a tree of size  $u$ , given that  $m = 0$  and  $m > 0$ , respectively. The probability,  $S_L$ , that a larva in batch B survives to final instar is then

$$S_L = p_n \{P(m = 0)g(u) + P(0 < m \leq k - 1)h(u)\} \\ = [p_n(1 - p_n)^{(n-1)}g(u) \\ + \{[S_B - p_n(1 - p_n)^{(n-1)}]h(u)\}. \tag{6}$$

To calculate  $S_L$  for different  $n$  and  $k$ , parameters of logistic regressions (see Eq. 2) were used to calculate probability functions  $p_n$ ,  $g(u)$  and  $h(u)$ . The probability function for egg batch predation,  $p_n$ , was calculated from data at site TII2 ( $\beta_0 = 0.871$ ,  $\beta_1 = 0.142$ ): the mean egg batch number was highest at this site; and it therefore gave estimates of proportion survival for a large range of batch densities (Table 3). The other probability functions were calculated from data combined from all sites sampled. Although clutch size influences within-cohort survival (Table 4), its effects are relatively minor compared to tree size and batch density, and for the purposes of simplicity, clutch size was assumed to be a constant (300; the approximate mean across sites and years) in the models.

Batch survival increases as the number of batches on the tree increases toward carrying capacity, with larger  $n$  reducing the likelihood of batch predation ( $S_B = p_n$ ). However, above  $k$ ,  $S_B$  levels off and starts to decrease as the probability of resource depletion increases (Fig. 6a). As carrying capacity is a function of tree size, batch survival is highest on large trees when the number of batches is close to the carrying capacity. The effects of  $n$  and  $k$  on larval survival are similar to those on batch survival, except that increased  $k$  leads to higher survival even at low  $n$  (Fig. 6b). This results from the positive effect that tree size has on larval survival.

Eqs. 5 and 6 assume that predation is independent for different batches on the same tree. However, at low  $n$ , within-tree predation was not independent in the field (Table 2). If we assume that batches on a

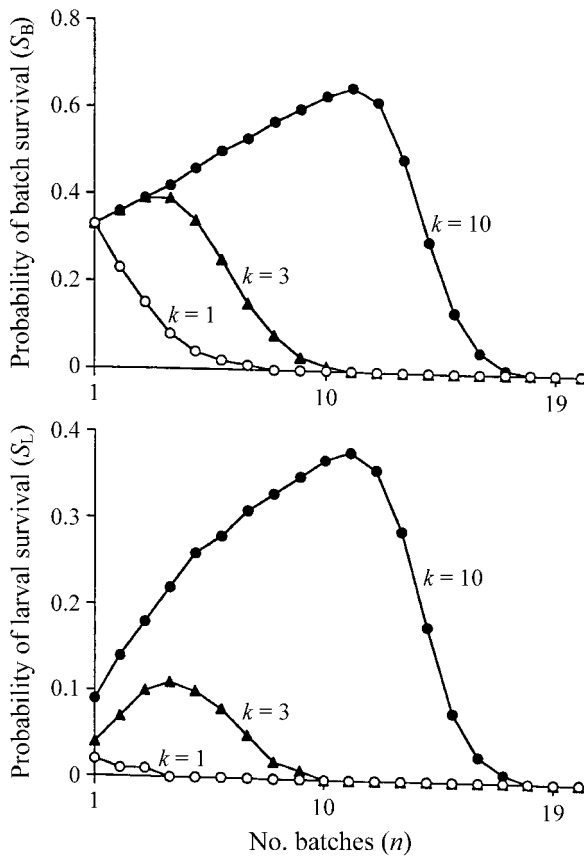


FIG. 6. Probability of (a) a batch (B) and (b) a larva in batch B surviving as a function of the number of batches,  $n$ , present on the tree and the carrying capacity of the tree,  $k$ .

tree either all survive or are all destroyed by predators, the probability that a larva in batch B survives to final instar then becomes the following:

$$\begin{aligned} S_L &= p_1 g(u) && \text{when } n = 1 \\ S_L &= p_n h(u) && \text{when } 1 < n \leq k \\ S_L &= 0 && \text{when } n > k. \end{aligned} \quad (7)$$

Eqs. 6 and 7 form the upper and lower bounds of a set of models, with the probability,  $p_d$ , of other batches surviving predation, given that batch B survives, ranging from  $p_n$  to 1 (Fig. 7).

*Simulations of oviposition behavior:  
estimating the MRD*

Using Eqs. 6 and 7, two numerical models were formulated to predict female oviposition behavior. In each simulation, the number and size of trees, and the number of egg batches in the model universe corresponded to those sampled at a specific locality. Females were introduced sequentially. Each female deposited her eggs on a tree so as to maximize the survival of her offspring,  $S_L$ , given the size of the tree and the number of batches already present. Values of  $S_L$  were calculated

from Eq. 6 for Model I, and Eq. 7 for Model II. In each model, females continue to deposit eggs on the same tree until  $S_L$  drops below the probability of offspring survival on another tree ( $s_2$  in Fig. 7). This occurs when ( $n > z$ ) in Model I (refer to Fig. 7), and when ( $n > k$ ) in Model II. As Eqs. 6 and 7 represent two extremes of a continuous set of models, with  $p_d$  ranging from  $p_n$  to 1, the predicted distribution of batches at a site is such that the number of batches on any particular tree is ( $n = 0$ ) or ( $k \leq n \leq z$ ). This range includes the number of batches that maximizes overall larval survival on the tree ( $s_{\max}$  in Fig. 7), and hence leads to the minimum risk distribution, MRD, for the population, which is similar to the spatial distribution produced by Model II.

The distribution of egg batches was predicted from Models I and II for each locality, and compared against that observed in the field. At most localities, the variance of egg batches per tree in the field was relatively low (Fig. 8a), with females ovipositing on a greater number of trees than predicted by Models I or II (Fig. 9). At four localities, the observed distribution had a similar variance to Model II; however, the spatial patterns that produced the variance were significantly different (Table 5). At each of these localities, particular trees received more egg batches than predicted by Model I ( $n > z$ ), while other trees received less egg batches than predicted by Model II ( $n < k$ ) (Fig. 9). At all localities, many trees received ( $n < k$ ) batches, and more trees received a single batch than predicted by either model (Fig. 8b). This was true not only for woodland habitats, where habitat structure could obscure

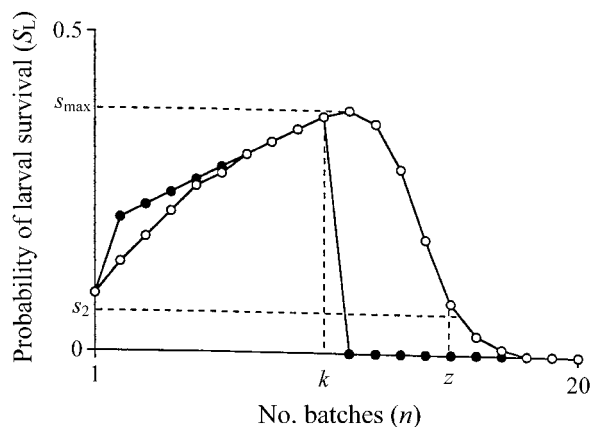


FIG. 7. Probability of larval survival,  $S_L$ , in batch B as a function of the number of batches,  $n$ , present on the tree and the carrying capacity of the tree,  $k$  ( $= 10$ ). Eq. 6 (open symbols): predation of batch B has no effect on the probability of predation of other batches on the tree. Eq. 7 (solid symbols): all other batches suffer the same fate as batch B (either all survive or all perish). Values:  $s_{\max}$  = maximum survival in Eq. 6;  $s_2$  = the probability of larval survival on a second tree, such that females switch to another host when  $S_L < s_2$ ;  $z$  = maximum number of batches oviposited before females switch to another host (i.e., when  $S_L < s_2$ ).



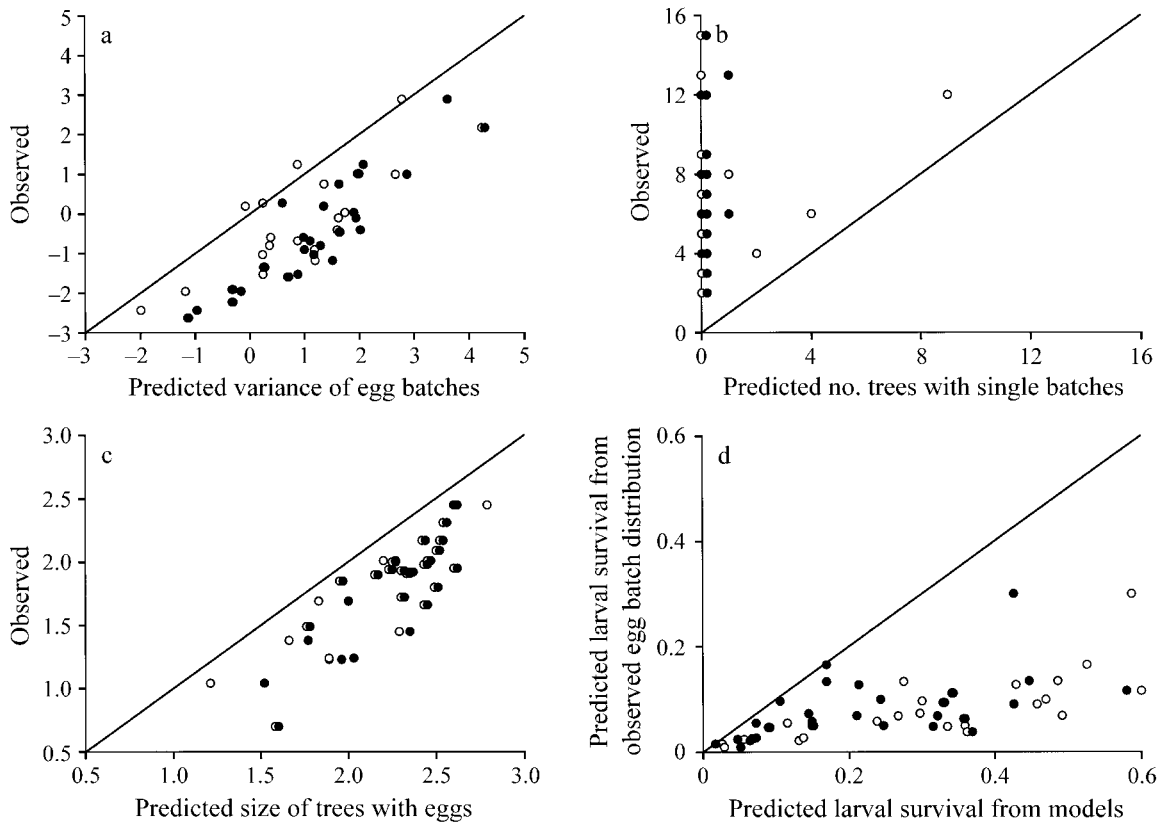


FIG. 8. Tests of Model I (solid symbols) and Model II (open symbols) at 28 localities, showing the relationship between predictions and observations: (a) variance of egg batches across trees; (b) number of trees with a single egg batch; (c) mean size of trees on which females oviposited; (d) predicted larval survival given the predicted and observed distributions of egg batches.

high quality hosts (Floater and Zalucki 2000), but also for open habitats where all hosts were relatively conspicuous (Fig. 9, Table 5). This suggests that constraints exist that prevent females from discriminating accurately between potential hosts on the basis of plant quality (in terms of offspring performance), even when hosts are relatively conspicuous. Females also oviposited on smaller trees than expected (Fig. 8c), particularly in closed habitats, where larger trees could be obscured by surrounding vegetation. These attributes of observed egg batch distributions reduced the probability of larval survival. Overall survival from observed distributions was related to survival predicted from Model II ( $r^2 = 606$ ,  $P < 0.0001$ ); however, the slope of the relationship was significantly less than unity ( $b = 0.2$ ,  $t = 25.4$ ,  $P < 0.0001$ ), indicating that as the potential for higher survival rates increased, actual survival increased absolutely ( $b > 0$ ), but decreased relative to the MRD ( $b < 1$ ) (Fig. 8d).

*Effect of habitat structure on spatial divergence from the MRD*

A combination of habitat characteristics and population density gave a highly accurate prediction of the

degree of divergence of actual egg batch distributions from the MRD in different habitats ( $r^2 = 0.959$ ,  $P < 0.0001$ ) (Fig. 10). Actual distributions diverged from the MRD as egg batch density increased, with the difference between predicted and actual oviposition behavior producing more pronounced effects as more females entered the habitat (Table 6). After accounting for the effect of density, habitat variables explained 85% of the remaining variance in the degree of association. As mean host tree size increased, mean cover increased (cover index I:  $\rho = 0.65$ ,  $P = 0.009$ ; cover index II:  $\rho = 0.50$ ,  $P = 0.057$ ), and variation in cover decreased (cover index I:  $\rho = -0.56$ ,  $P = 0.029$ ; cover index II:  $\rho = -0.47$ ,  $P = 0.079$ ). Mean tree size, mean background cover, and variation in background cover affected the relationship between the MRD and observed distributions, with variables associated with late successional, heterogeneous habitats leading to increased distributional mortality risk (Table 6).

The effect of habitat complexity on the divergence of actual egg batch distributions from the MRD led to a significant reduction in survival ( $r^2 = 0.952$ ,  $P < 0.0001$ ). Increases in overall egg batch density in the habitat and large host tree size led to increased pre-

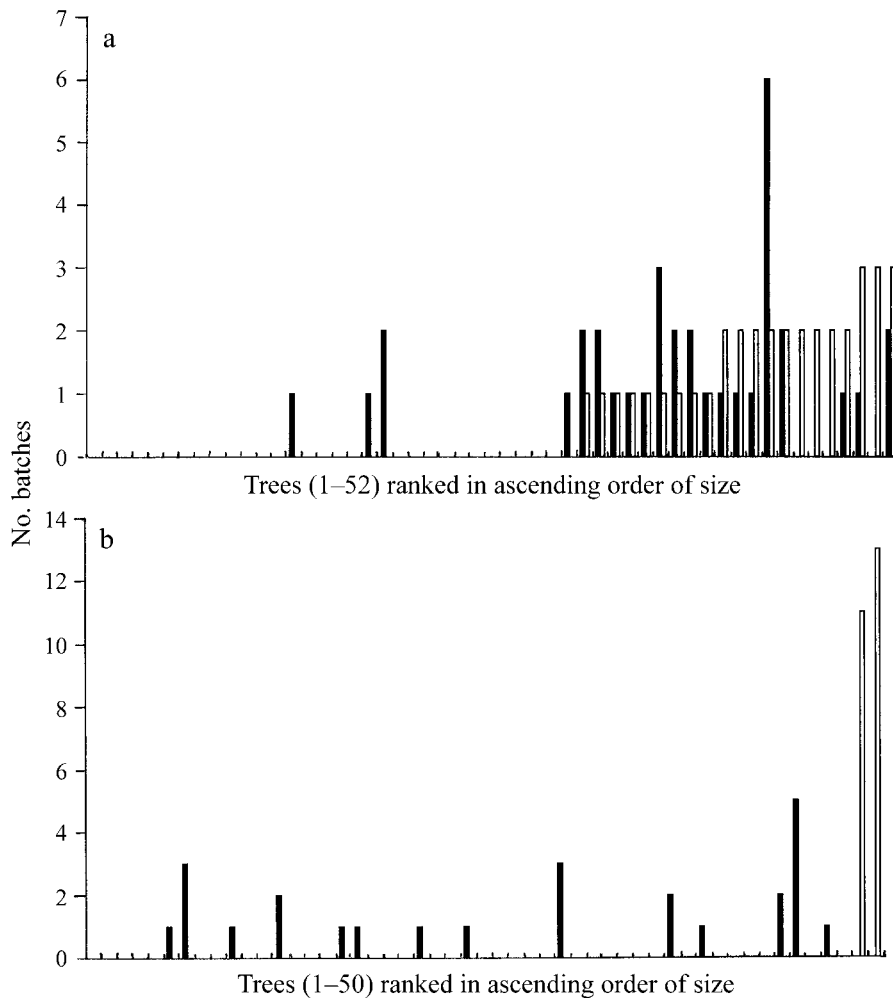


FIG. 9. Relationship between the distribution of egg batches and tree size predicted by Model II (white bars) and that observed in the field (dark bars) at (a) an early successional, open habitat (J2) where most trees were generally conspicuous, and (b) a late successional, woodland habitat (P1) where the amount of cover surrounding host trees was highly variable. Tree size range (trunk diameter): 6–70 mm at J2; 50–270 mm at P1 ( $n = 50$ ).

dicted survival (Table 6). In contrast, increased habitat interference (abundance and variation in background cover around host trees) led to reduced overall survival in the habitat. Furthermore, although survival from actual distributions increased with average host tree size in the habitat, it increased at a lower rate than predicted from the MRD. Thus, as mean tree size increased, the degree of divergence between survival from observed distributions and survival from the MRD increased ( $r^2 = 0.64$ ,  $P < 0.0001$ ).

#### DISCUSSION

##### *Benefits of aggregation*

Cohorts of *Ochrogaster lunifer* displayed several benefits of aggregation, including higher rates of establishment on the host, higher growth rates in later instars, and reduced predation mortality, agreeing with other studies of aggregative insect species (e.g., Long

1955, Morimoto 1967, Morimoto and Masuzawa 1974, Tsubaki 1981, Stamp 1982, Lawrence 1990).

Results of manipulating cohort size in *O. lunifer* revealed a strong reduction in early stage larval survival and development when caterpillars were reared singly or in groups of two or three. Group size can be especially crucial to insect performance when larvae first begin to feed (Ghent 1960, Nakamura 1977, Tsubaki 1981). In *O. lunifer*, large cohort size in the early larval stages could well facilitate feeding by individuals. The early instar larvae feed side by side in a double row along the edge of a leaf. The two rows feed along the same front, with one row positioned on the upper surface and the other on the lower surface of the leaf. Consequently, all the larvae feed in a highly localized area (Floater 1996a). This feeding behavior is found in other gregarious Lepidoptera (e.g., Lawrence 1990), and probably increases the feeding efficiency of each individual.

TABLE 5. Comparison of egg batch distributions predicted by Models I and II with those observed at 28 localities.

Locality	df	Model I		Model II	
		$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
TI12	10	46.7	< <b>0.0001</b>	30.0	<b>0.0009</b>
BC4	16	48.0	< <b>0.0001</b>	48.3	< <b>0.0001</b>
DH1	5	20.6	<b>0.001</b>	14.6	<b>0.012</b>
P3	13	44.3	< <b>0.0001</b>	36.5	<b>0.0005</b>
J2	3	16.0	<b>0.001</b>	17.1	<b>0.0007</b>
WW1	9	18.2	<b>0.033</b>	9.9	0.355
G6	2	3.3	0.185	1.8	0.394
BR1	12	28.0	<b>0.006</b>	27.0	<b>0.008</b>
P2	6	26.0	<b>0.0002</b>	22.0	<b>0.001</b>
P1	11	24.0	<b>0.013</b>	24.0	<b>0.013</b>
Y1	5	18.1	<b>0.003</b>	13.1	<b>0.023</b>
J1	5	16.1	<b>0.007</b>	10.0	0.076
MC12	8	7.1	0.526	7.1	0.526
MN1	13	15.0	0.307	15.0	0.307
D1	13	16.0	0.249	16.0	0.249
L123	15	37.0	<b>0.001</b>	37.0	<b>0.001</b>
N1	7	11.0	0.140	7.3	0.398
TF412	8	10.1	0.259	6.1	0.634
TH4	9	10.0	0.350	10.0	0.350
TH12	13	17.0	0.199	17.0	0.199
LR1	4	3.1	0.538	3.1	0.538
TH3	2	2.0	0.363	2.0	0.363
MG3	13	6.0	0.946	6.0	0.946
TF6	5	6.0	0.305	6.0	0.305
TH6	2	4.0	0.129	2.0	0.363
BC23	15	5.0	0.992	5.0	0.992
EK1	7	2.0	0.959	2.0	0.959
WR2	4	0.5	0.974	0.5	0.974

Notes: Trees were grouped into size categories of  $k = 0, 1, 2, 3$ , etc. for goodness of fit tests, where  $k$  is the tree's carrying capacity (i.e., the number of batches that a tree can support). Localities are ranked in order of egg batch density from highest (TI12) to lowest (WR2); localities with high mean tend to show a significant difference between observed and predicted distributions. Statistically significant ( $P < 0.05$ ) results are highlighted by bold type.

Larger group sizes also enhanced larval survival in later instars. When transferred to the field, fourth instar larvae in groups of <100 went extinct before completing development (cf. Watanabe and Umeya 1968, Morris 1972). Furthermore, larval survival and growth

was enhanced when several clutches, deposited on the same tree, amalgamated in later instars. Larger groups of late stage larvae may enhance the effectiveness of nest web construction (Shiga 1976, Tsubaki 1981), and aggregative defense (Itô and Miyashita 1968, Morimoto 1976, Morris 1976, Brown and Cameron 1979, Lawrence 1990). Breuer and Devkota (1990) found that the larval nest of *Thaumetopoea pityocampa* (Den. and Schiff.), a species related to *O. lunifer* with a similar ecology and life history, stores thermal energy due to the aggregation of the larvae and the insulation afforded by the web and frass in the nest. The nest web of *O. lunifer* also helps to shield the larvae from tachinid parasitoids (Floater 1996a).

As well as increasing larval performance through its effects on feeding efficiency, aggregation reduced predation in the egg and early instar stages. Although laying eggs in large batches did not prevent entire batches from being destroyed by dermestid predation, the aggregation of the batches themselves was found to have a significant effect on batch predation, with single batches having a high probability of extinction. The inverse density-dependent spatial pattern of dermestid attack was almost certainly due to the random spatial pattern of these generalist predators across trees, combined with predator satiation; each predator can destroy a limited number of egg batches, leaving batches with reduced risk when aggregated.

Costs of aggregation

While the benefits of aggregation in *O. lunifer* are many, living in groups also carries associated costs, including reduced early stage survival in very large batches, and the increased risk of host defoliation and scramble competition. While larval survival in experimental cohorts increased with group size (with manipulated group sizes ranging from one to 200 in early stage experiments, and three to 150 in late stage experiments), larval survival in natural cohorts observed in the field was lower in larger batches (with the number

FIG. 10. Effect of habitat complexity and population density on the divergence of spatial patterns of egg batches from the minimum risk distribution, MRD. Independent variables include: mean host tree size, mean quantity and degree of vegetative cover around host trees, variation in the degree of cover around host trees, and mean number of egg batches per host tree (see Table 6). The dependent variable is the  $\chi^2$  value calculated in Table 5. The high correlation between the predicted and observed divergence of egg batch spatial distribution demonstrates that higher habitat complexity leads to spatial distributions with higher mortality risk and therefore lower population growth.

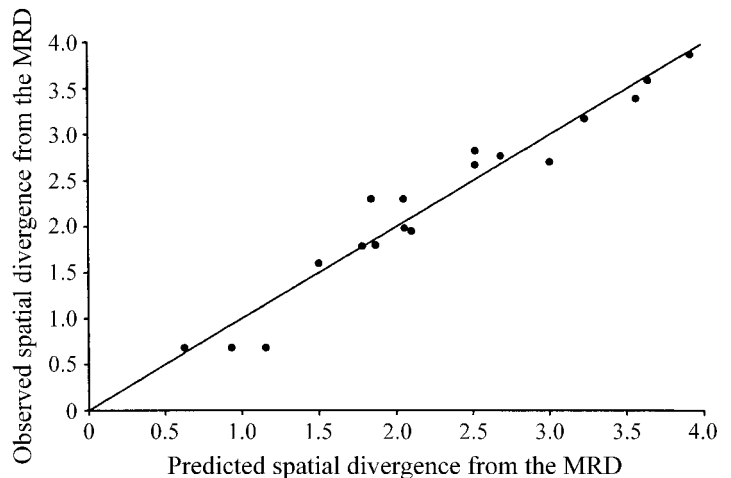


TABLE 6. Effects of population density (mean number egg batches per tree) and habitat characteristics on the spatial distribution and survival of egg batches of *O. lunifer* using multiple linear regression.

Habitat characteristic	Effect on spatial distribution†			Effect on survival‡		
	<i>b</i> §	<i>t</i>	<i>P</i>	<i>b</i> §	<i>t</i>	<i>P</i>
Population density	0.6	10.56	<0.0001	0.02	4.59	0.0008
Mean tree size	0.5	5.28	0.0003	0.08	9.46	<0.0001
Mean cover (index I)	1.1	3.71	0.003	-0.08	-4.35	0.001
Mean cover (index II)	-0.8	-3.88	0.003	...	...	...
CV   cover (index I)	...	...	...	-0.13	-3.75	0.003
CV cover (index II)	0.8	2.32	0.041	...	...	...

† The effect of habitat characteristics on the divergence of observed egg batch distributions from the minimum risk distribution, MRD (using  $\chi^2$  values from Table 5).

‡ The effect of habitat characteristics on predicted survival from observed egg batch distributions in different habitats.

§ *b* = regression coefficient.

|| CV = coefficient of variation.

of eggs per batch ranging from 140 to 555). Combining field and experimental data, the optimal clutch size for larval survival was estimated to be 150 eggs. Batches that give rise to >200 second instar larvae may suffer reduced survival at the feeding initiation stage, as the entire cohort cannot feed on a single leaf simultaneously, which may reduce larval feeding efficiency. Alternatively, larger egg batches and larger cohorts of early stage larvae may suffer proportionately higher rates of parasitism and predation from species other than dermestids (Floater 1996a). Whatever the mechanisms that increase mortality risk for larger batches, they clearly operate in the egg and/or early larval stages when batches deposited on the same host remain independent. By the fourth instar, different batches occupying the same host amalgamate into a single large cohort, leading to increased larval survival in the later stages.

The most important mortality risk associated with the aggregation of eggs and larvae is the risk of host defoliation. Defoliation risk increases with smaller host size, a higher number of batches surviving dermestid predation, and larger batch size. Of these, the most significant factors are tree size and batch number. Defoliation does not necessarily lead to the mortality of larvae, as a cohort can travel to a secondary host and complete development. This was observed at the Lytton site (L123) where a cohort on a small sapling traveled to a second sapling growing one meter away. Furthermore, larvae can travel relatively long distances; final instar larvae can travel >100 m from the host before entering prepupal diapause. However, the success rate of larvae finding a secondary host is low (Floater 1996c), with an estimated probability of success in the present study of 11%. Larvae require a constant supply of food, particularly in the later stages, and probably cannot survive without food for more than a day or two. While emigration success was assumed to be zero in models of female behavior, a higher success rate would increase the benefits of egg batch aggregation, predicting a higher variance of egg batch distributions

than predicted by the models. In contrast, observations of egg batch distributions demonstrated a significantly lower batch variance than predicted by the models.

In early successional, open habitats, the probability of emigration success is probably higher than in late successional habitats where distances between hosts are generally greater, and the presence of other tree species reduces the probability of a cohort locating a suitable secondary host. However, it was in open habitats, where females had a greater choice of conspicuous hosts, that egg batches tended to be clustered on larger trees, suggesting that there is a strong link between oviposition behavior and increased offspring survival on larger trees. Furthermore, in early successional habitats, where all acacia hosts are relatively young and small, the probability of a larval emigration event is higher (some hosts cannot support a single batch to pupation), and as larvae can travel longer distances in later instars, even small differences in tree size in young habitats may lead to a significantly different likelihood of larvae locating a secondary host. This, combined with higher levels of larval performance on larger trees, has probably led to strong directional selection on female oviposition behavior. That females in late successional, closed habitats (habitats where the range of tree size is much greater than in younger habitats) do not locate and oviposit on larger hosts, suggests that constraints, or greater counteractive selection pressures, exist that are associated with female searching behavior.

#### *The cost-benefit trade-off: quantifying the MRD*

With females constrained to laying a single batch of eggs, the MRD for *O. lunifer* resulted from the spatial distribution of entire batches. Host quality (with regard to larval performance) can be defined almost entirely in terms of host tree size for *O. lunifer* larvae; differential leaf chemistry in the field has relatively little effect on oviposition and larval performance (Floater and Zalucki 2000). Female fitness is, therefore, in-



creased by ovipositing on large trees, and the resulting MRD for *O. lunifer* is a nonrandom pattern of egg batches with regard to tree size.

Of all the costs and benefits associated with the aggregation of egg batches in *O. lunifer*, the dominant two were dermestid predation (with mortality risk decreasing with aggregation) and resource depletion (with mortality risk increasing with aggregation). While the risk of dermestid predation can be reduced by aggregating egg batches on the same tree, this carries the risk of resource depletion, scramble competition, and high (often 100%) mortality. The minimum risk distribution (MRD) for egg batches of *O. lunifer*, therefore, displays a high aggregation of batches on the largest trees in the habitat, with the number of batches on each tree approaching the tree's carrying capacity.

The deposition of a single batch of eggs by a female in her lifetime is a high risk strategy given the high frequency of batch extinctions in each generation. Furthermore, offspring survival in the field was significantly lower in larger clutches, and higher when several batches were deposited on the same host, suggesting that fitness would be increased substantially if females laid several smaller clutches (even if laid on the same tree) rather than all eggs in a single clutch. When clutch size was manipulated below the range of clutch sizes present in the field, larval performance was reduced significantly; the optimal clutch size was estimated to be 150 eggs, corresponding to the smallest clutches observed in the field.

A plausible reason for females depositing larger clutches than expected is that protection of the eggs would be compromised if laid in separate batches. Although egg predation from dermestids is high, loss of eggs from predation and parasitism would be significantly higher were it not for the protective scale covering over the eggs. Field experiments have shown that the likelihood of egg batch loss from predation increases significantly when the scale covering is artificially removed (Floater 1998). The provision of an effective scale covering for several batches may be more difficult than covering a single batch (both in the systematic way in which the female removes the scales from her abdomen and due to the increased surface area several batches would create). The important protective role of deciduous scales could, therefore, contribute to the maintenance of single clutches.

As long as females are constrained to laying a single clutch, fitness is maximized by maximizing the number of eggs; for although the absolute number of survivors approximates to a constant at higher densities (with higher densities leading to proportionately higher mortality), larval growth rates continue to increase with density. With females constrained to laying a single batch in their lifetime, the MRD for *O. lunifer* is solely a consequence of the spatial distribution of batches rather than the number of eggs per batch.

#### *Habitat interference: the divergence of herbivore spatial patterns from the MRD*

The divergence of actual egg batch spatial patterns from the MRD was due to habitat interference, with the density and variation of vegetative cover around hosts interfering with the ability of females to locate the highest quality hosts for larval survival in the habitat. Large average tree size and high levels of vegetation cover were associated with dense, late successional habitats, where egg batches tended to be aggregated on a few exposed hosts on habitat edges or in clearings (see also Floater and Zalucki 2000).

As females are constrained to laying a single batch of eggs, characteristics of the host tree on which the batch is laid (including the number of other batches present on the tree) have important consequences for female fitness and represent strong selection pressures on female oviposition behavior. However, although these selection pressures are strong, the time that females can spend searching for higher quality hosts for higher offspring performance is limited; and therefore a quantitative increase in habitat interference (due to background vegetation) leads to an egg batch spatial pattern diverging from the MRD. Constraints on searching time appear to involve, at least in part, the short life-span of the adult female; females possess no functional mouthparts, and can only survive two to three days.

While the presence of egg batches or other females can influence oviposition decisions in some species of Lepidoptera, leading to "cohesive aggregation" (e.g., Tsubaki 1981), females of *O. lunifer* do not aggregate before oviposition, and there is no evidence from egg batch distributions that oviposition is influenced by the presence of other batches on a tree. Rather, the aggregation of egg batches is a direct consequence of habitat and host heterogeneity ("adhesive aggregation"), a phenomenon that is probably more widespread in herbivorous insects than is generally thought (Desouhant et al. 1998).

Although quantitative effects of habitat heterogeneity on the divergence of actual spatial distributions from the MRD are unknown for other herbivore species, there is substantial evidence that the link between oviposition and subsequent larval performance is weak in many taxa (Wiklund 1975, Chew 1977, Morrow 1977, Jermy and Szentesi 1978, Thompson 1988, Roininen and Tahvanainen 1989, Price 1991), even in some gall-forming and leaf-mining species (Burstein and Wool 1993, Marini-Filho et al. 1997), which are generally regarded as having a strong preference-performance linkage (Price 1991). Evidence suggests that poor linkage is often due to females ovipositing on "apparent" host plants (Cromartie 1975, Feeny 1976, Rausher 1979, Dempster and Hall 1980, Courtney 1982, Fowler 1984, Wiklund 1984, Day 1986, Soberón et al. 1988, Firempong and Zalucki 1990, Chew and

Courtney 1991, Damman 1991), and consequently, the level of habitat interference (which governs variation in resource apparency in the habitat) should have a significant effect on the divergence of actual herbivore distributions from the minimum risk distribution for many herbivore species.

*Habitat interference and herbivore spatial patterns: consequences for population stability*

Most population biologists agree that density-dependent factors must exist in nature for populations to remain stable over time, although the form that these factors take has been debated by regulationists (Sinclair 1989) and advocates of population limitation with resource ceilings (Milne 1957, Dempster 1971). However, the search for density-dependent factors in natural systems has often diverted attention away from the link between the evolutionary principle of individual fitness and associated population growth rates, and without a firm foundation in evolutionary ecology, traditional population theories have been open to criticisms of untestable post hoc assumptions (Royama 1992).

The present paper attempts to circumvent the impasse in the density dependence debate by providing a different framework for population stability that links individual fitness, spatial interference, and population growth, leading to a number of associated hypotheses that can be tested. This is not to say that this framework is a substitute for regulation, resource limitation, or spreading of risk theories, but that it can provide new insights into all these dynamical models.

While the framework of system interference should combine the effects of adhesive and cohesive aggregation (Fig. 1), this paper concentrates on the former, as an increasing literature on cohesive aggregation has already started to develop (e.g., Walde and Murdoch 1988, Hassell et al. 1991, Taylor 1993, Van den Meer and Ens 1997). The following six hypotheses can be erected from the premise that spatial interference, and in particular habitat complexity, governs population stability. (1) Spatial patterns of individuals should diverge from the MRD as habitat complexity (i.e., spatial interference) increases. (2) Stable population dynamics should be more common in complex habitats, while a higher frequency of site-wide outbreaks and crashes should be observed in simple habitats (e.g., in plantations, crops, open environments). (3) If population spatial patterns are governed by "adhesive aggregation," the level of aggregation (measured as the CD or CV) should increase with habitat complexity. (4) The action (and detection) of spatially density-dependent predation/parasitism should become more pronounced with habitat complexity as the variance in host density increases (this applies to regulating and non-regulating density dependence). (5) The link between herbivore host preference and subsequent performance should be stronger in simple habitats. (6) If populations are limited by subdivided resource ceilings, habitat complex-

ity (spatial interference) should increase stability by increasing the frequency of localized outbreaks (e.g., defoliated plants); and, thereby, decreasing site-wide outbreaks.

In the *O. lunifer* system, results of the present study appear to satisfy Hypotheses 1 and 5 explicitly, while there is some evidence that Hypothesis 4 also holds true. Data yet to be published will be used to test Hypotheses 2, 3, and 6.

*Hypothesis 1.*—Habitat complexity governs the divergence of herbivore spatial patterns from the MRD in two ways. First, by interfering with host-searching, habitat structure leads to a distribution of herbivores on lower quality hosts, and so leads directly to a weaker preference–performance linkage (Hypothesis 5). The actual distribution need not have a higher variance than the MRD, and therefore its divergence cannot be tested by examining the statistical properties of the herbivore distribution alone; divergence from the MRD is governed as much by the distribution of host quality as by the degree of herbivore aggregation. Second, habitat interference also tends to lead to a more aggregated herbivore distribution with higher variance. As variance increases, density dependent predation (Hypothesis 4) and scramble competition will become more pronounced.

The effect of this on population growth can be seen in Fig. 11. Maximum population growth occurs when *O. lunifer* batches are aggregated to the carrying capacity of trees in the habitat (Fig. 11a). However, habitat interference leads to many trees with one or two batches which are prone to higher predation risk, while a few apparent trees receive very high aggregations of batches that are prone to resource depletion with resulting starvation (Fig. 11b). The number of batches in the habitat that are at low risk is, therefore, reduced significantly from that under the MRD.

*Hypothesis 2.*—Many outbreaks of pest species on crops and plantations are known to display more stable dynamics in natural habitats. To test that this is due to altered pest spatial patterns and within-population movements, rather than increased resource ceilings or lower levels of natural enemies, will require linking outbreaks to spatial interference. Indirect evidence comes from Andow's (1990) comprehensive study of resource ceilings and natural enemies in the *Epilachna* bean system, which found that non-host plant interference was the most important component governing population density.

*Hypothesis 3.*—Species that evolve in complex habitats, with high spatial interference, may experience less intense selection for cohesive aggregation than those in simple habitats, and adhesive aggregation is probably much more prevalent in natural systems than presently acknowledged (Desouhant et al. 1998). That being so, many species should display increasing levels of aggregation with increasing habitat complexity. The link between habitat complexity and aggregation

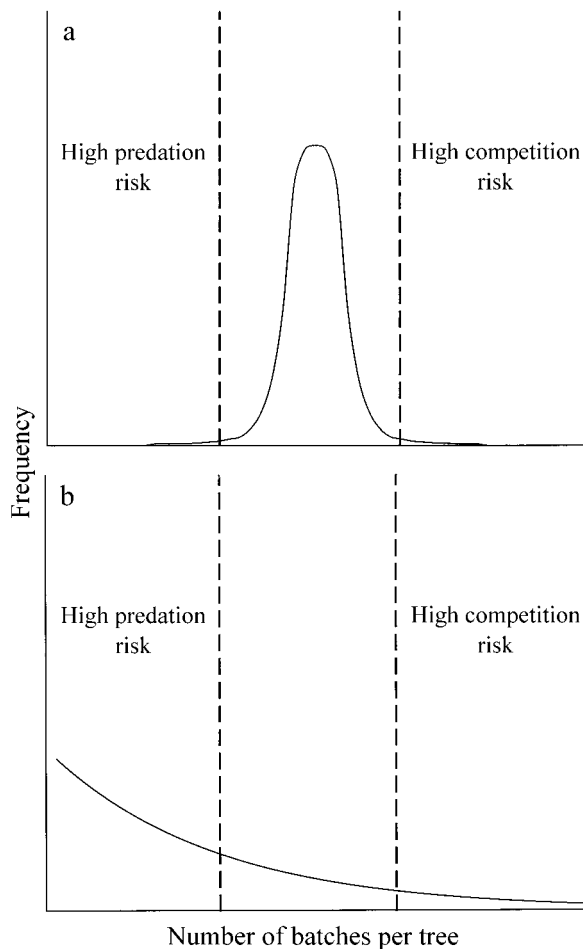


FIG. 11. Effects of spatial interference (habitat complexity) on the divergence of herbivore spatial patterns from the minimum risk distribution, MRD. (a) In simple habitats, without interference from background vegetation, the distribution of herbivores approaches the MRD, with a high frequency of egg batches that avoid the risks of predation at low densities, while avoiding the risks of competition at high densities. (b) In complex habitats, with high levels of background interference, many plants receive low herbivore densities that are at risk from inverse density-dependent predation, while a few trees receive extremely high densities that are at risk from resource depletion and scramble competition. For simplicity, all plants are assumed to be of equal size in the habitat.

should hold both temporally (e.g., increasing habitat complexity with succession, reduced habitat complexity with disturbance) and spatially (between different habitat types).

**Hypothesis 4.**—In predicting the stabilizing effects of natural enemies on herbivore population dynamics, researchers have generally sought empirical solutions from highly specific interactions, notably between herbivores and parasitoids (Walde and Murdoch 1988, Hochberg 1996). This is in part because the less coupled the interaction between natural enemy and prey, the less likely that each can stabilize the other's dynamics. However, theoretical studies have also high-

lighted the potential role of generalist natural enemies in the population dynamics of their prey (Murdoch and Oaten 1975, Southwood and Comins 1976, Hassell and May 1986). Clearly, neither inverse density-dependent nor density-independent predation can stabilize herbivore dynamics alone, as they cannot check the increase in herbivore abundance; but they can be vital components of stability by reducing population growth rates. In the dermestid-*O. lunifer*-acacia system, dermestid predation can increase stability in at least two ways. First, by increasing *O. lunifer* mortality, predation reduces the high population growth rates that can destabilize an otherwise stable system. Second, inverse density-dependent predation results in a greater number of empty trees in the habitat that may be used by larvae dispersing from defoliated hosts. Even if successful dispersal from one tree to another is rare (as in *O. lunifer*), it could be enough to prevent site-wide extinction.

**Hypothesis 5.**—There is a large literature on the link between host preference and larval performance for insect herbivores (Thompson 1988, Floater 1997). However, the relative effects of host quality and host apparency on the overall spatial distribution of herbivores within habitats have rarely been assessed (Floater and Zalucki 2000), and there is great potential for investigating the effects of habitat complexity on the preference-performance link.

**Hypothesis 6.**—In the *O. lunifer* system, habitat complexity clearly leads to over aggregation on apparent trees with resulting defoliation and scramble competition. Whether these frequent resource ceilings are the density-dependent factors that actually govern the stabilization of populations needs to be tested more rigorously over longer time scales. What is clear, is that resource ceilings on trees with over-aggregated batches, combined with inverse density-dependent predation directed at under-aggregated batches, significantly reduce the population growth rate and so contribute to population stability (Fig. 11).

The interference of habitat structural complexity on herbivore spatial patterns also has consequences for herbivore establishment in new habitats, and maintenance in mature habitats. In the case of *O. lunifer*, the potential for larval survival, and therefore establishment, in young habitats, is relatively low because host trees are relatively small. Small hosts increase the cost of aggregation due to scramble competition, thereby leading to an MRD with a low degree of aggregation and increased predation risk. However, these young habitats are relatively open, and egg batches tend to be concentrated on the larger trees in the habitat, thereby approaching the MRD for the habitat (Fig. 11a), and nearing the potential for maximum population growth (albeit low) for the habitat, leading to maximum likelihood of establishment (Floater and Zalucki 2000).

In mature habitats, the potential for larval survival is high because egg batches can be highly aggregated

on large hosts without costs of scramble competition, while increasing the benefits of reduced predation risk. However, mature habitats tend to be more complex than younger habitats, with high densities of different plant species interfering with the ability of females to aggregate their batches effectively on the largest, high quality hosts in the habitat. The high level of divergence between the actual egg batch distribution and the MRD in these mature, complex habitats may consequently reduce the destabilizing effects of high population growth rates (Fig. 11b).

The MRD will take different forms in different species with different costs and benefits of aggregation or regularity. However, although it is difficult to predict whether particular types of MRD will lead to higher or lower levels of association between predicted and actual animal spatial patterns without studies on different taxa, knowledge of the association itself should be a highly effective means of predicting trends in population dynamics. Species with a low potential for population growth (due to risk trade-offs that result in high mortality costs at all levels of aggregation), or that have a low association between their actual spatial distribution and their MRD, may display relatively stable dynamics at low population levels. In contrast, species with high potential for survival coupled with a high level of association between their actual spatial distribution and their MRD should experience frequent outbreaks. Spatial interference, and in particular the degree of habitat complexity, may therefore prove a key predictor of herbivore population persistence or extinction.

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#### APPENDIX

A description of 29 habitat localities for populations of *O. lunifer* in southeast Queensland, with code references and the number of trees sampled at each site is available in ESA's Electronic Data Archive: *Ecological Archives* M071-006.