

Sandra E. Helms · Mark D. Hunter

Variation in plant quality and the population dynamics of herbivores: there is nothing average about aphids

Received: 29 February 2004 / Accepted: 3 February 2005 / Published online: 11 May 2005
© Springer-Verlag 2005

Abstract In the attempt to use results from small-scale studies to make large-scale predictions, it is critical that we take into account the greater spatial heterogeneity encountered at larger spatial scales. An important component of this heterogeneity is variation in plant quality, which can have a profound influence on herbivore population dynamics. This influence is particularly relevant when we consider that the strength of density dependence can vary among host plants and that the strength of density dependence determines the difference between exponential and density-dependent growth. Here, we present some simple models and analyses designed to examine the impact of variable plant quality on the dynamics of insect herbivore populations, and specifically the consequences of variation in the strength of density dependence among host plants. We show that average values of herbivore population growth parameters, calculated from plants that vary in quality, do not predict overall population growth. Furthermore, we illustrate that the quality of a few individual plants within a larger plant population can dominate herbivore population growth. Our results demonstrate that ignoring spatial heterogeneity that exists in herbivore population growth on plants that differ in quality can lead to a misunderstanding of the mechanisms that underlie population dynamics.

Keywords Density dependence · Plant–insect interactions · Plant quality · Population dynamics · Spatial scale

Introduction

Ecologists are often interested in answering large-scale questions while conducting experiments at small scales. The general approach is to assume that results of small-scale studies can be used to make larger scale predictions. However, as we make predictions about processes on larger spatial scales, we are incorporating greater spatial heterogeneity. Inherent in this heterogeneity is variation in plant quality both within and among plant species (Hunter et al. 1996).

Variation in plant quality can have a profound influence on herbivore populations through changes in fecundity, survival, movement, mortality due to natural enemies, and rates of competition (Price et al. 1980; Denno and McClure 1983; Denno et al. 1995; Abrahamson and Weis 1997; Lill et al. 2002). We should also expect that the strength of density dependence, and herbivore population dynamics, will vary with host plant quality (Hunter et al. 2000; Hunter 2001). For example, host plant genotype, which influences phenotypic variation in plant quality traits (Underwood and Rausher 2000; McIntyre and Whitham 2003), including plant secondary chemistry (Hunter et al. 1996; Larsson et al. 2000) has been shown to influence herbivore population dynamics. The strength of density dependence can have considerable impact on population dynamics as its value determines the difference between exponential and density-dependent growth. Several recent studies have demonstrated that the strength of density dependence can vary among host plants (Underwood and Rausher 2000, 2002; Rotem and Agrawal 2003).

Here, we present some simple models and analyses designed to examine the impact of variable plant quality on the dynamics of insect herbivore populations. Specifically, we concentrate on the consequences of variation in the strength of density dependence among host plants. We illustrate that (a) average values of herbivore population growth parameters, calculated from plants that vary in quality, do not predict overall population

Communicated by Craig Osenberg

S. E. Helms (✉) · M. D. Hunter
Institute of Ecology, University of Georgia,
Athens, GA 30602-2202, USA
E-mail: shelms@uga.edu
Fax: +1-706-5424819

growth, and (b) the quality of a few individual plants within a larger plant population can dominate herbivore population growth.

Materials and methods

Field observations of aphid populations (Helms et al. 2004) have served as the basis for many of the ideas presented in this paper. In a common garden of *Asclepias* plants in Athens (GA, USA) we have observed exponential growth of *Aphis nerii* populations within a single growing season despite considerable variation in the strength of density dependence among individual plants. We explore this phenomenon here with a series of population models. The initial models are extremely simple, to make some general points. We then increase model complexity and incorporate some real data from our common garden.

Because aphids have overlapping generations, continuous time models have been used. Specifically, these models are all variations of the basic form:

$$\frac{dN}{dt} = N \times (r + b \times N) \quad (1)$$

where N is the size of the population, r is the maximum per capita growth rate, and b is the strength of density dependence. The quantity $(r + b \times N)$ is the R-function and represents the realized reproductive rate (or per capita population growth rate) (Berryman 1999). If we make the assumption that r is non-zero and positive, the behavior of the population is dependent on b . In this case, we can have three outcomes:

1. $b > 0$: The population will experience inverse density dependence and exhibit hyper-exponential growth.
2. $b = 0$: The population will be density independent and exhibit exponential growth.
3. $b < 0$: The population will experience density dependence and will reach a stable equilibrium.

A simple model

Our first step in examining the effect of variation in plant quality is to consider a very simple hypothetical system in which there are ten individual plants hosting aphid populations. We assume that the aphid populations experience the same arbitrary maximum growth rate ($r=0.9$) on each plant; however aphids realize exponential growth ($b=0$) on one of these plants while experiencing density dependence (we have arbitrarily chosen $b=-0.005$) on the other nine plants. These ten individual populations are each simulated using Eq. 1. When the ten plants are considered together as one large population, total population growth is the sum of the population densities from each of the individual plants at each time step.

Variable growth parameters

To make the simple model used above slightly more realistic, we can allow the growth parameters to vary randomly among host plants. These parameters are estimated from the following normal distributions: $r \sim N(0.9, 0.0025)$ and $b \sim N(-0.005, 0.000025)$, where the first value in the bracket is the average parameter estimate, and the second value is the variance around the mean. Note that the average of b favors density-dependent growth ($b < 0$). Ten values for each parameter are generated at random from these distributions and used to simulate populations on each of the ten individual plants using Eq. 1. Once again, we can sum the densities on individual plants to find total aphid population size. We can compare the model output from runs with variable parameters with a simple model that uses the average parameter values from all ten plants. In this case, we calculated mean parameter values from the ten variable parameter simulations, and used these to simulate an average population.

Hierarchical Bayesian parameter estimation

Rather than assuming that all variation around a mean estimate of a parameter value is due simply to sampling error and will tend to zero as sample size increases, hierarchical Bayesian methods allow for some of this observed variation to be real biological variation among individuals (see Clark 2003; Sauer and Link 2002). Hierarchical Bayesian methods were used to estimate the parameters r and b from aphid population data. Population densities of the aphid *Aphis nerii* growing in a common garden of *Asclepias* plants in Georgia were monitored from July to October 2001. The common garden consisted of between 50 and 100 plants of each of six different *Asclepias* species. Naturally occurring aphid densities (calculated as number of aphids per gram of plant tissue) were recorded from each plant in the garden every two weeks from July 14 to October 22. Again, aphids have overlapping generations, with a generation time of approximately 1 week. Complete details of our sampling protocols are provided in Helms et al. (2004).

Values for r and b were estimated by fitting linear regressions between the realized growth rate (R) and the population density on individual *Asclepias* plants (i.e., (x, y) coordinates are $(N_t, \ln(N_{t+1}/N_t))$). The intercept of this line represents r , while the slope is the value for b , such that $R = r + b \times N$. Only plants that hosted aphids for at least four consecutive sampling dates were used in the analysis, giving a total of 171 individual plants.

The observational data collected from the field, $R_{i,j}$ (where $i=1, 2, \dots, 171$ denotes individual plants, and $j=1, 2, \dots, 5$ denotes time period) is assumed to follow a normal distribution such that $R_{i,j} \sim N(\mu_{i,j}, \sigma^2)$ and $\mu_{i,j} = r_i + b_i \times N_{i,j}$ and σ^2 follows a flat inverse gamma distribution. Both r_i and b_i are given normal

prior distributions: $[r_i | \mu_r, \tau_r^2] \sim N(\mu_r, \tau_r^2)$ and $[b_i | \mu_b, \tau_b^2] \sim N(\mu_b, \tau_b^2)$.

Hyperpriors (distributions of the parameters of the distribution of r_i and b_i) have been defined as diffuse normal distributions for the means (i.e., $[\mu_r] \sim N(0.0, 1000^2)$ and $[\mu_b] \sim N(0.0, 1000^2)$) and flat inverse gamma distributions for the variances (i.e., $[\tau_r^2] \sim \text{Inv-gamma}(0.1, 0.1)$ and $[\tau_b^2] \sim \text{Inv-gamma}(0.1, 0.1)$). In all cases, standard non-informative priors and hyperpriors for Bayesian analysis have been used (Spiegelhalter et al. 1999). The program WinBUGS (Spiegelhalter et al. 1999) was used to complete this analysis. After specifying the model, the program carries out the Bayesian analysis with a Markov chain Monte Carlo (MCMC) procedure.

As a comparison to Hierarchical Bayesian methods, standard statistical methods were also used to examine the values of r and b . These parameters were first estimated by using pooled data for all 171 plants. Pooling these data gave 761 data points consisting of the realized growth rate and population density. A linear regression, as well as mean estimates and standard deviations of r and b , for the pooled data were determined using PROC REG in SAS (1999). Values for r and b were also estimated by fitting a linear regression between the realized growth rate and population density for each individual plant and then averaging the resulting parameter values over all 171 plants.

Models with movement

Most insect herbivores have the ability to move among plants either within or between generations, and so we added migration to our original models. The results of aphid movement can be considered analytically. Here, we consider only two populations: one that supports exponential growth and one that has density-dependent growth. The two-patch model considered here is very similar to models in Underwood (2004), Holt (1985), Hastings (1993), and Freedman and Waltman (1977).

Let N be the population with density-dependent growth and P be the population with exponential growth.

Then,

$$\frac{dN}{dt} = N \times (r_1 + b \times N) - m_1 \times N + m_2 \times P \quad (2)$$

$$\frac{dP}{dt} = r_2 \times P - m_2 \times P + m_1 \times N. \quad (3)$$

Here, r_1 and r_2 are the maximum growth rates of N and P , respectively. The strength of density dependence is b (here $b=0$ for P), and m_1 and m_2 are the rates of movement of individuals from populations N and P , respectively. The following set of assumptions will be made:

1. $r_2 > 0$ (necessary for exponential growth)
2. $m_1, m_2 > 0$
3. $b < 0$ (necessary for density-dependent growth)

This set of equations (Eqs. 2, 3) was solved to find the conditions necessary for equilibrium (i.e. $N^* > 0$ and $P^* > 0$).

Results

A simple model

In a deterministic model with aphids on nine plants exhibiting density-dependent growth and aphids on one plant exhibiting exponential growth, the total population exhibits exponential growth (Fig. 1). This rather obvious result stems from the fact that exponential growth on a single plant comes to dominate the whole population over time.

Variable growth parameters

When average population growth is density dependent ($b < 0$), but is varied randomly from a normal distribution of the type described above, total population growth is exponential (Fig. 2; because the parameter values for each individual plant are generated from a normal distribution, it should be noted that the run of this model shown in Fig. 2 is representative of other runs of this model). Although individual plants exhibit either exponential or density-dependent growth, the sum of the population shows exponential growth. Furthermore, by averaging the parameter values over the ten variable parameter simulations, the parameters are those of density-dependent growth. These results indicate that

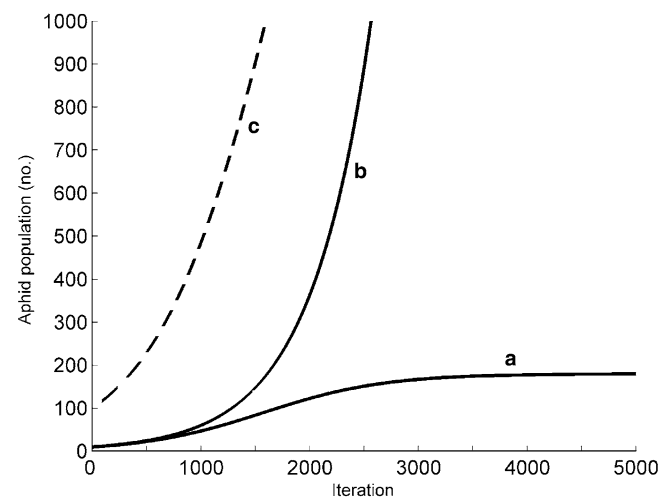


Fig. 1 Aphid population growth as simulated using a deterministic model (Eq. 1) for **a** the mean of nine plants with density-dependent growth, **b** one plant with exponential growth, and **c** the total aphid population on these ten plants

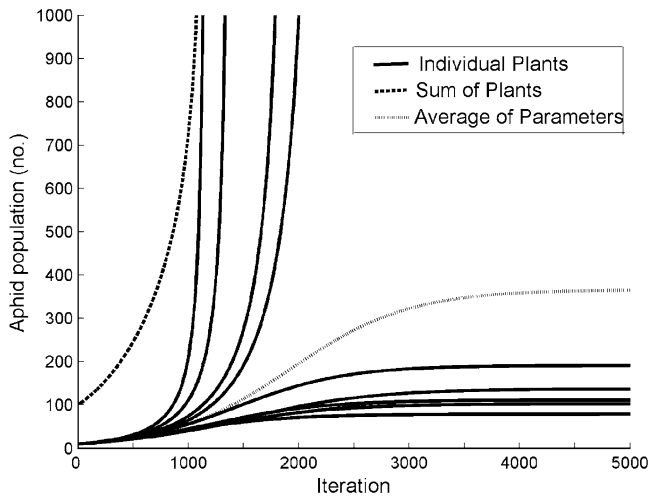


Fig. 2 Aphid population growth with the parameters r (maximum population growth rate) and b (strength of density dependence) varying randomly among host plants. Individual plants exhibit either density-dependent growth or exponential growth (solid lines). The dashed line represents the totals of these populations. The dotted line represents the output of a model that uses the average parameter values from all ten plants

total population growth can be exponential even when average parameter values favor density-dependent growth.

This process can occur in nature. Figure 3 shows the behavior of *A. nerii* populations on 15 different *Asclepias* plants in Georgia (recalculated from data in Helms et al. 2004) as well as the sum of these populations. Once again, there exist both density-dependent and exponential growth on the individual plants, but the sum of the population shows exponential growth.

The level of variance in parameter values among populations on different host plants will likely have a significant impact on the dynamics observed in the

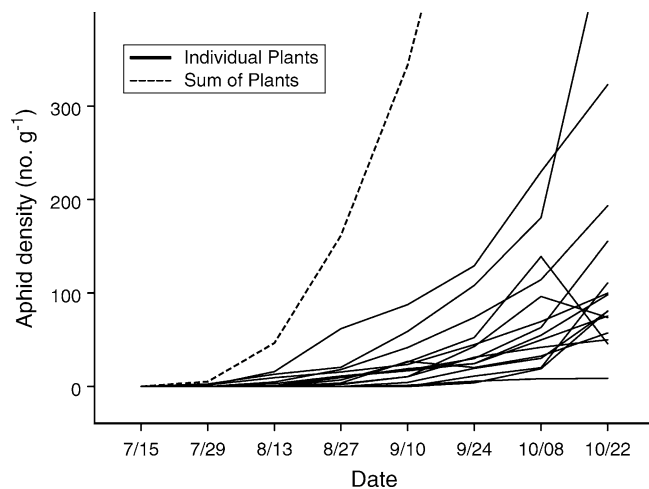


Fig. 3 Population growth of *Aphis nerii* on 15 different *Asclepias* plants growing in a common garden in Athens, Georgia in 2001 (recalculated from data in Helms et al. 2004)

population as a whole. This variance represents the variation in plant quality that is central to our current discussion. The effect of increasing variance in the parameter b (strength of density dependence) can be examined by plotting the probability of observing exponential growth in the total aphid population (i.e., b is non-negative) against the variance.

Under a normal distribution, as variance in the estimate of the strength of density dependence (b) increases, so does the probability of generating a plant upon which aphids will exhibit exponential growth. The probability of exponential growth also depends on the mean of the parameter b ; as the mean of b decreases, so does the probability of exponential growth. This effect can be seen in Fig. 4. In other words, the greater the variation among individual plants, the more likely it is that overall population growth will be determined by a few plants exhibiting exponential growth.

Hierarchical Bayesian parameter estimation

Using Bayesian analysis, we have generated distributions for the parameter values r and b from *A. nerii* populations growing in a common garden of *Asclepias* plants in Georgia. The mean value for r is 1.174 with a 95% credible interval (1.004, 1.336) and the mean value for b is -0.004 with a 95% credible interval (-0.01 , 0.006). A 95% credible interval is the interval that contains 95% of the data. The values for these parameters approximate the following normal distributions: $r \sim N(1.174, 0.064^2)$ and $b \sim N(-0.004, 0.006^2)$. Using the marginal distribution for b , the probability of observing a specific number of individual plants on which aphid populations grow exponentially is shown in Fig. 5. According to this table, in a population of ten plants

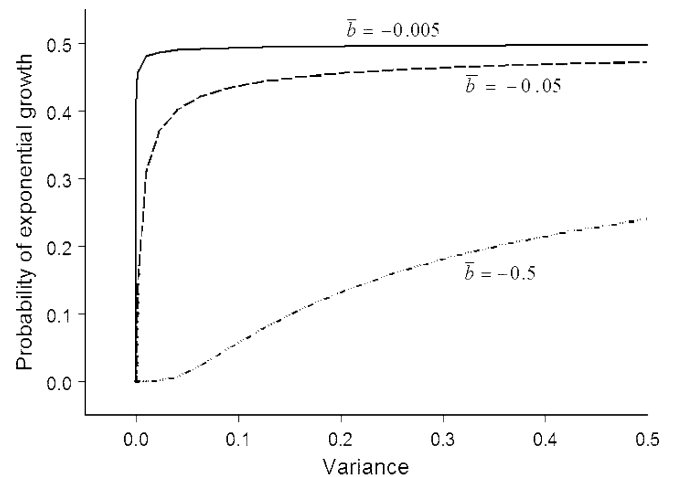


Fig. 4 The probability of observing a plant upon which aphids will exhibit exponential growth as the variance in the estimate of the strength of density dependence (b) increases. The parameter b is assumed to follow a normal distribution, and these results are shown for three different values of the mean of b : -0.005 , -0.05 , -0.5

with the distribution of parameter values found here, there will be one or more plants supporting exponential growth in 93.6% of cases, despite average parameter values favoring density-dependent growth.

A comparison of estimated values for r and b from the hierarchical Bayesian analysis (HB) with the standard statistical methods used is shown in Table 1. The pooled data linear regression gave a mean value for r of 1.05 with a 95% confidence interval of (0.992, 1.108) and a mean value for b of -0.0017 with a 95% confidence interval of $(-0.0021, -0.0013)$. Averaging the parameter estimates for linear regressions on each individual plant gave a mean value for r of 1.183 with a 95% confidence interval of (1.102, 1.263) and a mean value for b of -0.002 with a 95% confidence interval of $(-0.006, 0.002)$.

Models with movement

Upon solving Eqs. 2 and 3 to find the conditions necessary for equilibrium (i.e. $N^* > 0$ and $P^* > 0$), we found that both of the following conditions must be met in order for this system to have an equilibrium:

$$r_1 > \frac{r_2 \times m_1}{r_2 - m_1} \quad (4)$$

$$r_2 < m_2 \quad (5)$$

If condition 5 is violated, then there is no equilibrium for this system and both plants experience exponential growth. So if population growth rate on the exponential plant is larger than the rate of emigration from that exponential plant, both populations will grow exponentially (see Fig. 6a, $r_1 = r_2 = 0.9$, $b = -0.005$, $m_1 = m_2 = 0.1$).

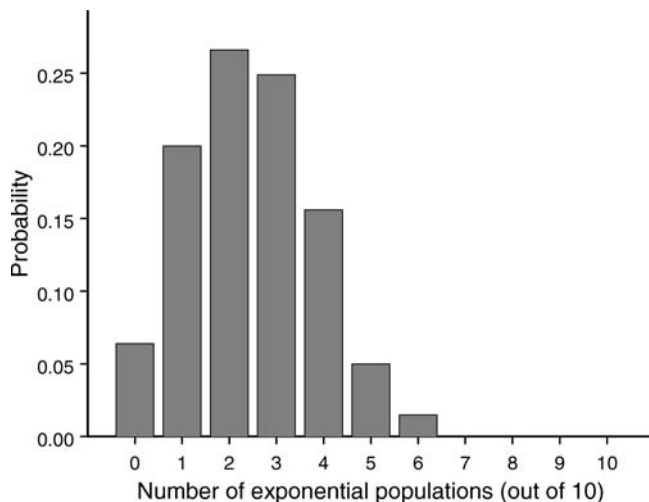


Fig. 5 The probability that, in a population of ten *Asclepias* plants, there will be a given number of plants on which *A. nerii* populations grow exponentially despite average growth parameters favoring density dependence. For example, there is a 20% probability of one plant supporting exponential aphid growth and only a 6.4% probability that all plants will exhibit density-dependent growth

Table 1 Comparison of estimates for r (maximum per capita growth rate) and b (strength of density dependence) using hierarchical Bayesian analysis (HB), a linear regression for the pooled data (pooled), and an average of values from linear regressions on each individual plant (average). 95% CI is the 95% credible interval for the HB analysis and the 95% confidence interval for the pooled and average analyses

	Mean	Standard deviation	95% CI
<i>r</i>			
HB	1.174	0.0640	(1.004, 1.336)
Pooled	1.050	0.8182	(0.992, 1.108)
Average	1.183	0.5403	(1.102, 1.263)
<i>b</i>			
HB	-0.0040	0.0060	$(-0.01, 0.006)$
Pooled	-0.0017	0.0055	$(-0.0021, -0.0013)$
Average	-0.0020	0.0310	$(-0.006, 0.002)$

If condition 5 holds and $r_1 > 0$, there is always an equilibrium for this system. Populations on both plants will reach a stable population size, with the exponential population $(-m_1/(r_2 - m_2))$ times larger than the density-dependent population (see Fig. 6b, $r_1 = 0.9$, $r_2 = 0.8$, $b = -0.005$, $m_1 = 0.5$, $m_2 = 0.9$).

However, if condition 5 holds and $r_1 < 0$, condition 4 can be re-written as

$$\frac{r_2}{r_1} < \frac{r_2 - m_2}{m_1} \quad (6)$$

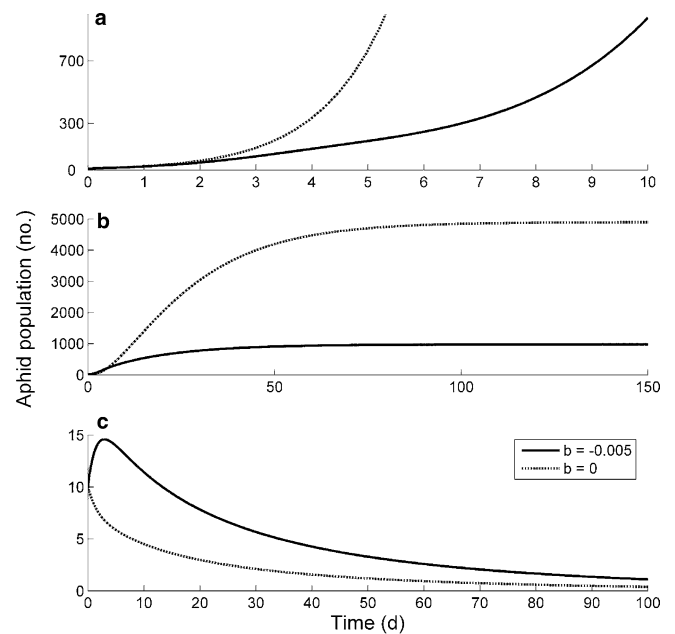


Fig. 6 Aphid population growth as simulated using a deterministic model (Eqs. 2, 3) which allows aphids to move among host plants. Here, we assume that there are two host plants, one with density-dependent growth (solid line, $b = -0.005$) and one with exponential growth (dashed line, $b = 0$). Possible outcomes of this model are represented by the following combinations of parameter values: **a** $r_1 = r_2 = 0.9$, $b = -0.005$, $m_1 = m_2 = 0.1$, **b** $r_1 = 0.9$, $r_2 = 0.8$, $b = -0.005$, $m_1 = 0.5$, $m_2 = 0.9$, and **c** $r_1 = -0.2$, $r_2 = 0.5$, $b = -0.005$, $m_1 = 0.1$, $m_2 = 0.8$ (see text for details)

If Eq. 6 is true, we will see an equilibrium similar to that in Fig. 6b. This demonstrates that plants that are unable to sustain positive aphid growth ($r_1 < 0$) can still exhibit equilibrium aphid densities as a result of immigration from plants supporting exponential growth. However, if Eq. 6 is false, then both populations will go extinct (see Fig. 6c, $r_1 = -0.2$, $r_2 = 0.5$, $b = -0.005$, $m_1 = 0.1$, $m_2 = 0.8$).

In summary, to prevent exponential aphid growth on all plants, aphid population growth rate on the exponential plant must be less than the rate of emigration from the exponential plant. Furthermore, if aphid growth rate on the exponential plant is less than the rate of aphid emigration from that plant and the second plant is a sink, i.e. unable to sustain population growth ($r < 0$), then populations on both plants will go extinct unless condition 6 holds.

Discussion

The spatial scale at which insect herbivore populations are examined can have considerable influence on the assessment of factors underlying population dynamics. Using a simple deterministic model, we have demonstrated that exponential growth by an herbivore on a single plant in a population will dominate the whole population over time, even when the other plants favor density-dependent growth by the herbivore population (Fig. 1). While this simple example may seem obvious, it underscores an important point—when individual plants vary in quality for herbivores, the dynamics of the herbivore population as a whole can be driven by the quality of a few individual plants. As a consequence, average growth parameters calculated from the entire plant population may be poor predictors of overall population growth.

In nature, both the strength of density dependence, b , and the maximum per capita growth rate, r , of herbivores can vary among host plants (Underwood and Rausher 2000, 2002; Rotem and Agrawal 2003; Fig. 3). When we allowed these parameters to vary around a given mean, such that the average parameter values favored density-dependent growth, we found either density-dependent or exponential growth on individual plants, but exponential growth for the herbivore population as a whole (Fig. 2). Furthermore, as variability around the mean value of b increased, we were more likely to observe one or more plants supporting exponential growth (Fig. 4) while the growth of the whole herbivore population was determined by these few plants. What we have not explored here is the potential for aphid populations on an individual plant to vary between exponential and density-dependent growth over time. Temporal changes in the quality of individual plants might cause such changes in aphid growth and will be considered in future work.

Given that variation among host plants in both the maximum per capita growth rate and the strength of density dependence of insect herbivores should be common (Hunter et al. 2000; Hunter 2001) and has been demonstrated experimentally (Rotem and Agrawal 2003; Underwood and Rausher 2000, 2002), we should begin exploring the use of statistical methods that allow for such variability in parameters to be expressed as “real” variation among individuals rather than as measurement error. Using standard statistical procedures, measurement error declines towards zero as sample size increases.

Standard statistical analyses conducted on data from *A. nerii* populations on *Asclepias* plants showed the strength of density dependence estimated from the smaller spatial scale of individual plants (Table 1, “average”) to be only slightly stronger than that from pooled data over the entire field. However, there was a fairly large difference in the 95% confidence intervals between the two methods. Using the pooled data, the 95% confidence interval for b contains only negative values, while that for the average of individual plants allows for both negative and positive numbers. However, this may just be an artifact of the differences of sample size ($N = 761$ for pooled data versus $N = 171$ for average of individual plants).

Instead of all variance being due to measurement error and decreasing towards zero as sample size increases, HB allows for some variation to be real variation among individuals. While variance due to measurement error does decline as sample size increases, hierarchical Bayesian statistics also allows estimation of real variance that exists among plants. For the data from *A. nerii* populations on *Asclepias* plants, not only does the HB detect a much stronger average value of density dependence (-0.004), but the 95% credible interval contains both negative and positive values for b and allows for much more variability than does either of the standard statistical methods used in this paper. An added strength of HB is the generation of distributions of the values of r and b for each individual plant (not shown here). With standard statistical methods, treating each plant individually would only allow for a point estimate for each of the values of r and b . In addition, with the HB, we find that in a population of ten plants, we will observe exponential growth for the whole population 93.6% of the time (Fig. 5), despite the average value of b favoring density-dependent growth. These results are supported by our field observations (Helms et al. 2004) where we found the total population exhibiting exponential growth, but aphid populations on individual host plants exhibiting either density-dependent or exponential growth (Fig. 3).

Standard statistical approaches such as those used in this paper are likely to be inappropriate for scaling up from small studies to larger studies, where true variation among plants is likely to increase with spatial scale (Hunter et al. 1996). Hierarchical Bayesian methods should provide a better approach to parameter estima-

tion (Clark 2003; Sauer and Link 2002) because they produce distributions of parameters rather than simple mean estimates. These distributions encompass real variation among individuals, can be used to make predictions about local dynamics (Fig. 5) and may be useful tools in the attempt to scale up results from small-scale studies to large-scale predictions.

There are an increasing number of studies suggesting that measures of spatial variance are essential to understanding processes that determine population dynamics. Including measures of spatial variance and covariance can give qualitatively different results than simply using mean values estimated from a single spatial scale (Inouye 2005, Melbourne & Chesson 2005, Underwood 2004). Spatial variance has been shown to explain coexistence of competing species that exhibit strong competitive interactions at smaller spatial scales (Inouye 2005) and to influence population abundance for insect herbivores (Underwood 2004).

Shima and Osenberg (2003) demonstrated an analogous situation in populations of reef fish. They found that differences in patch quality caused an underestimation of the effect of density dependence. Aggregation of data over large spatial scales in this study underestimated the strength of density dependence by approximately 97%. Because habitat quality covaries with population density, the strength of density dependence becomes obscured in a heterogeneous habitat. Shima and Osenberg (2003) termed this phenomenon “cryptic density dependence.” Further support for the existence of cryptic density dependence in reef fishes has been provided by Forrester and Steele (2004) and is likely to be found in many other systems. Several studies of insect herbivores have found that the detection of density dependence is only possible at smaller spatial scales (Hassell et al. 1987; Jones et al. 1987; Southwood et al. 1989). Hastings (1993) showed in a two-patch model that the degree of coupling between the dynamics of the two patches will influence the detection of density dependence at larger spatial scales. If the dynamics in the two patches are weakly coupled, then density dependence will be much less apparent at the level of the whole population even though there is clear density dependence at the level of a patch.

Consistent with the results of the two-patch model of Hastings (1993), the effect of exponential growth on a single plant dominating the dynamics of the whole population will decline if the rate of emigration from the exponential population is large in relation to its maximum population growth rate. In this case, sufficient emigration from the exponential population causes the whole population to exhibit either density-dependent growth or go extinct depending on values of the other model parameters (Fig. 6b, c). In our *Asclepias*–*A. nerii* system, movement among plants is sufficiently rare within a growing season and the estimated parameter values for r are sufficiently high (Table 1) such that exponential aphid growth on some individual plants does indeed dominate the dynamics of the whole pop-

ulation (Fig. 3). However, the production of alate aphids at very high density (Groeters 1989) might alter the effects of the plants that support exponential growth on the entire aphid population. The final outcome will depend upon the relative values of dispersal and population growth rate (Eq. 5).

Other recent studies have also demonstrated that for herbivores that move among plants, variability in plant quality can influence herbivore population dynamics (Underwood 2004). Specifically, this study showed that increasing variance in quality among host plants leads to increasing effects on herbivore population size. Furthermore, Underwood (2004) found that herbivore mobility increased the effect of variance in plant quality. It is clear that variation in rates of movement among individual plants should be considered along with variation in rates of increase and density dependence if we wish to understand the role of variable plant quality in population dynamics (Pulliam 1988; Gilpin and Hanski 1991).

An appreciation for the role of variation in plant quality in the population dynamics of herbivores is growing (Foster et al. 1992; Rossiter 1994; Belovsky and Joern 1995; Larsson et al. 2000; Underwood and Rauscher 2000, 2002; Helms et al. 2004; Rotem and Agrawal 2003). As we have demonstrated in this paper, ignoring the spatial heterogeneity that exists in herbivore population growth on plants that differ in quality can lead to a misunderstanding of the mechanisms that underlie observed population dynamics. Counting herbivores on plants and taking averages of population size, per capita growth rate, and the strength of density dependence is simply not sufficient (Hunter et al. 2000). Plant-derived variation in herbivore population parameters should be described explicitly, using appropriate statistical techniques, and incorporated directly into population models. Until this becomes the rule rather than the exception, our basic understanding of herbivore population ecology will continue to be inadequate.

Acknowledgements We thank Jeff Diez, Ron Pulliam, Pejman Rohani, Caralyn Zehnder, and Chris Frost for discussion and comments on the manuscript. This work was supported by NSF grant DEB-9906366 to MDH. We thank two anonymous reviewers for constructive criticism of an early version of this manuscript.

References

- Abrahamson WG, Weis AE (1997) Evolutionary ecology across three trophic levels. Princeton University Press, Princeton
- Belovsky GE, Joern A (1995) Regulation of rangeland grasshoppers: differing dominant mechanisms in space and time. In: Cappuccino N, Price PW (eds) Population dynamics: new approaches and synthesis. Academic, San Diego, pp 359–386
- Berryman AA (1999) Principles of population dynamics and their application. Stanley Thornes Publishers, Cheltenham
- Clark JS (2003) Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology* 84:1370–1381
- Denno RF, McClure MS (eds) (1983) Variable plants and herbivores in natural and managed systems. Academic, New York

- Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annu Rev Entomol* 40:297–331
- Forrester GE, Steele MA (2004) Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology* 85:1332–1342
- Foster MA, Schultz JC, Hunter MD (1992) Modeling gypsy moth-virus-leaf chemistry interactions: implications of plant quality for pest and pathogen dynamics. *J Anim Ecol* 61:509–520
- Freedman HI, Waltman P (1977) Mathematical models of population interactions with dispersal. I: stability of two habitats with and without a predator. *SIAM J Appl Math* 32:631–648
- Gilpin ME, Hanski I (1991) *Metapopulation dynamics: empirical and theoretical investigations*. Academic, London
- Groeters FR (1989) Geographic and clonal variation in the milkweed-oleander aphid, *Aphis nerii* (Homoptera: Aphididae), for winged morph production, life-history, and morphology in relation to host plant permanence. *Evol Ecol* 3:327–341
- Hassell MP, Southwood TRE, Reader PM (1987) The dynamics of the viburnum whitefly (*Aleurotrachelus jelinekii*): a case study of population regulation. *J Anim Ecol* 56:283–300
- Hastings AH (1993) Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* 74:1362–1372
- Helms SE, Connelly SJ, Hunter MD (2004) Effects of variation in plant species on the interaction between an herbivore and its parasitoid. *Ecol Entomol* 29:44–51
- Holt RD (1985) Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor Pop Biol* 28:181–208
- Hunter MD (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic Appl Ecol* 2:295–309
- Hunter MD, Malcolm SB, Hartly SE (1996) Population-level variation in plant secondary chemistry, and the population biology of herbivores. *Chemoecology* 7:45–56
- Hunter MD, Forkner RE, McNeil JN (2000) Heterogeneity in plant quality and its impact on the population ecology of insect herbivores. In: Hutchings MA, John EA, Stewart AJA (eds) *The ecological consequences of environmental heterogeneity*. Blackwell, Oxford, pp 155–179
- Inouye BD (2005) Scaling up from local competition to regional coexistence across two scales of spatial heterogeneity: insect larvae in the fruits of *Apeiba membranacea*. *Oecologia*. DOI 10.1007/s00442-005-0059-7
- Jones RE, Nealis VG, Ives PM, Scheermeyer E (1987) Seasonal and spatial variation in juvenile survival of the cabbage butterfly *Pieris rapae*: evidence for patchy density dependence. *J Anim Ecol* 56:723–737
- Larsson S, Ekblom B, Bjorkman C (2000) Influence of plant quality on pine sawfly population dynamics. *Oikos* 89:440–450
- Lill JT, Marquis RJ, Ricklefs RE (2002) Host plants influence parasitism of forest caterpillars. *Nature* 417:170–173
- McIntyre PJ, Whitham TG (2003) Plant genotype affects long-term herbivore population dynamics and extinction: conservation implications. *Ecology* 84:311–322
- Melbourne BA, Chesson P (2005) Scaling up population dynamics: integrating theory and data. *Oecologia*. DOI 10.1007/s00442-005-0058-8
- Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu Rev Ecol Syst* 11:41–65
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661
- Rossiter MC (1994) Maternal effects hypothesis of herbivore outbreak. *Bioscience* 44:752–763
- Rotem KA, Agrawal AA (2003) Density dependent population growth of the two-spotted spider mite, *Tetranychus urticae*, on the host plant *Leonurus cardiaca*. *Oikos* 103:559–565
- SAS (1999) *SAS/STAT user's guide*. SAS Institute, Cary
- Sauer JR, Link WA (2002) Hierarchical modeling of population stability and species group attributes from survey data. *Ecology* 83:1743–1751
- Shima JS, Osenberg CW (2003) Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology* 84:46–52
- Southwood TRE, Hassell MP, Reader PM, Rogers DJ (1989) Population dynamics of the viburnum whitefly (*Aleurotrachelus jelinekii*). *J Anim Ecol* 58:921–942
- Spiegelhalter DJ, Thomas A, Best NG (1999) WinBUGS, Version 1.2, user manual. MRC Biostatistics Unit
- Underwood N (2004) Variance and skew of the distribution of plant quality influence herbivore population dynamics. *Ecology* 85:686–693
- Underwood N, Rausher M (2000) The effects of host-plant genotype on herbivore population dynamics. *Ecology* 81:1565–1576
- Underwood N, Rausher M (2002) Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. *Am Nat* 160:20–30