Notes and Comments

Variation in and Correlation between Intrinsic Rate of Increase and Carrying Capacity

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abstract: Intrinsic population growth rate and density dependence are fundamental components of population dynamics. Theory suggests that variation in and correlations between these parameters among patches within a population can influence overall population size, but data on the degree of variation and correlation are rare. Replicate populations of a specialist aphid (*Chaetosiphon fragaefolii*) were followed on 11 genotypes of host plant (*Fragaria chiloensis*) in the greenhouse. Population models fit to these census data provide estimates of intrinsic growth rate and carrying capacity for aphid populations on each plant genotype. Growth rate and carrying capacity varied substantially among plant genotypes, and these two parameters were not significantly correlated. These results support the existence of spatial variation in population dynamic parameters; data on frequency distributions and correlations of these parameters in natural populations are needed for evaluation of the importance of variation in growth rate and density dependence for population dynamics in the field.

Keywords: carrying capacity, intrinsic population growth rate, *Fragaria chiloensis*, *Chaetosiphon fragaefolii*, environmental variation, density dependence.

Early models of temporal population dynamics (e.g., the Ricker [Ricker 1954] and the logistic [Hutchinson 1978] models) consider individuals within populations to be subject to a uniform environment. However, like most simplifying assumptions, we know this is not always true; habitat quality can vary within populations or metapopulations. For example, populations of herbivorous insects that move among host plants experience an environment

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of patches (plants) that can vary in quality (Underwood and Rausher 2000; Agrawal et al. 2004). Models that incorporate spatial variation in habitat quality within populations or metapopulations (see, e.g., Holt 1985; Pulliam 1988; Hastings 1993; Underwood 2004) suggest that variation in the quality of the habitat (biotic or abiotic) within a single population should affect the population's ecological or evolutionary dynamics when organisms move among areas of different quality.

Models of regulated population dynamics have at least two parameters, either of which could be affected by spatial variation in habitat quality: one controlling the rate of population growth at low densities (the intrinsic growth rate) and one controlling density dependence. Density dependence is sometimes expressed directly (as in the generalized Ricker model) and sometimes expressed as equilibrium population size (as in the logistic model). Although the concept of equilibrium populations has rightly been challenged (because populations may rarely be at stable equilibria), the idea that populations are affected by density dependence is well accepted. In models such as the logistic model, equilibrium population size can be a useful parameter even if equilibrium is rarely reached, because it is a component of the strength of density dependence acting on a population.

Models of spatial variation in population dynamics account for spatial variation by manipulating the two fundamental population dynamic parameters in several different ways. Some models consider only differences in intrinsic rate of population growth among patches (see, e.g., Pulliam 1988; Hastings 1993; Pascarella and Horvitz 1998), some consider only differences in equilibrium population size (Holt 1985), and some consider differences in both parameters (see, e.g., Underwood 2004; M. Donahue, N. Underwood, B. Melbourne, and P. Chesson, unpublished manuscript). Many empirical studies have documented variation in intrinsic population growth rate (e.g., Horvitz and Schemske 1995; Helms et al. 2004) or density dependence (e.g., references in Krebs 2002; Shima and Osenberg 2003) among patches within populations; fewer

studies have examined spatial variation in both intrinsic growth rate and density dependence or equilibrium population size simultaneously (Bell 1990; Underwood and Rausher 2000; Agrawal et al. 2004). There are thus relatively few data to address the question of whether variation in habitat quality within populations can be thought of as variation predominantly in intrinsic population growth rate, predominantly in density dependence, or both.

If, as one might expect, patches within populations vary substantially in both of the basic population dynamic parameters, we can also consider whether and how growth rate and density dependence or equilibrium population size might be correlated. Models including variation in both growth rate and equilibrium population size (Underwood 2004; M. Donahue, N. Underwood, B. Melbourne, and P. Chesson, unpublished manuscript) suggest that variation in equilibrium population size among patches alone, or with uncorrelated variation in population growth rate, can reduce overall equilibrium population sizes. These models also suggest that correlations between equilibrium population size and intrinsic growth rate can strongly modify the effect of variation on equilibrium population size. In particular, correlation between growth rate and carrying capacity across patches influences whether the effect of variation in quality among habitat patches on equilibrium population size will be positive or negative. In these models, if growth rate and carrying capacity are positively correlated such that patches that promote high growth also support large numbers of organisms, the equilibrium population size across all patches is larger than would be expected without variance. When the two are negatively correlated, equilibrium population size is smaller than would be expected without variance or with variance in carrying capacity alone (fig. 1; Underwood 2004). It is important to note that increasing movement among patches can also magnify the effect of variation.

Theory thus suggests that to understand fully the dynamics of a given population, we may need information about the variation in and correlation between population dynamic parameters within populations. Unfortunately, little is known about how these parameters might be correlated among patches within a larger population. We might predict positive correlations because, for example, patches with faster resource renewal should promote rapid growth at low density and support higher densities of organisms. On the other hand, negative correlations could also be expected, for example, if temperature increases growth rates but decreases equilibrium populations because energy needs are higher at higher temperatures (Hutchinson 1978). To my knowledge, no data exist that bear directly on these correlations among patches within populations or metapopulations, and data on differences in population dynamic parameters among environments
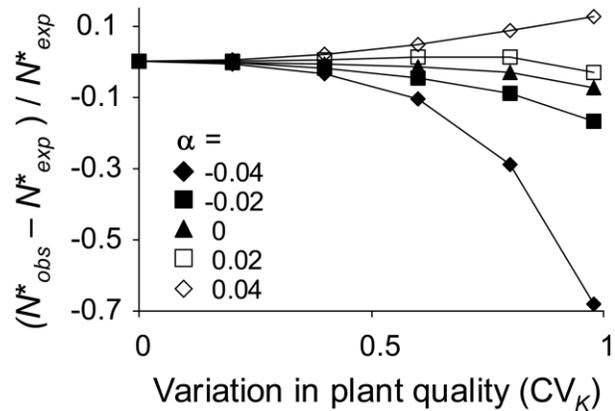
Figure 1: Effect of variation in carrying capacity (K) among patches on the equilibrium population size across patches in a simulation model. Population dynamics are modeled as logistic equations in each patch, linked by global migration. The observed equilibrium population size (N^*_{obs}) in simulations is expressed relative to the expected population size (N^*_{exp}) in the absence of an effect of variation (i.e., average carrying capacity across patches). Each point indicates equilibrium population size in a single run of the model; α indicates the correlation between r and K. Redrawn from Underwood (2004).

that could exist at the within-population scale are rare (but see Bell 1990).

Data addressing variance in and correlations between the fundamental population dynamic parameters are likely to be logistically difficult to gather in many systems because they require measuring growth and density dependence in different patches in isolation; migration among patches will alter the observed population dynamic parameters within patches. Because plant-insect-herbivore systems can often be relatively small scale and have rapid population dynamics, these systems are a good tool for looking at correlations between population dynamic parameters. As a step toward examining the relationship between growth rate and carrying capacity across environments, I measured the intrinsic rate of increase and equilibrium population size of a specialist aphid across genotypes of its host plant in the greenhouse. Like many herbivorous insects, these aphids move among plants in the field (N. Underwood, personal observation), so individual plants represent environmental patches within the insect population. Using greenhouse experiments and model fitting, I asked (1) whether environments represented by different host-plant genotypes differ in aphid population growth rate and/or equilibrium population size and (2) whether these parameters were correlated across host-genotype environments.

Wild strawberry (*Fragaria chiloensis*) and the strawberry aphid (*Chaetosiphon fragaefolii*, a specialist on *Fragaria*) are native to the Pacific coast of the Americas. *Fragaria chiloensis* is a perennial herb that is easily cloned from asexual runners. Strawberry plants for this experiment were collected in the field (Sonoma County, CA; genotypes Wrights 2, Doran 1, and Doran 3) or obtained from the National Clonal Germplasm Repository (Corvallis, OR; genotypes 34, 37, 39, 59, 55, 340, 361, and 1312). Some genotypes from the Germplasm Repository were chosen for high or low resistance to arthropods (mostly mites), but most (including those from the field) were chosen without any knowledge of their effects on aphids. All plants used in this experiment resulted from at least two rounds of asexual propagation in a common greenhouse environment. *Chaetosiphon fragaefolii* for this experiment were collected from several locations in the field (Sonoma County, CA) and reared for at least 6 months in the greenhouse, a minimum of 10 overlapping aphid generations. The aphid colony was initiated and occasionally refreshed with individuals from multiple field populations and thus probably contained a mixture of genotypes. The aphid colony was reared on a mixture of strawberry genotypes not used in the study so that a feeding bias would not develop within the aphid population. All aphids in this experiment were parthenogentic females (sexual reproduction is extremely rare in coastal populations; Schaefers and Allen 1962).

I rooted six individuals of each of the 11 strawberry genotypes listed above in separate 3.8 × 21-cm tubes (Cone-tainers, Stuewe, Corvallis, OR) filled with University of California–Davis (UC Davis) research mix. Plants were grown in a UC Davis entomology department greenhouse and were watered and fertilized as necessary with Miracle-Gro (Scotts, Marysville, OH). The tubes were placed in six racks (each rack constituted a spatial block), with one individual of each genotype per rack. Each plant was enclosed in a mesh bag (Fibe-Air Sleeve, Kleen Test, Milwaukee, WI) that prevented aphid movement among plants. I began the experiment by placing either one (for two of the six blocks) or two (for the other four blocks) adult aphids on each plant. Starting with slightly different aphid densities provided additional information for estimating population dynamic parameter values (Pascual and Kareiva 1996). Aphid populations were counted in situ biweekly for 10–14 censuses; two blocks were started later than the other blocks, and in eight cases, individual plants died before the end of the experiment, resulting in shorter time series (plants that died were genotypes 361 [four cases], 340 [two cases], and 37 and 34 [one case each]). If an aphid population became extinct while the plant was

alive, the population was restarted with either one or two new adult aphids, as appropriate for that block.

I fit the logistic model—$dN/dt = rN[1 - (N/K)]$, where N is population size, r is intrinsic rate of increase, and K is the equilibrium population size (carrying capacity)—to the time series of aphid population sizes for each strawberry genotype (e.g., fig. 2) separately. For all genotypes, a logistic model was a much better fit to the data than was the simpler exponential. I fit two alternative maximum likelihood models, one with observation noise and one with process noise (de Valpine and Hastings 2002). Poisson error resulted in better model fits than did normal or lognormal error; parameter estimates were similar regardless of the type of error used. This procedure resulted in estimates of r and K for aphids on each of the strawberry genotypes. Estimates using process and observation noise were significantly correlated for both r (Pearson correlation coefficient: $r = 0.77$, $P = .02$) and K ($r = 0.85$, $P = .003$); results are shown only for observation error. I calculated contours around the best-fit estimates of r and K that indicate significant differences at the $P = .05$ level for likelihood ratio tests. Genotypes for which the confidence contours do not overlap can therefore be considered to have population dynamic parameters significantly different at the $P = .05$ level. As an additional test for effect of plant genotype on aphid population dynamics, I used a likelihood ratio test (Edwards 1992) to compare a global mean model to one including separate population dynamic parameters for each plant genotype. I calculated a Spearman's rank correlation coefficient as a description of the strength of association between the most likely growth rate and equilibrium population size across plant genotypes and tested whether this correlation was significantly different from 0 (results using a Pearson correlation coefficient were very similar). Finally, I conducted a power analysis for the correlation.
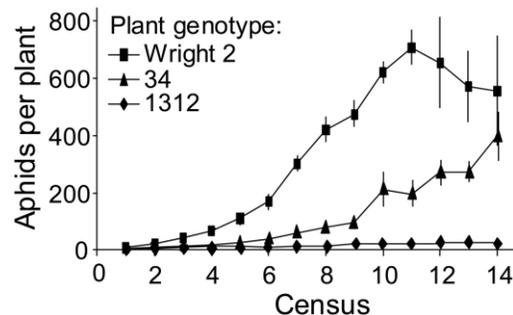
Figure 2: Dynamics of aphid populations on three of the 11 genotypes of wild strawberry in the greenhouse. $N = 6$ for each point; error bars indicate ± 1 SE.

Results and Discussion

Theory suggests that variation in and correlations between population dynamic parameters within populations should affect overall population size. In this study, I found significant variation in intrinsic population growth rate and carrying capacity and no significant correlation between parameters across host plants.

Aphid populations on different strawberry genotypes differed substantially in estimates of both intrinsic growth rate and carrying capacity (figs. 2, 3). The confidence contours around estimates for the parameters for individual genotypes did not overlap, and a model including separate parameters for each genotype had a significantly lower negative log likelihood than a global mean model (likelihood ratio test statistic = 274,116.8, df = 22, $P = 0$), indicating significant differences in parameter estimates among strawberry genotypes. The confidence with which these parameters could be estimated varied widely (cf. the estimates of r for genotypes 39 and 361). Because the study was carried out in the greenhouse, after several generations of greenhouse propagation, these differences are probably due to genetic differences among the plants, although lingering maternal effects of the environments from which the plants were collected are possible. Although evidence is abundant that plant traits can influence herbivore performance and behavior (Fritz and Simms 1992), few studies have shown that differences among host species or genotypes influence longer-term population dynamics (both growth rate and density dependence). Many studies examining plant effects on herbivore populations have demonstrated differences in population growth rates across either plant species or genotypes (see, e.g., Agrawal et al. 2004; Helms et al. 2004). Fewer have attempted to measure differences in carrying capacity or density dependence (but see Underwood et al. 2000; Agrawal et al. 2004).

The plant genotypes used in this study were collected from many different natural populations across several states, so the results cannot tell us the distribution of population dynamic parameters in any one population in the field. However, two of the genotypes in the experiment (Doran 1 and Doran 3) were collected from the same population (Doran Park, Sonoma County, CA) and differ significantly in both r and K, so variation in these parameters within populations in the field does exist. Although *Fragaria chiloensis* appears to reproduce primarily asexually by means of runners, its populations contain genetic variation greater than would be expected as a result of asexual reproduction alone (Alpert et al. 1993). Aphid growth rate and carrying capacity also varied in a field experiment on a subset of the same strawberry genotypes used in this study (although the rank order of plant quality
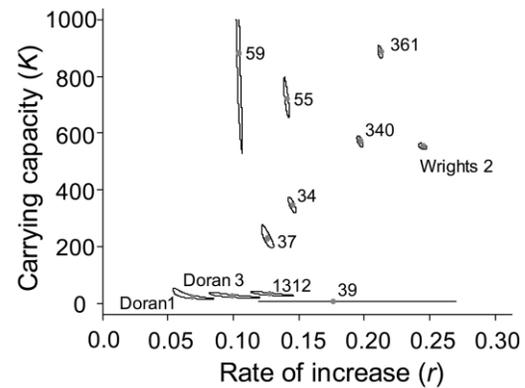

Figure 3: Maximum likelihood estimates of strawberry-aphid population growth rates and carrying capacities on 11 different genotypes of wild strawberry. Each point indicates a different genotype. Contours indicate parameter values significantly different from the maximum likelihood estimates at the $P = .05$ level, on the basis of likelihood ratio tests.

was not identical; N. Underwood, unpublished manuscript), suggesting that the kind of differences in parameters observed in the greenhouse are detectable even with natural variation in weather, predators, and competitors. Results of this study thus suggest that variation in population dynamic parameters among wild strawberries has the potential to influence aphid population size in the field. Models (Underwood 2004; M. Donahue, N. Underwood, B. Melbourne, and P. Chesson, unpublished manuscript) show that increasing variation of the kind observed in this study can cause increasing deviations from the equilibrium population sizes expected for populations in homogeneous environments (fig. 1).

The magnitude and sign of the effect of variation in population dynamic parameters can also in theory be affected by correlations between population growth rate and carrying capacity across plants (fig. 1). With no correlation, variation in carrying capacity alone should have a negative effect on equilibrium population size. A negative correlation between parameters should cause a stronger negative effect of variation in K, and a positive correlation should cause a positive effect of variation in K. In this study, aphid growth rate and carrying capacity were not significantly correlated across wild strawberry genotypes ($r = 0.41$, $P = .20$), although the trend was toward a positive correlation (power to detect a significant correlation = 0.75).

There are two aspects of correlations between r and K to consider: whether there is a fundamental association between plant traits that influence herbivore growth rate and carrying capacity and what the association between growth rate and carrying capacity might be in any particular population of interest. The lack of correlation be-

tween r and K in this study suggests that there is not a strong fundamental association between plant traits influencing these parameters. Because the variation in r and K measured in this study is a property of the aphids' environment (the plant) rather than of traits of the aphids themselves, either negative or positive correlations between r and K across plants could have been expected. For example, plants with high throughput of nitrogen might have supported both fast aphid reproduction at low densities and larger aphid densities, whereas trade-offs between inducible and constitutive plant resistance might have produced a negative correlation between r and K or no correlation. Plants with high constitutive resistance should produce aphid populations with low intrinsic growth rates but carrying capacities set by other factors in the environment. Plants with inducible resistance, on the other hand, might allow high growth rates for herbivores at low density (r), when resistance has not yet been induced, but also might contribute to lowering herbivore carrying capacity because inducible resistance can be density dependent (Underwood 2000).

The lack of a strong fundamental association between plant traits influencing aphid growth rate and carrying capacity in this study also means that any particular population of wild strawberry plants could have anything between a positive and a negative association between r and K. That is, from any pool of plant genotypes, one could select a group of plants with negative or positive correlations and thus different predicted effects of variation on equilibrium population size. In one other study of genotype-by-environment correlations between r and K in *Chlamydomonas*, Bell (1990) found a negative but also nonsignificant correlation between r and K. Unless correlations between r and K across environments turn out to be stronger and more consistent than indicated by these studies, prediction of the influence of such correlations within any particular population may not be possible until the distribution of population dynamic parameters is determined for that particular population.

The results reported here suggest that both population growth rate and density dependence can vary among patches within populations and thus should be accounted for in theoretical and empirical studies of the effects of heterogeneity on population processes. Variation in and correlation between population dynamic parameters within populations has the potential to influence equilibrium population sizes, as long as there is movement within populations. No correlation was found in this study, but more data are clearly necessary to determine how often strong correlations exist and whether they play an important role under field conditions (given the influence of other factors affecting population size). In addition to among-patch variation (a function of the environment of the focal population), there might also be genetic variation among individuals within the focal population in traits contributing to these parameters (Mueller et al. 1991). The actual dynamics of any given population are likely to be a function of the mean and variance of parameters both among environments and among individuals. A full understanding of population dynamics may thus require describing the distributions of and correlations between population dynamic parameters both among individuals as a result of their own traits and among environmental patches within populations.

Acknowledgments

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