

Travel costs, oviposition behaviour and the dynamics of insect–plant systems

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Abstract Insect attack can have major consequences for plant population dynamics. We used individually based simulation models to ask how insect oviposition behaviour influences persistence and potential stability of an herbivore–plant system. We emphasised effects on system dynamics of herbivore travel costs and of two kinds of behaviour that might evolve to mitigate travel costs: insect clutch size behaviour (whether eggs are laid singly or in groups) and female aggregation behaviour (whether females prefer or avoid plants already bearing eggs). Travel costs that increase as plant populations drop lead to inverse density dependence of plant reproduction under herbivore attack. Female clutch size and aggregation behaviours also strongly affect system dynamics. When females lay eggs in large clutches or aggregate their clutches, herbivore damage varies strongly among plants, providing probabilistic refuges that permit plant reproduction and persistence. However, the population dynamics depend strongly on whether insect behaviour is fixed or responds adaptively to plant population size: when (and only when) females increase clutch size or aggregation

as plants become rare, refuges from herbivory weaken at high plant density, creating inverse density dependence in plant reproduction. Both herbivore travel costs themselves, and also insect behaviour that might evolve in response to travel costs, can thus create plant density dependence—a basic requirement for regulation of plant populations by their insect herbivores.

Keywords Density dependence · Oviposition behaviour · Herbivory · Phytophagous insects · Population regulation · Travel costs

Introduction

Despite a long history of research into interactions between phytophagous insects and their host plants, the population- and community-level consequences of these interactions remain incompletely understood (Halpern and Underwood 2006; Maron and Crone 2006). There is little doubt that phytophagous insects can have important impacts on plant population dynamics: they can reduce plant population sizes (Harris 1986; Bach 1994; Louda 2001; Maron et al. 2002), reduce rates of population growth (Fagan and Bishop 2000; Maron et al. 2002; Maron and Crone 2006), cause local plant extinctions (van der Meijden 1979; McConnachie et al. 2003) and provide apparently stable density-dependent regulation at low plant density (Moran et al. 2005; Rose et al. 2005; Halpern and Underwood 2006). It is much less clear what aspects of insect or plant ecology determine herbivore impacts on plant population dynamics, and in particular whether and when herbivore attack imposes density dependence in plant reproduction and can therefore regulate plant population size. One factor of obvious interest, however, is among-plant variance in

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herbivore attack. In general, spatial variation in consumer impact is thought to stabilise exploitative interactions, including predator–prey (Taylor 1984), parasite– and parasitoid–host (Anderson and May 1978; Hassell and May 1988) and plant–herbivore (Caughley and Lawton 1981; Crawley 1983) interactions.

Whilst herbivore attack and damage are often highly variable among plants within a population (e.g. Monro 1967; van der Meijden 1979; Wellings 1987; Eber 2004), few studies have connected this variation to plant population dynamics. Importantly, herbivore attack is often variable even without underlying variation in quality of plants for herbivores (or at least, variation in attack does not correlate well with plant quality). We focus here on variation in herbivore attack that can arise even in the absence of plant quality variation. A few plant–herbivore (and related parasite–host) models have incorporated such variation usually, by imposing a negative binomial distribution of consumers over resource patches (plants or hosts, e.g. Anderson and May 1978; Caughley and Lawton 1981; Crawley 1983; Taylor 1988; Rose et al. 2005). However, the ecological mechanisms controlling herbivore distribution are often unknown, and spatial variation generated by different mechanisms can produce very different herbivore distributions and have different consequences for the dynamics of populations and communities (e.g. compare Atkinson and Shorrocks 1981; Green 1986; Heard and Remer 1997).

One important way in which spatial variation in consumer density can be generated is through the behaviour of females as they distribute eggs among potential oviposition sites (plants). Egg distributions may be heterogeneous because female movements during oviposition are influenced by the spatial arrangement of oviposition sites (Remer and Heard 1998), because females lay eggs in clutches (Sevenster and van Alphen 1996; Heard and Remer 1997; Heard 1998) or because females aggregate to particular oviposition sites (Hassell and May 1988). Some consequences of egg distribution behaviour have been examined for competitive (e.g. Ives 1991; Heard and Remer 1997; Remer and Heard 1998) and host–parasitoid (e.g. Hassell and May 1988; Rohani et al. 1994) interactions, but for plant–herbivore systems, only a few verbal models have been available (except see Myers 1976). Oviposition behaviour varies greatly among phytophagous insects (e.g. Johannesen and Loeschke 1996) and could play an important role in determining the outcome of herbivore–host plant interactions (e.g. Myers et al. 1981; Zwölfer and Völkl 1997).

We sought to understand the consequences of insect oviposition behaviour for the population dynamics of plant–herbivore systems by building models explicitly addressing two major issues: first, how oviposition behav-

our can contribute to among-plant variance in herbivore attack, and second, how this variance might mediate connections between insect behaviour and plant population dynamics. We were especially interested in insect behaviours that could generate (plant-) density-dependent impacts of herbivory, as such effects could lead to stable regulation of plant populations by herbivore attack. It is unknown how common such regulation is for native plants (Halpern and Underwood 2006; Maron and Crone 2006), but it is central to successful biological control of invasive plants by herbivores (e.g. Moran et al. 2005).

We focused on two particular aspects of oviposition behaviour: clutch size and the aggregation of clutches across plants (by a “clutch”, we mean the set of eggs deposited by one female during one visit to one host plant). Our interest in clutch size stems from the possibility that females might adjust clutch sizes as an adaptive response to variation in host plant density (laying fewer, larger clutches to avoid travel costs when plants are rare; Heard 1998; Shea et al. 2000). Previous suggestions about the effects of such behaviour on the stability of exploitative systems have been contradictory (compare Hassell 1980; Taylor 1988; Cronin and Strong 1999), and ours is the first model to address these effects explicitly. Aggregation of clutches is of interest, among other reasons, because it has been offered as an explanation for stability in the successful biological control of *Opuntia* by *Cactoblastis* (Myers et al. 1981). Although previous studies have largely considered aggregation as a fixed behaviour, travel-costs arguments suggest that (like clutch size), aggregation behaviour might be under selection to respond to plant density. Our models make novel predictions about the effects of travel costs, and the herbivore oviposition behaviours that would be expected to evolve in response to those costs, on the stability of plant–herbivore interactions.

Methods

We used simulation models written in QuickBASIC (Microsoft 1988) to examine the effects of oviposition behaviour on the persistence of an insect–host plant system. In these simple models, all plants are identical, insect and plant generation times are the same (for instance, annual plants and univoltine insects), and plant generations are non-overlapping (i.e. there is no persistent soil seed bank). We modelled the common case where relatively sedentary larvae are distributed over host plants by adult females; therefore, we did not permit dispersal among plants by larvae. Whilst these assumptions are fairly restrictive, our intention was to provide a clear focus on simple oviposition behaviours rather than to produce a detailed model of any particular insect–plant species pair.

We were primarily interested in how different oviposition behaviours affected two properties of insect–plant dynamics. First, we recorded the persistence time for the plant–herbivore system. Second, we tested for the presence or absence of density dependence in plant reproduction; when inverse density dependence arises, it is possible for insect herbivory to regulate the plant population.

Oviposition

In our model, each generation begins with H (for ‘herbivore’) adult insects exploiting an array of P host plants. Each insect is designated male or female with equal probability (therefore, we allow for stochastic extinction of small populations due to a lack of females). For each female, a first host plant is chosen (see below) and a clutch of c eggs is laid on it. A second host plant is then chosen and a second clutch (again of size c) is laid. This continues until the female exhausts her supply of λ_h eggs (λ_h being total herbivore fecundity, and $c \leq \lambda_h$) and is repeated for each female. We assume that each female begins with a fixed egg supply and cannot replace eggs that are laid, an assumption met by many insects (Büning 1994). Females incur costs of travel in the form of a mortality risk (for plant population size P , dying with probability $q_p = k_1/\sqrt{P+k_2}$) associated with each movement to a plant (including the first). Our expression for travel costs includes a component scaled to the expected distance between host–plant individuals (k_1/\sqrt{P}), plus a component associated with each visit to a plant independent of the distance traveled to get there (k_2). Note that in some simulations, we used values of k_1 and k_2 that could make $q_p > 1$ for small P . Whilst the interpretation of q_p as a mortality risk could be preserved simply by capping q_p at 1.0, in practice, we never saw P take values that would have required application of this rule.

In our simplest models, clutch size is constant (for all females in all generations), and a plant is chosen at random to receive each clutch. In more complex models, we relax each stricture in turn: first, we allow clutch sizes to respond to changes in plant population density, and second, we allow females to discriminate either for or against plants already bearing eggs. We will return to these complications after describing the simplest model in full. We ignore the possibility of spatial structure arising when females move locally (i.e. primarily among neighbouring plants). Such spatial structure is likely to have interesting consequences (Remer and Heard 1998), but is outside the scope of this manuscript.

Intraspecific competition

Once all individuals have laid their eggs, a modified Hassell–Comins competition equation (Hassell and Comins 1976; Heard and Remer 1997) determines the number of

adults emerging from each host plant. Let y_i be the yield of adults from host plant i ; these adults are the survivors of the e_i eggs that were laid there:

$$y_i = e_i(1 + ae_i)^{-b} \quad (1a)$$

$$\text{where } a = 2 \left[(\lambda_h/2)^{1/b} - 1 \right] / (\lambda_h K). \quad (1b)$$

Here, b defines the shape of the competition function along a continuum from contest to scramble, and a represents the strength of competition among larvae on a single plant. In the expression for a , λ_h is the herbivore fecundity and K the carrying capacity of a single plant (the number of adult insects produced at equilibrium by one plant replaced each generation). Except as otherwise indicated, we used a standard set of parameter values: $b=1$ (contest competition), $\lambda_h=16$, and $K=4$. These values were chosen as representative; other values change persistence times, but do not change trends in persistence times with changes in oviposition behaviour.

Plant reproduction

After simulating insect competition, we evaluated damage done to each host plant. Herbivore damage will be relevant to plant population biology whenever it has a measurable impact on plant reproductive output. We modelled the reproductive output of plant i as

$$R_i = \lambda_p(1 - y_i/E)^d \quad (2)$$

where the exhaustion load E is the number of herbivores required to reduce a plant’s reproduction to zero, and λ_p the reproduction expected of an undamaged plant (we set $\lambda_p=4$). Note that λ_p and R_i are small because they do not represent seed set but rather recruitment of new adult plants (henceforth, we refer to this simply as ‘‘plant reproduction’’). Herbivore attack could reduce R_i by reducing seed set or through reductions in seed provisioning resulting in lower germination or survival of offspring seeds or seedlings. The parameter d controls the shape of the herbivore load–plant reproduction curve: $d=1$ makes the relationship linear, whilst $d < 1$ makes the curve concave down, as it will be if plants show tolerance to herbivory. We explored d values between 0.2 and 1, using $d=0.3$ except as otherwise indicated because we expect most d values in nature to be small (most plant species show substantial tolerance; Hendrix 1988, Stowe et al. 2000, Tiffin 2000, Fornoni et al. 2003). We added reproduction across all individual plants to obtain population-level reproduction.

The treatment above does not incorporate any self-regulation of the plant population (there is no inherent density dependence of plant reproduction). We adopted this somewhat unrealistic approach so that any regulation of the

plant population imposed by herbivory would be clearly evident. To keep computational demands reasonable, though, we did cap the plant population at $P_{\max}=400$ individuals, and many simulations have the plant population persisting at that cap. To ensure that our neglect of plant density dependence did not colour our results, we implemented an alternative model with linear density dependence of plant reproduction at all plant densities. Qualitative results did not differ between the two models, but interpretation of herbivory effects was much more straightforward in the former model, and so we do not discuss the plant-density-dependent alternative further.

In our simulations, we generally set the carrying capacity K of a host plant (for herbivores) equal to its exhaustion load E ($E=K=4$). Although this may seem restrictive, only when $E \approx K$ are plant–insect interactions of much ecological interest ($E \approx K$ when the number of herbivores required to reduce plant reproduction to zero is not much different from the maximum number the plant can support). E can never be much less than K because when $E \ll K$, even very low herbivore loads completely suppress plant reproduction: if such plants existed, herbivores would quickly drive them to extinction. On the other hand, when $E \gg K$, even heavy herbivore infestation does not affect plant reproduction—so there are no population-dynamic consequences of herbivory to be studied. That E is often close to K is evident from the fact that many plants suffer measurable, and sometimes severe, impacts from herbivory.

Iterating the model

After each generation, the number of emerging adult insects, the number of plants and the clutch size calculated above were used as starting conditions for the next generation. A simulation ended either when the host plant or herbivore went extinct or after 10,000 generations without extinction. Ten thousand generations exceed the expected timescales of both environmental perturbations and evolutionary change, and so we consider longer term behaviour of our models of little interest (Heard and Remer 1997). We considered a species extinct when it was represented by fewer than two individuals, and we report persistence times (generations before extinction) averaged over 100 simulations.

We do not report formal statistical tests of patterns in our results because those results are so clear. In all plots of our simulation results, 95% confidence intervals are approximately the size of the symbols.

Clutch size adjustment

In some simulations, we let insects alter their clutch size in response to plant population density. This behaviour is

interesting because as plants become rare, the costs of travel among plants should increase ($k_1 > 0$ in our travel-costs equation). Females can minimise travel costs by allocating eggs to larger but fewer clutches (and therefore visiting fewer plants), but large clutches impose high sib competition costs. A female behaving optimally should balance these costs by increasing clutch size when plants are rare (to minimise travel costs), but decreasing clutch size when plants are plentiful (to avoid sib competition costs; Heard 1998). To easily distinguish population-dynamic effects of travel costs per se from effects of clutch size adjustments to those costs, we first imposed clutch size adjustment in the absence of travel costs and then later combined the two effects.

Each simulation began with a large plant population and insects laying a specified initial (and minimum) clutch size, c_{\min} . If plant population density dropped, clutch size increased (but never above λ_h); if the plant population subsequently rebounded, herbivore clutch size decreased (but never below c_{\min}). We considered clutch size responses of different strengths:

$$c = \text{round} \left\{ 1 + s(\lambda_h - 1) \left(1 - \frac{P}{P_{\max}} \right) \right\}, \quad (3)$$

except that we imposed a lower bound of c_{\min} and an upper bound of λ_h . In Eq. 3, c is the clutch size, s is the strength of the herbivore response, λ_h is herbivore fecundity, P is the plant population density, and P_{\max} is the highest plant density allowed. This function has the clutch size small when plants are abundant, and increasing stepwise-linearly (with slope s , but only integer sizes are allowed) as plants become less common (the first two 1s set the minimum clutch size at 1 rather than 0). All females are assumed to respond identically to plant population density, so clutch size is constant within each generation.

Female aggregation and overdispersion

In further simulations, we controlled the degree to which egg-laying visits were either aggregated or overdispersed among plants. Among real phytophagous insects, some species show aggregated egg-laying visits (e.g. Morris et al. 1992; Reed 2003; Ulmer et al. 2003), whilst others show overdispersion (e.g. Anderson and Löfqvist 1996; Dempster 1997; Diaz-Fleischer and Aluja 2003). Aggregation may arise simply because oviposition sites vary in ease of location or visitation or may be favoured by ovipositing females because it provides larvae an advantage in cooperative feeding (Heard and Buchanan 1998; Inouye and Johnson 2005) or parasitoid avoidance (Rohlf and Hoffmeister 2004); overdispersion may arise through avoidance of larval competition (e.g. Roitberg and Prokopy 1983). For a given herbivore at a given time, the actual distribution of clutches is likely to reflect a compromise among these and other factors.

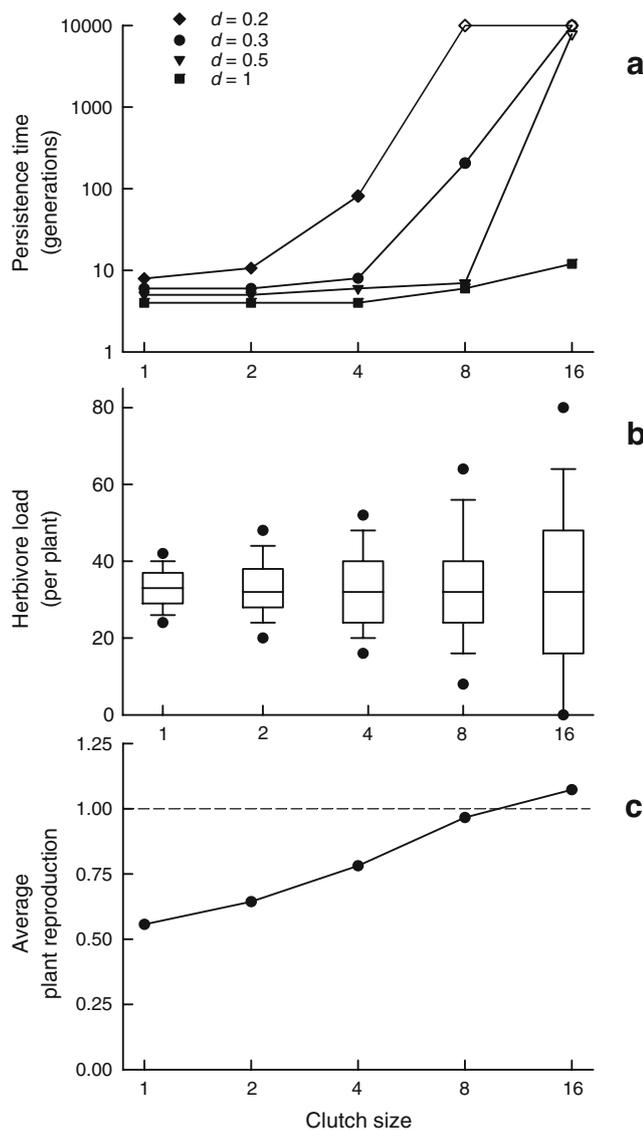


Fig. 1 Effects of fixed clutch size behaviour on insect–plant persistence. **A** Persistence times; *open symbols* indicate underestimates because some or all simulations ran the full 10,000 generations without extinction. **B** Distributions of herbivore loads over plants. *Boxes* show 25th to 75th percentiles, *whiskers* 10th and 90th percentiles, and *circles* 5th and 95th percentiles. Values are for plants and insects at their carrying capacities (1,600 herbivores on 400 plants). **C** Average (across the population) reproductive output of plants with herbivore load distributions from **B**. When average reproduction is less than 1.0 (*dashed line*), the plant population is overexploited and declines. Parameter values not indicated are as listed in the text

In our models, we began with the case where aggregation or overdispersion exists independent of plant density. If egg-laying visits are to be aggregated, a female directed to an eggless plant (one that has not previously been visited) skips or rejects that plant with probability R_{empty} . If egg-laying visits are to be overdispersed, a female directed to a plant that already holds eggs skips or rejects that plant with probability R_{used} . These two parameters produce a contin-

uum in clutch distribution from highly aggregated (R_{empty} near 1) through random ($R_{\text{empty}}=R_{\text{used}}=0$) to highly overdispersed (R_{used} near 1).

The distribution of egg-laying visits might also change with plant density. For example, in some phytophagous insects, females relax their avoidance of egg-laden patches when they have not recently encountered hosts (Roitberg and Prokopy 1983). Alternatively, if females aggregate their clutches because some plants are difficult to locate or visit, then females might avoid this aggregation only at an increased travel cost, and an optimal strategy will then be to avoid aggregation more assiduously when plants are abundant and travel is cheap. To model insects that relax overdispersion when plants are rare, we set $R_{\text{used}}=0.95$ (strong overdispersion) when plants are at their maximum density, but let it decline linearly to zero as plants became vanishingly rare ($P \rightarrow 0$). To model insects that avoid aggregation when plants are abundant, we set $R_{\text{empty}}=0.95$ (strong aggregation) when plants are vanishingly rare and let it decrease linearly to 0 as $P \rightarrow P_{\text{max}}$.

Testing for density dependence

We were particularly interested in whether insect herbivores could regulate plant population size by imposing inverse density dependence in plant reproduction (Halpern and Underwood 2006). Therefore, we ran additional simulations in which we held all model parameters constant whilst varying P , the size of the plant population. We set insect population size H to track the plant population size (that is, $H = KP$). Insect behaviour responded to P as specified by the model parameterisation (for example, with clutch size adjustment if $s > 0$). We then calculated average per-capita plant reproduction for the set values of H and P (that is, for this purpose, we simulated only a single generation) and plotted plant reproduction vs. P to reveal the presence or absence of density dependence.

Results and discussion

When the outcome of a simulation is extinction, in most cases, the plant goes extinct first and the herbivores, having no other resources, follow. Because extinction in our models is generally due to overexploitation, factors that delay or prevent extinction tend to work by reducing average herbivore impact on the plants. They can do so in (plant) density-independent fashion, which means the system can persist with plants and insects at the system-wide carrying capacity (P_{max} plants and KP_{max} insects), or they can do so in (plant) density-dependent fashion, which makes possible regulation of the plant population below P_{max} .

Fixed clutch sizes

Initially, we let plant population density respond to herbivore pressure, but kept herbivore clutch size constant. Regardless of other parameter values, for larger herbivore clutch sizes, persistence of the host plant–herbivore system is extended (Fig. 1A). Both the strength of the clutch size effect and the persistence time for any particular clutch size increase with smaller values of the tolerance parameter d . Smaller d means more herbivore damage is required before plant reproduction is much reduced; recall that we expect small d values to be common in nature.

Large clutches extend persistence because increasing clutch size increases the heterogeneity of herbivore attack among plants (Fig. 1B). At the herbivore densities in our simulations, without spatial variation in herbivore load, plants are quickly driven extinct. In contrast, when herbivore attack is heterogeneous, some plants suffer from high herbivore loads and do not reproduce at all, whilst others have light herbivore loads and produce seeds that recruit to establish the next generation (Fig. 1B, right). Only an increased variance (not a decreased mean) of herbivore attack is necessary to allow reproduction by some plants. Clutch laying reduces overall herbivore damage (and increases average plant reproduction; Fig. 1C) because compared to plants with the average herbivore load, lightly infested plants gain more reproductive output than heavily infested plants lose.

This result bears a superficial resemblance to a stabilizing effect of large clutches in Myers' (1976) plant–herbivore model. However, in Myers' model, the plant population was unaffected by herbivory, and any plant with an herbivore load above carrying capacity had complete larval mortality (pure scramble competition). As a result, insect extinction occurred not because the host plants became extinct but because every host plant was overcrowded and no insect larvae survived. In both models, large clutch sizes leave some individual plants as uncrowded refuges—but in Myers' model, these plants were refuges for the insects, whereas in our model, these plants are refuges from the insects (allowing plants to set seed).

Travel costs

The addition of travel costs, implemented as a mortality risk, reduces overall herbivore reproduction because some individuals die before laying all their eggs. In general, increasing travel costs extend persistence, whether those costs are fixed per visit (Fig. 2A) or scale with interplant distances (Fig. 2B). The striking prolongation of persistence at small clutch sizes is not surprising, as individuals must make more movements (and thus pay more travel costs) when clutches are small.

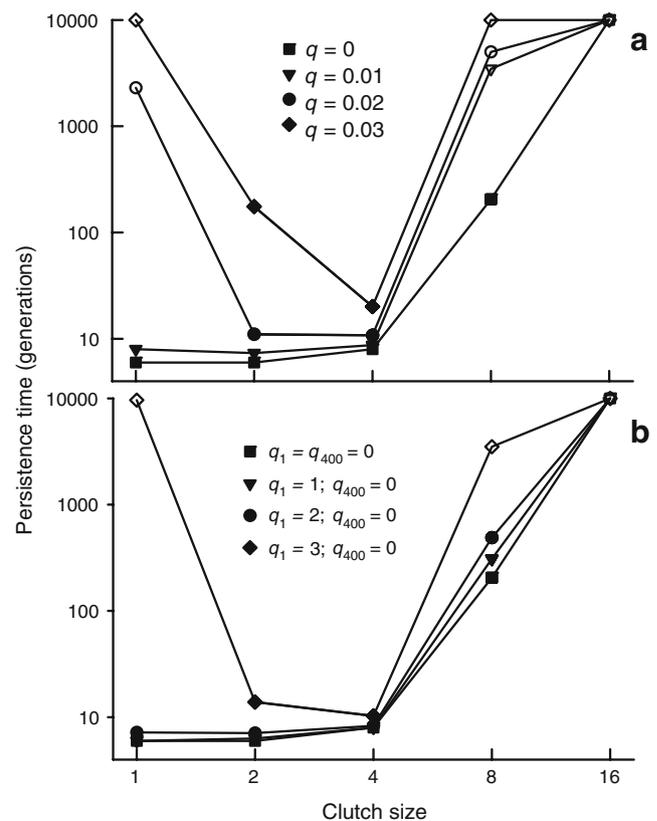


Fig. 2 Effects of travel costs on insect–plant persistence. *Open symbols* indicate underestimates because some or all simulations ran the full 10,000 generations without extinction. **A** Travel costs constant (costs per plant visit do not depend on plant population size). To achieve $q=0, 0.01, 0.02$ and 0.03 , we set $k_1=0$ and $k_2=0, 0.01, 0.02$ and 0.03 , respectively. **B** Travel costs scale with expected interplant distance. To achieve $q_1=0, 1, 2$ and 3 whilst holding $q_{400}=0$, we set $(k_1, k_2)=(0, 0), (1.053, -0.053), (2.105, -0.105)$ and $(3.158, -0.158)$, respectively. Parameter values not indicated are as listed in the text

Whilst the two panels in Fig. 2 look rather similar, the two kinds of travel costs (fixed or scaling with interplant distances) have very different consequences for the stability of insect–plant population dynamics. Higher fixed travel costs reduce insect reproduction, and hence increase per-capita plant reproduction, but this increase is (plant-) density-independent (Fig. 3, compare open circles and squares). Persistence is extended because overexploitation of the plants is reduced, but when plants persist indefinitely, they do so at their carrying capacity free of any demographic impact of herbivory. In contrast, travel costs that scale with interplant distances make density-dependent regulation possible (Fig. 3, filled triangles) because those costs rise, and so herbivore loads fall and per-plant reproduction increases, as plants become scarcer.

Clutch sizes sensitive to plant density

When travel costs scale with interplant distances, herbivores should balance sib competition costs and travel costs and

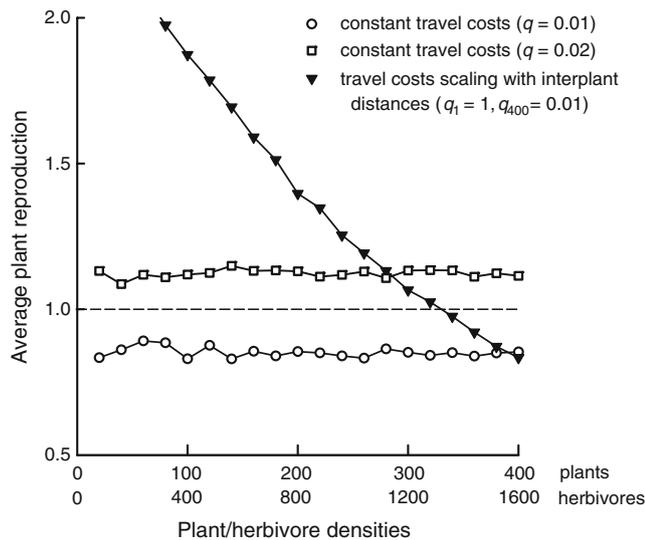


Fig. 3 Plant reproduction vs. plant population density with different travel-cost functions. Across the *horizontal axis*, plant density increases, and the herbivore population tracks the plants at its carrying capacity. The *dashed line* indicates plant reproduction just sufficient to maintain the population; when a reproduction curve crossing this line (with negative slope), herbivory can regulate the plant population. *Hollow symbols*: travel costs per plant visit do not depend on plant population size; to achieve $q=0.01$ and 0.02 , we set $k_1=0$ and $k_2=0.01$ and 0.02 , respectively. *Solid symbols*: travel costs scale with expected interplant distance; to achieve $q_1=1$ and $q_{400}=0.01$, we set $k_1=1.042$ and $k_2=-0.042$. Parameter values not indicated are as listed in the text

increase clutch sizes as host plant density falls (Heard 1998). We began by examining such clutch size behaviour in the absence of any actual cost of travel to clearly distinguish between effects of travel costs and effects of clutch size responses to those costs.

Behaviour adjusting clutch size in response to plant abundance ($s>0$) extends persistence (Fig. 4, squares), as did larger but fixed clutch sizes (Fig. 1). However, we draw the same contrast we drew for travel costs: herbivore clutch sizes that are large but fixed increase per-capita plant reproduction (Fig. 1C), but the increase is (plant-) density-independent (Fig. 5, compare circles and squares) and plants persist at P_{max} . In contrast, behaviour in which clutch size responds to plant density makes possible density-dependent regulation at low plant density (Fig. 5, triangles).

As we motivated the idea of clutch size responses to host plant density as a way insects might avoid travel costs, it is critical to consider the joint effect of travel costs and clutch size responses to those costs. The existence of travel costs actually strengthens the effect of clutch size behaviour on persistence (Fig. 4, compare plots). Furthermore, the existence of travel costs increases the strength of inverse density dependence created by clutch size behaviour (Fig. 5, compare triangles and diamonds). This is interesting because from the point of view of insect reproduction, clutch size behaviour mitigates travel costs; essentially,

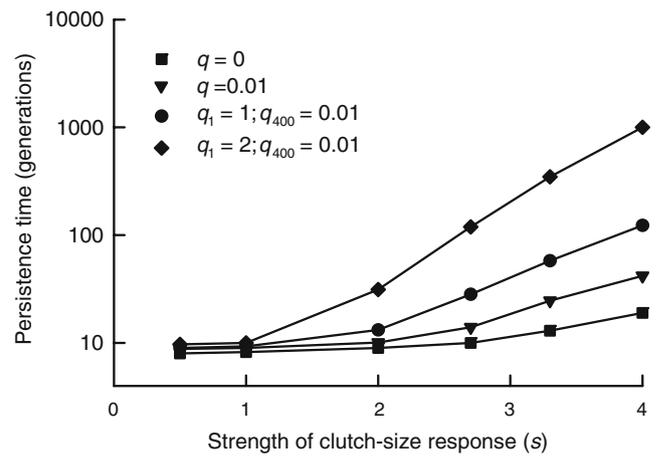


Fig. 4 Persistence time vs. strength of clutch size response (s) to plant density. Minimum clutch size (c_{min})=4. To achieve $q=0$ and 0.01 we set $k_1=0$ and $k_2=0$ and 0.01 , respectively; to achieve $q_1=1$ and 2 whilst holding $q_{400}=0.01$, we set $(k_1, k_2)=(1.042, -0.042)$ and $(2.095, -0.095)$, respectively. Other parameter values as listed in the text

insects can avoid one fitness cost by paying the other. From the point of view of plant reproduction, though, clutch size behaviour reinforces rather than mitigates the stabilising effect of travel costs. Travel costs are stabilising (Figs. 2 and 3) because they reduce mean herbivore load as plants become rare, whilst clutch sizes responses are stabilising

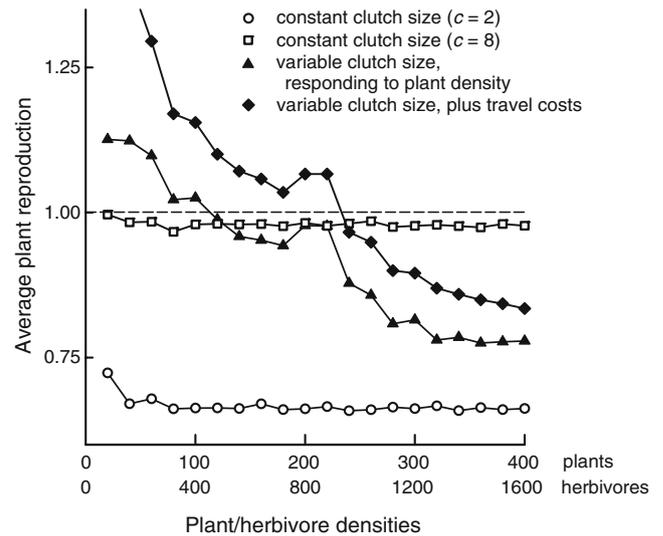


Fig. 5 Plant reproduction vs. plant population density with different herbivore clutch size behaviours. Across the *horizontal axis*, plant density increases, and the herbivore population tracks the plants at its carrying capacity. The *dashed line* indicates plant reproduction just sufficient to maintain the population; when a reproduction curve crossing this line (with negative slope), herbivory can regulate the plant population. *Hollow symbols*: fixed clutch size behaviour ($c=2$ vs. 8). *Solid symbols*: clutch size responding to plant abundance ($s=1$; either without travel costs). Simulations with travel costs (*diamonds*) have $q_1=1$, $q_{400}=0.01$ ($k_1=1.042$, $k_2=-0.042$). The lines wiggle because clutch sizes are constrained to integer values. Parameter values not indicated are as listed in the text

because they increase spatial variance in herbivore load as plants become rare (Figs. 1 and 5).

Female aggregation and overdispersion

The effects of aggregation behaviour are very similar to those of clutch size behaviour because from the point of view of the plant, two small clutches together have the same impact as one large one. As a result, we provide only a brief summary of our aggregation results (further details available on request). Aggregation of egg-laying visits to plants increases spatial heterogeneity in herbivore attack, and therefore increases persistence times. Overdispersion of egg-laying visits has the opposite effect and accelerates extinction. When female increasingly accept aggregation when plants become rare, then herbivore load is most heterogeneous when plants are rare, making plant reproduction inversely density-dependent. Therefore, female clutch distribution behaviour that responds to plant abundance can provide a strong stabilising force in plant–herbivore interactions.

Our models and real plant–herbivore systems

For many years, the potential for insect herbivores to regulate host plant populations received much less attention than the analogous potential for other consumers to regulate other resources (for instance, predators to regulate prey; Louda 2001; Halpern and Underwood 2006; Maron and Crone 2006). In part, we suspect that this reflects emphasis on plant defences that deter herbivory and on trophic cascades featuring control over herbivores by their predators (Hairston et al. 1960, and a vast ensuing literature). However, attention has been refocused on herbivore–plant dynamics by the continuing crisis of plant invasions (Mack et al. 2000; Simberloff et al. 2005; Colautti et al. 2006). The notion that invasiveness arises at least in part through escape from herbivores that control populations in the invader's native range (Wolfe 2002; DeWalt et al. 2004; Torchin and Mitchell 2004) obviously depends on the ability of herbivores to exert that control (Raghu and Dhileepan 2005). Furthermore, the existence of success stories in the apparently stable biocontrol of invasive plants by insect herbivores (Dhileepan 2001; McConnachie et al. 2003; Moran et al. 2005) strongly suggests that plant populations can be regulated by insect herbivory, at least some of the time.

Our models address the kinds of ecological mechanisms that might give rise to plant regulation by insect herbivores. In our results, there are in general two components to such a mechanism: first, the generation of probabilistic refuges from herbivory and second, the provision of more such refuges as plant density falls (i.e. the creation of inverse

density dependence). Probabilistic refuges are generated in our models by the laying of eggs in clutches and by the aggregation of egg-laying visits over plants. Spatial heterogeneity in herbivore attack achieved via clutch laying or via female aggregation, coupled with plant tolerance of moderate levels of herbivory, allows some individual plants to substantially or completely escape the effects of herbivory. Similar probabilistic refuges are known from other models of exploitative systems and may be generated by a variety of mechanisms, including prey dispersing to predator-free areas (e.g. Huffaker 1958) or the spatial aggregation of searching predators or parasitoids (Ives 1992). Our models add clutch laying and aggregated egg-laying visits by adult herbivores to the list of mechanisms by which probabilistic refuges may be generated. Travel costs play a somewhat different role: they reduce herbivore attack and make refuges more effective, but they do so by decreasing system-wide average herbivore load.

Responses of herbivore behaviour to host plant abundance are plausibly adaptive for females distributing eggs over spatially structured resources, but have not been extensively studied in the field. For clutch size, adaptively behaving females should increase clutch sizes as host plants become rare (Heard 1998). However, little is known about such behaviour in real insects (Cronin and Strong 1999; Heard 1998 and references therein). Among phytophagous insects, we are aware of no estimates of parameters like our s , although some observations suggest that butterfly clutch sizes differ between individuals (Courtney 1986) or species (Benson et al. 1975) exploiting rare vs. common host plants. For female aggregation, some laboratory data suggest relaxed overdispersion when host plants are rare (Roitberg and Prokopy 1983), and at least one agricultural study has found greater herbivore aggregation when hosts are in polyculture rather than monoculture (Harmon et al. 2004). However, few field studies have measured the distribution of female egg-laying visits (i.e. of clutches, not of eggs or larvae), and none to our knowledge have related these distributions to plant densities. Field studies of female aggregation (or overdispersion) behaviour across a range of host plant densities are sorely needed.

Interestingly, in at least two plant–herbivore systems, seed-set refuges resulting from aggregated egg laying have been invoked to account for the persistence of plant populations under insect attack: *Urophora* tephritids on knapweed (Myers and Harris 1980) and *Cactoblastis* moths on *Opuntia* (Monro 1967; Myers et al. 1981). In neither case is it known whether female aggregation is sensitive to plant abundance. For one species of *Urophora*, spatial heterogeneity in attack is greatest where plants are rare (Zwölfer and Völkl 1997), but this pattern has not been explicitly connected to female aggregation behaviour and is complicated by a tendency for females to avoid the habitats in which plants are most

common. For *Cactoblastis*, one data set (Monro 1967, our analysis of data in his Tables 3 and 4) shows a trend toward stronger aggregation of clutches at sites where host plants are rare (egg-stick variance/mean ratio vs. *Opuntia* density, $r = -0.56$, one-tailed $P = 0.075$). Whether or not this relationship is real is a critical question, because our models suggest (contra Myers et al. 1981) that aggregated egg laying alone likely cannot account for the stable regulation of *Opuntia* at low density—but aggregation that increases when plants are rare might do so. More field studies of oviposition behaviour in *Cactoblastis* are clearly called for.

Conclusions

Our results indicate that oviposition behaviour of herbivorous insects can influence the severity of herbivore damage and the stability of plant–insect interactions. Through their impacts on spatial heterogeneity in herbivore attack, clutch laying and female aggregation generate probabilistic refuges from herbivory for some individual plants. In turn, these refuges allow some plants to escape herbivore damage and found the next generation. When clutch laying and aggregation behaviour are plausibly adaptive (with insects increasing clutch size and/or aggregation as plant populations decline), then the generation of refugia becomes inversely density-dependent, and regulation of the plant population by its herbivores becomes possible. Even the existence of travel costs that are sensitive to plant population size, in fact, can lead to plant density dependence. If many insect species adjust the size and/or distribution of their clutches in response to changes in plant density, oviposition behaviour may play an important role in the population dynamics of plants and the phytophagous insects associated with them.

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