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Population density and area: the role of within- and between-generation processes over time

Stephen F. Matter *

University of Virginia, Blandy Experimental Farm, Boyce, VA 22620, USA

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Abstract

The density–area relationship has received considerable attention recently. A limitation of empirical examinations of the density–area relationship is that they have been conducted over short time spans, focusing on within-generation mechanisms such as dispersal and ignoring potential between-generation effects. I used simulation modeling to investigate the effects of both within- and between-generation factors that vary with patch size on the density–area relationship. In general, between-generation factors had a greater effect on long-term density–area patterns than within-generation processes, but within-generation processes are important under certain conditions. Interactions between within- and between-generation processes produced several non-intuitive results. The results of this study demonstrate that to fully understand density–area patterns both within- and between-generation patterns must be investigated. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Density–area relationship; Resource concentration; Patch; Density; Metapopulation; Dispersal

1. Introduction

Much recent research in spatial population ecology has addressed how population density varies with the size of habitat patches—the density–area relationship. Understanding how populations respond to patches of varying size underlies basic ecological theory and is pertinent to conservation issues (Andrén, 1994; Matter, 1996, 1997; Bowers and Matter, 1997; Bender et al., 1998; Connor et al., 1999). An implicit assumption of most metapopulation models is that the abundance of organisms is proportional to the size of the patch, in other words, density does not vary with patch size (Hanski, 1991; Hanski and Thomas, 1994). Positive or negative density–area relationships result in individuals being clustered in larger or smaller patches, changing the relative importance of patches of different size and potentially altering predictions concerning metapopulation dynamics and persistence. The equilibrium theory of island biogeography also incorporates the assumption that density of individual species is constant with patch or island area (MacArthur

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* Present address: Department of Ecology and Systematics, Division of Population Biology, University of Helsinki, PO Box 17 (Arkadiankatu 7), FIN-00014 Helsinki, Finland. Tel.: + 358-9-1917378; fax: + 358-9-1917492.

E-mail address: steve.matter@helsinki.fi (S.F. Matter)

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Table 1
Parameter values used in the simulations[a]

Parameter values							
Carrying capacity coefficient (A)	−1.75	−1.50	−1.25	1.00	1.25	1.50	1.75
Dispersal coefficient (B)	0.40	0.60	0.80	1.00	1.20	1.40	1.60
Population growth rate (r)	1.00	1.50	2.00	2.50	3.00	3.50	4.00
Proportion dispersing (m)	0.15	0.25	0.35	0.45	0.55	0.65	0.75
Coded values							
Carrying capacity coefficient (A)	−1.00	−0.86	−0.71	0.00	0.71	0.86	1.00
Dispersal coefficient (B)	−1.00	−0.67	−0.33	0.00	0.33	0.66	1.00
Population growth rate (r)	−1.00	−0.67	−0.34	−0.01	0.32	0.65	0.98
Proportion dispersing (m)	−1.00	−0.67	−0.33	0.00	0.33	0.66	1.00

[a] Because the design was not completely orthogonal, factor levels were coded before use in the response surface analysis.

and Wilson, 1967; Connor et al., 1999). From a management perspective how population density varies with reserve size is central to the single-large or several-small (SLOSS) debate (Simberloff, 1988).

Observational and experimental studies have shown that there is considerable variability in density–area patterns with different species showing positive, negative and neutral relationships (Root, 1973; Cromartie, 1975; Raupp and Denno, 1979; Denno et al., 1981; Kareiva, 1981, 1985; Kindvall and Ahlen, 1982; MacGarvin, 1982; Bach, 1988; Funderburke et al., 1990; Foster and Gaines, 1991; Dooley and Bowers, 1996; Förare and Solbrek, 1997; Matter, 1997 c.f. Bowers and Matter, 1997; Bender et al., 1998; Connor et al., 1999 for reviews). Despite this variability, there appear to be consistent taxonomic differences. The density of insects and birds generally increases with the size of habitat patches (Bender et al., 1998; Connor et al., 1999) while mammals tend to show constant densities across patches of different size (Bowers and Matter, 1997; Connor et al., 1999).

Root (1973) suggested as part of the 'resource concentration hypothesis' that a positive density–area pattern would result from the net movement of individuals out of smaller patches and a tendency to immigrate to and remain on larger patches (Root, 1973; Kareiva, 1985). Following this lead, most theoretical and empirical examinations of density–area patterns have focused on mechanisms, such as dispersal, acting within generations and between patches. Studies examining patterns of movement and density with patch size have often found greater emigration rates for smaller patches or higher immigration to larger patches, along with positive density–area relationships. Together these results have been accepted as confirmation of the role of dispersal as

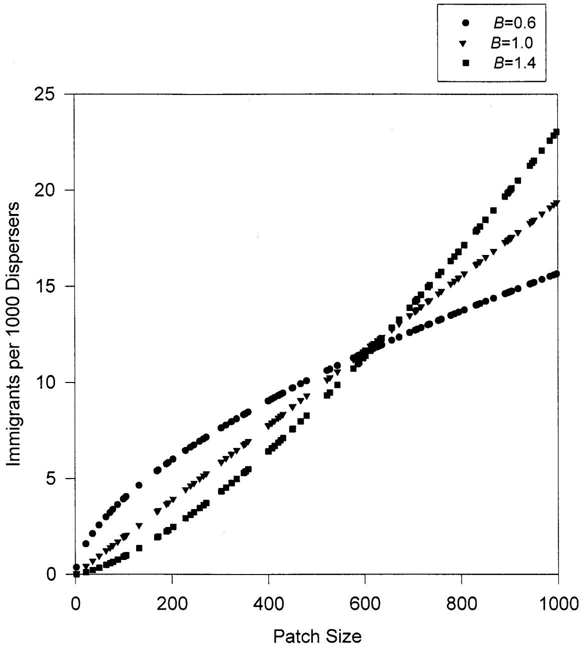


Fig. 1. A sample dispersal pattern for increasing immigration with patch size ($B = 1.4$), constant immigration with patch size ($B = 1.0$) and decreasing immigration with patch size ($B = 0.6$). Values shown are the number of immigrants per 1000 dispersers for a set of 100 patches uniformly random in size from 1 to 1000.

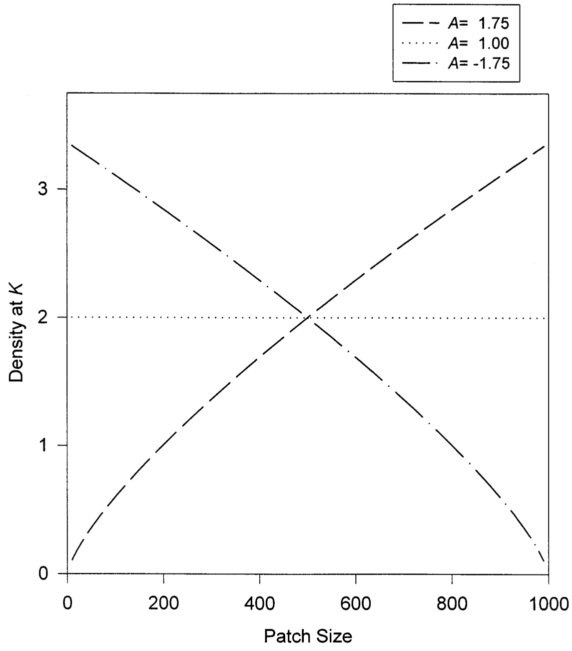


Fig. 2. The population density at the carrying capacity (K) for patterns of increasing ($A = 1.75$), constant ($A = 1.00$) and decreasing ($A = -1.75$) density at K with patch size.

the main mechanism producing density–area patterns (Root, 1973; Fahrig and Merriam, 1985; Kareiva, 1985; Turchin, 1986, 1987; Dooley and Bowers, 1996; Bowers and Matter, 1997). However, a variety of other mechanisms have been proposed to account for density–area relationships. Both predator efficiency and predatory risk from edge predators have been shown to be higher for small patches, producing positive density–area relationships (Denno et al., 1981; Risch, 1981; Andrén, 1992; Matter et al., 1996). For small mammals negative density–area relationships may arise from social interactions where dominant individuals maintain territories on larger, presumably higher-quality habitats and smaller habitats contain higher densities of non-territorial, sub-dominant individuals (Dooley and Bowers, 1996; Bowers and Matter, 1997).

Despite the conceptual importance of the density–area relationship, a limitation of most studies examining this phenomena is that they have been conducted over short time spans, ignoring any potential between-generation effects (e.g. Root, 1973; Maguire, 1983; Kareiva, 1985; Bach, 1988; Funderburke et al., 1990, but see Root and Kareiva, 1984; Capman et al., 1990). Extrapolating the tenets of the resource concentration hypothesis to multi-generational situations requires special considerations. First, patterns of movement to either large or small patches could not continue in perpetuity. Over multiple generations patches would reach a point where increasingly high densities could not be supported, creating a

Table 2
Response surface regression analyses for the slope of the relationship between local population density and patch size[a]

After dispersal			
Source	df	Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	0.038	
Dispersal coefficient (B)	5	0.048	
Population growth rate (r)	5	0.016	
Proportion dispersing (m)	5	0.001	
Source		Type I SS	R^2
Linear	4	0.063	0.630
Quadratic	4	0.006	0.006
Interactions	6	0.017	0.167
Total Regression	14	0.086	0.858
Error	23 995	0.014	
After reproduction			
Source		Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	0.140	
Dispersal coefficient (B)	5	0.008	
Population growth rate (r)	5	0.001	
Proportion dispersing (m)	5	0.003	
Source		Type I SS	
Linear	4	0.146	0.922
Quadratic	4	0.001	0.003
Interactions	6	0.017	0.017
Total Regression	14	0.149	0.942
Error	23 995	0.009	

[a] On the top is the analysis after dispersal while on the bottom is after reproduction. Composite variables include the sums of squares due to the linear, quadratic and linear interactions versus the null hypothesis that the joint parameter estimate is zero. These joint sums of squares were used to estimate the sensitivity of the dependent variable to each parameter (see Section 2 for details). Below the composite variables are the overall response surface analyses.

Table 3
Response surface regression analyses for the z-transformed correlation coefficient between local population density and patch size[a]

After dispersal			
Source	df	Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	22 451	
Dispersal coefficient (B)	5	6809	
Population growth rate (r)	5	1398	
Proportion dispersing (m)	5	3102	
Source		Type I SS	R^2
Linear	4	23 452	0.675
Quadratic	4	272	0.008
Interactions	6	5017	0.145
Total Regression	14	28 742	0.828
Error	23 995	5979	
After reproduction			
Source		Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	45 240	
Dispersal coefficient (B)	5	2140	
Population growth rate (r)	5	466	
Proportion dispersing (m)	5	4992	
Source		Type I SS	
Linear	4	43 246	0.810
Quadratic	4	293	0.006
Interactions	6	4650	0.087
Total Regression	14	48 189	0.902
Error	23 995	5232	

[a] On the top is the analysis after dispersal while on the bottom is after reproduction. Composite variables include the sums of squares due to the linear, quadratic and linear interactions versus the null hypothesis that the joint parameter estimate is zero. These joint sums of squares were used to estimate the sensitivity of the dependent variable to each parameter (see Section 2 for details). Below the composite variables are the overall response surface analyses.

situation where survival, reproduction, movement, or a combination of these factors become density-dependent. Second, any potential between-generation factors that may directly affect density or that vary with patch size, such as predation, mating opportunities, or the amount of or ability to find resources must be considered. Finally, it should be noted that for many species, especially insects, the notion of between-generation processes occurring within a patch may be inappropriate. Many immature insects use different resources than adults. If hosts are short-lived, as in the case of annual plant species, between-generation processes may not be confined to a particular patch. Additionally, if patches simply represent ‘foraging units’ and an organism may visit many over its lifespan, population-level processes may be occurring at larger spatial scales than the patch (Hastings and Harrison, 1994).

The combination of within- and between-generation factors that vary with patch size may interact in complex ways to create density–area relationships, forming the basis for this research. Specifically, a simulation model was developed to examine the effects of both types of processes on the density–area relationship. The within-generation process was modeled considering the resource concentration hypothesis, i.e. movement patterns are patch size dependent. Because most alternatives to the resource concentration hypothesis involve mortality or survival that varies with patch size, the between-generation factor was modeled as a non-unique, density-dependent process that increases or decreases between generation survival or mortality relative to patch size. This between-generation process may be viewed as a ‘carrying capacity’ for each patch that can vary disproportionately with patch size. The results of this study should be pertinent to those interested in spatial population dynamics, patch and landscape scale studies and density–area questions in particular.

2. Methods

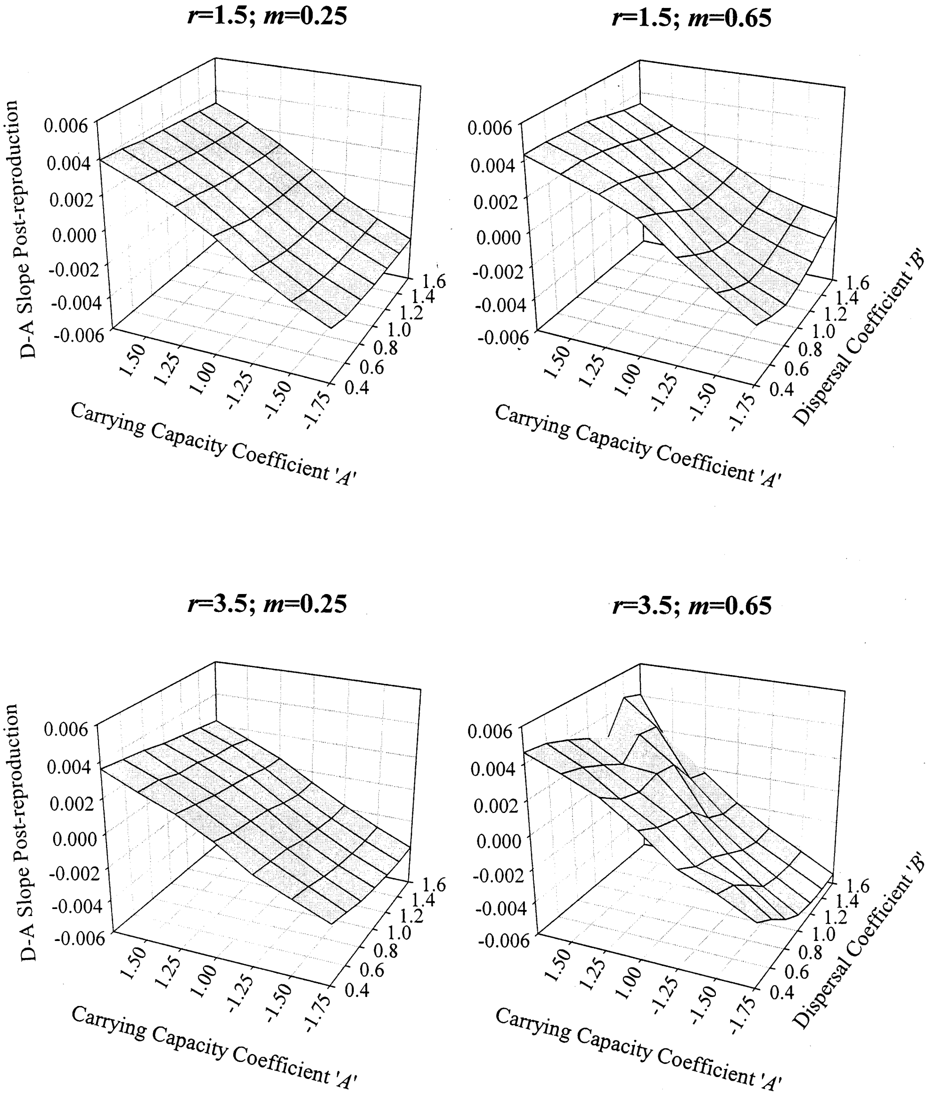
2.1. Model and parameters

A generalized life history was employed. At the beginning of a generation a proportion of the population disperses between patches. Parameter values for the proportion of the population dispersing (m) span the range from relatively sedentary to vagile species (Table 1). Organisms emigrate from patches independent of patch size or population density. The pattern of immigration with patch size was modeled as follows:

$$\mathrm{Imm}_i = (m^*X) * (\mathrm{S}_i^B / \Sigma_i^n \mathrm{S}_i^B)$$

where Imm_i is the number of immigrants to patch i, X is the total number of individuals across all patches, S_i is the size of patch i and B is the dispersal coefficient (Fig. 1). For values of B greater than one the number of immigrants is disproportionately increasing with patch size. The magnitude of this effect increases with increasing values of B. When B is equal to one, immigration is proportional to patch size and is proportionally greater to smaller patches for values of B less than one. Parameter values include patterns of movement ranging from dispersing strongly toward large patches (1.60) to strongly toward smaller patches (0.40).

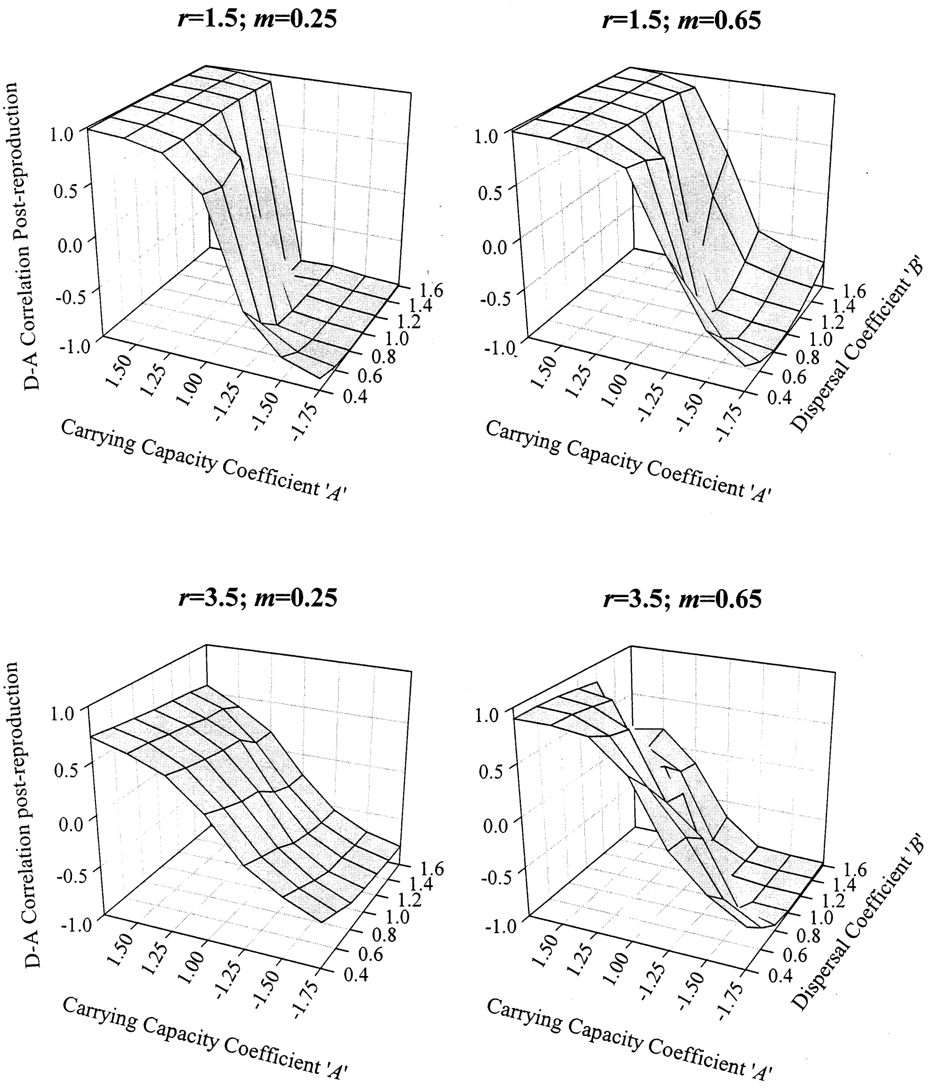
Following dispersal organisms reproduce. The number of individuals in each patch in the next generation occurs according to a discrete logistic function:



r=1.5; m=0.25 **r=1.5; m=0.65**

r=3.5; m=0.25 **r=3.5; m=0.65**

Fig. 3. The mean simulated ($n = 10$) slope of the relationship between population density and patch size following reproduction for each dispersal coefficient (B) and carrying capacity coefficient (A) under four combinations of the rate of dispersal (m) and population growth (r).


r=1.5; m=0.25

r=1.5; m=0.65

r=3.5; m=0.25

r=3.5; m=0.65

Fig. 4. The mean simulated ($n = 10$) correlation between insect density and patch size following reproduction for each dispersal coefficient (B) and carrying capacity coefficient (A) under four combinations of the rate of dispersal (m) and population growth (r). The figure shows the correlation coefficient (r). Statistical analyses were performed on the z-transformed correlation coefficient.

$$N_{i(t+1)} = N_{i(t)} + rN_{i(t)}\,(1 - (N_{i(t)}/K_i))$$

where K_i is the carrying capacity and N_i is the number of organisms in patch (i) at time t (Gotelli, 1995). Population growth rates (r) ranged from 1.0, where the population is simply replacing itself, to 4.0 spanning the range of dynamic situations from damped oscillations to chaos seen for single-population, discrete logistic models (May, 1974; Gotelli, 1995). To produce a proportionally varying carrying capacity with patch size, the density (D) of organisms that would occur at the carrying capacity for patch (i) was modeled using the function:

$$K_i = C\,S_i^A + L$$

where $D_i = K_i/S_i$. For constant density at carrying capacity situations, i.e. when the carrying capacity is proportional to patch size, $A = 1$. Values of A

greater than one indicate increasing density at carrying capacity with patch size, values of A less than negative one were used to produce decreasing densities at carrying capacity with patch size. The parameters C and L were adjusted to make densities and the correlation between density and area comparable between treatment levels (i.e. the expected number of individuals across the landscape should be the same for all values of A if all patches are at the carrying capacity). C and L were adjusted so that at the mean patch size (500) density at carrying capacity was 2.0 individuals per unit patch size for all values of A and so that the pattern was equal in magnitude for the same absolute values of A (e.g. the density at carrying capacity for $A = -1.75$ is the 'mirror image' of $A = 1.75$ about the mean patch size, Fig. 2). Because few comparative data exist, the patterns of

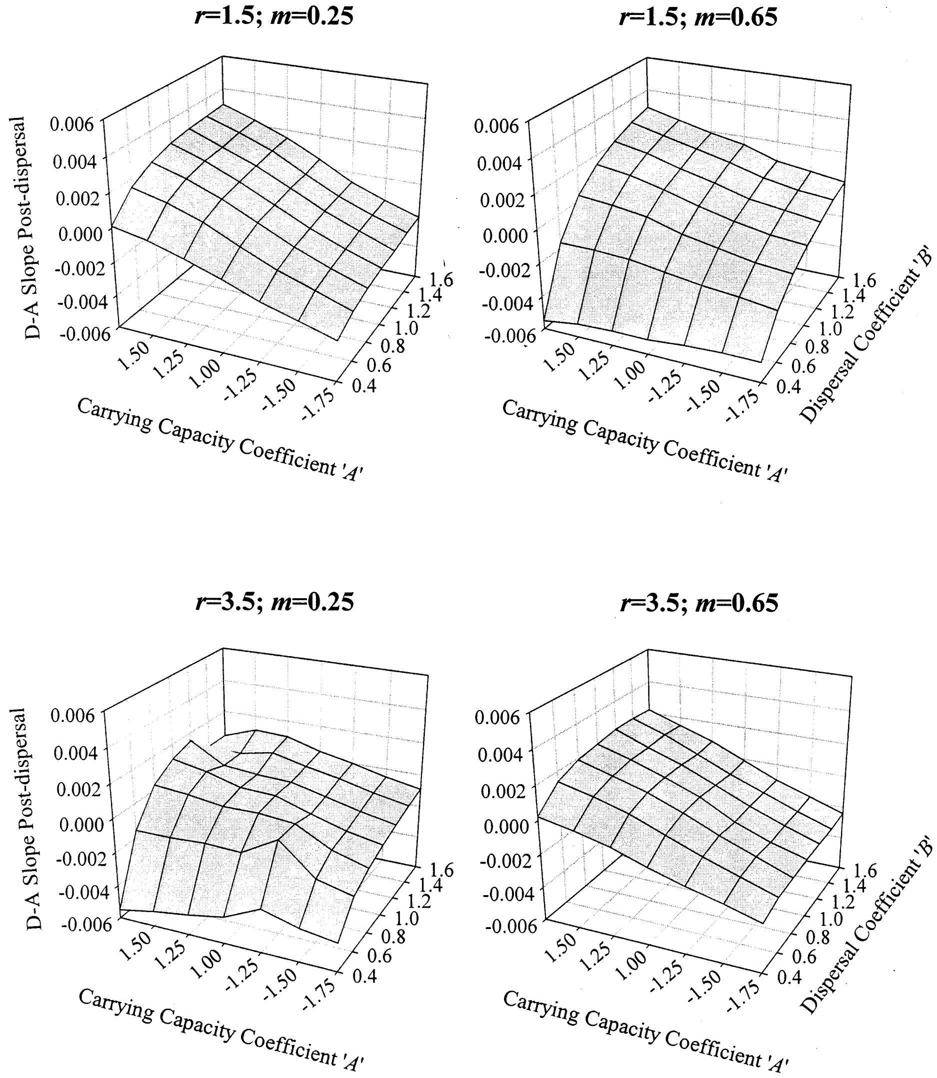


Fig. 5. The mean simulated ($n = 10$) slope of the relationship between population density and patch size following dispersal for each dispersal coefficient (B) and carrying capacity coefficient (A) under four combinations of the rate of dispersal (m) and population growth (r).

Table 4
Response surface regression analyses for the spatial variation in local population density[a]

After dispersal			
Source	df	Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	15 832	
Dispersal coefficient (B)	5	275 730	
Population growth rate (r)	5	78 896	
Proportion dispersing (m)	5	568	
Source		Type I SS	R^2
Linear	4	137 683	0.085
Quadratic	4	98 500	0.061
Interactions	6	67 421	0.042
Total Regression	14	303 606	0.187
Error	23 995	1 322 795	
After reproduction			
Source		Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	788	
Dispersal coefficient (B)	5	177	
Population growth rate (r)	5	50	
Proportion dispersing (m)	5	364	
Source		Type I SS	
Linear	4	1503	0.192
Quadratic	4	3008	0.385
Interactions	6	1193	0.153
Total Regression	14	5703	0.730
Error	23 995	2111	

[a] On the top is the analysis after dispersal while on the bottom is after reproduction. Composite variables include the sums of squares due to the linear, quadratic and linear interactions versus the null hypothesis that the joint parameter estimate is zero. These joint sums of squares were used to estimate the sensitivity of the dependent variable to each parameter (see Section 2 for details). Below the composite variables are the overall response surface analyses.

density at carrying capacity are meant to simulate a variety of potential scenarios regarding the relationship between a between-generation factor and patch size. Abundances were cropped at zero. If abundance on a particular patch became negative it was set to zero and the patch was allowed to be recolonized.

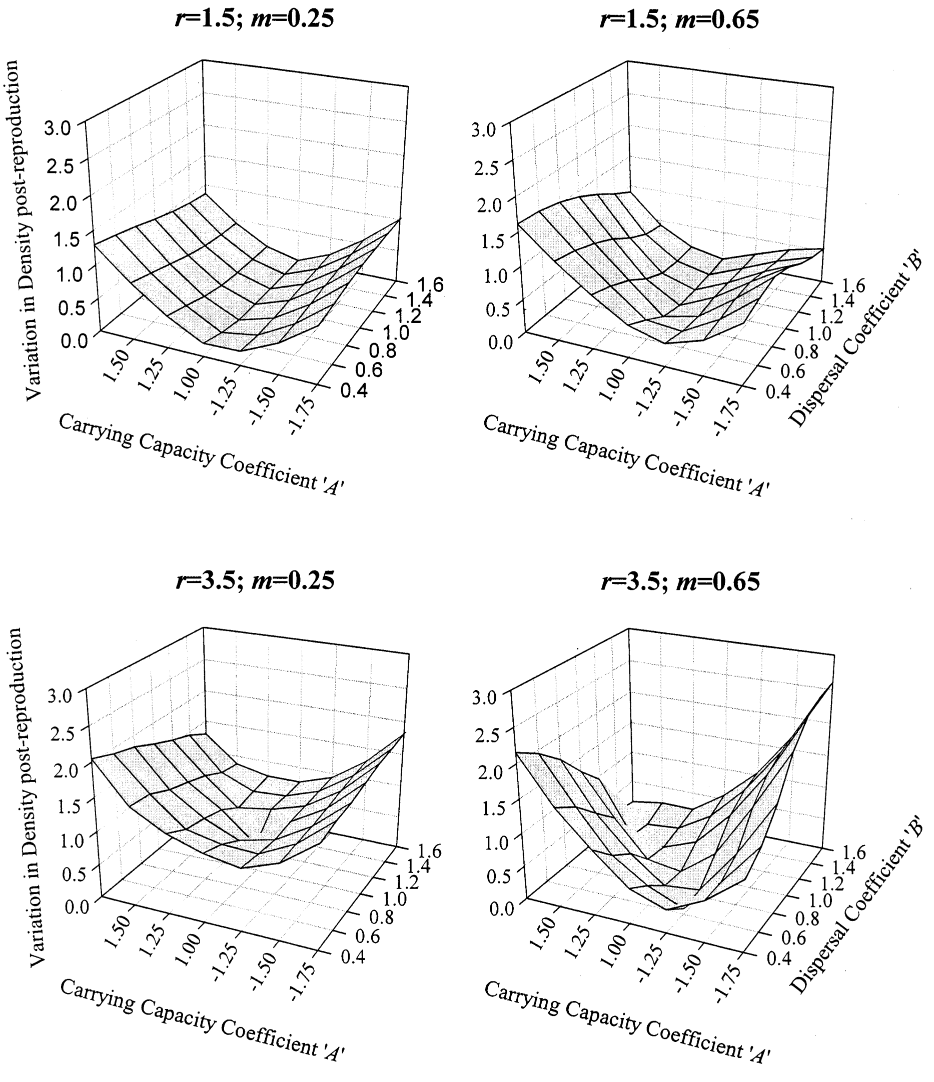
Although the main focus was to examine the combined effects of a within (dispersal) and a between (carrying capacity) generation factor on density–area relationships, it was necessary also to consider the magnitude of the process. For example, the pattern of dispersal to large patches may be quite strong, but if only a few individuals disperse the overall effect may be small. Therefore, both patterns of dispersal and density at carrying capacity were examined, as well as the underlying degree of dispersal and rate of population growth. Thus, the effects of four factors were investigated: patterns of dispersal (B) and density at carrying capacity (A), either increasing, decreasing or constant with patch size, proportion of the population dispersing (m) and population growth rate (r) (Table 1).

Because the objective of this simulation was to examine the relative impact and interactions of within- and between-generation factors, care had to be taken to avoid biasing the model through the choice of factor levels. Therefore levels of both patterns of carrying capacity and dispersal were chosen so that the initial effect of each on the density–area correlation was similar at the corresponding rank i.e. $A = 1.75$ and $B = 1.6$ should initially have similar effects on the density–area relationship. For a sample set of patches the correlation between density and patch area was $r = 0.995$ for $A = 1.75$ and $r = 0.994$ for $B = 1.6$ at $m = 0.65$. To generate a correlation due to movement it was assumed that all patches were initially at equal density and movement was then allowed to create the relationship. For the initial effect due to carrying capacity, the abundance of organisms in all patches was assumed to be at the carrying capacity. Sample density–area correlations were equally similar for other corresponding factor levels, indicating that there should be no initial bias in the magnitude of the effect of each factor on the density–area relationship.

For each simulation, 100 patches were randomly sampled from a uniform distribution of patch sizes ranging from 1 to 1000. Spatial structure of the landscape was inexplicit. I followed the ‘island model’ approach of Kareiva (1990), which assumes that either all patches are equally colonizable or that dispersal ability of the organism is not a limiting factor. Initial densities were drawn randomly from a uniform distribution ranging from 0 to 3.0 organisms per unit patch size. Thus, simulations were stochastic in only the initial densities of organisms and the configuration of patch sizes.

2.2. Response variables and statistical analyses

Four responses were considered. First and most important was the relationship between the density of organisms and patch size, which was evaluated by examining both the slope and the correlation of the relationship between density and patch size. The third response was variance in density across the 100-patch landscape. Variance in density is of importance because the strength of the correlation between density and area is partially dependent upon this variation. If there is little variation in density it is unlikely that there will be a relationship between density and patch size. Finally, the mean density of organisms across the landscape was investigated to determine if different parameter combinations system-


r=1.5; m=0.25

r=1.5; m=0.65

r=3.5; m=0.25

r=3.5; m=0.65

Fig. 6. The mean simulated ($n = 10$) spatial variation in density following reproduction for each dispersal coefficient (B) and carrying capacity coefficient (A) under four combinations of the rate of dispersal (m) and population growth (r).

Table 5
Response surface regression analyses for the mean local population density[a]

After dispersal			
Source	df	Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	733	
Dispersal coefficient (B)	5	1766	
Population growth rate (r)	5	389	
Proportion dispersing (m)	5	1208	
Source		Type I SS	R^2
Linear	4	2160	0.414
Quadratic	4	468	0.090
Interactions	6	734	0.141
Total Regression	14	3363	0.644
Error	23 995	1856	
After reproduction			
Source		Joint SS	
Composite variables			
Carrying capacity coefficient (A)	5	453	
Dispersal coefficient (B)	5	156	
Population growth rate (r)	5	124	
Proportion dispersing (m)	5	978	
Source		Type I SS	
Linear	4	914	0.302
Quadratic	4	194	0.068
Interactions	6	302	0.106
Total Regression	14	1411	0.493
Error	23 995	1451	

[a] On the top is the analysis after dispersal while on the bottom is after reproduction. Composite variables include the sums of squares due to the linear, quadratic and linear interactions versus the null hypothesis that the joint parameter estimate is zero. These joint sums of squares were used to estimate the sensitivity of the dependent variable to each parameter (see Section 2 for details). Below the composite variables are the overall response surface analyses

atically raise or lower density from the expected mean of 2.0 individuals per unit patch size, as is a consequence of other metapopulation models (Holt, 1985). As densities and the relationship between density and area are likely to be more greatly affected by the most recent factor affecting them (Matter, 1997), densities and patterns were evaluated both after dispersal and after reproduction.

For each generation, the mean and variance in density (spatial variation in density) across the 100 patches were calculated as well as the slope and correlation coefficient of the relationship between population density and patch size. Each simulation lasted 50 generations. This length was long enough to evaluate stability (see below) and capture the dynamics of the populations within the landscape. For each simulation, the mean of the densities, the mean of the spatial variation in density and the mean of the slopes and correlation coefficients, were calculated over the 50 generations and used in all analyses. Ten replicates were run under each factor level combination for a total of 24 010 simulations. Some factor combinations were unstable, resulting in extinction across all patches. Generally, global extinction happened quickly, after less than 20 generations.

Response surface methodology (RSM) was used to examine how changes in population growth and dispersal and patterns of movement and density at carrying capacity with respect to patch size affected mean density, spatial variation in density and the slope and correlation coefficient of the relationship between population density and patch area. The correlation coefficient was z-transformed prior to analysis to meet distribution assumptions (Sokal and Rohlf, 1981). RSM allows for inclusion of both linear and quadratic terms and interactions between linear terms while providing traditional regression statistics. The attractiveness of RSM lies in the ability to partition the effects of a single factor in all its forms by testing the null hypothesis that the joint parameter estimate is zero. An examination of the joint sums of squares from this test provides a measure of how sensitive the dependent variable is to each independent variable, making RSM a particularly powerful analysis for complex simulation models. What is of interest in these analyses is not the overall significance of any particular factor, but the relative amount of variation accounted for by each factor. Although an attempt was made to make the design completely orthogonal, it was not possible. Therefore, all factor levels were coded to span the range from -1 to 1 prior to analysis to ensure that factors with greater variation in levels do not exert excessive influence on the response surface design (Khuri and Cornell, 1987; Cornell, 1990).

3. Results

The between-generation pattern of density at carrying capacity had the greatest effect on the relationship between population density and patch size. Following reproduction the carrying capacity pattern accounted for the greatest amount of variation (95%; $0.95 = 0.140/0.152$) in the density–area slope (Table 2) and in the correlation between density and area following both dispersal (67%) and reproduction (86%) (Table 3). Following dispersal, however, the pattern of dispersal had the greatest effect on the density–area slope accounting for 47% of the variation in the slope, while the pattern of density at carrying capacity accounted for 37% (Table 2). The population growth rate and proportion of the population dispersing had relatively small effects on both

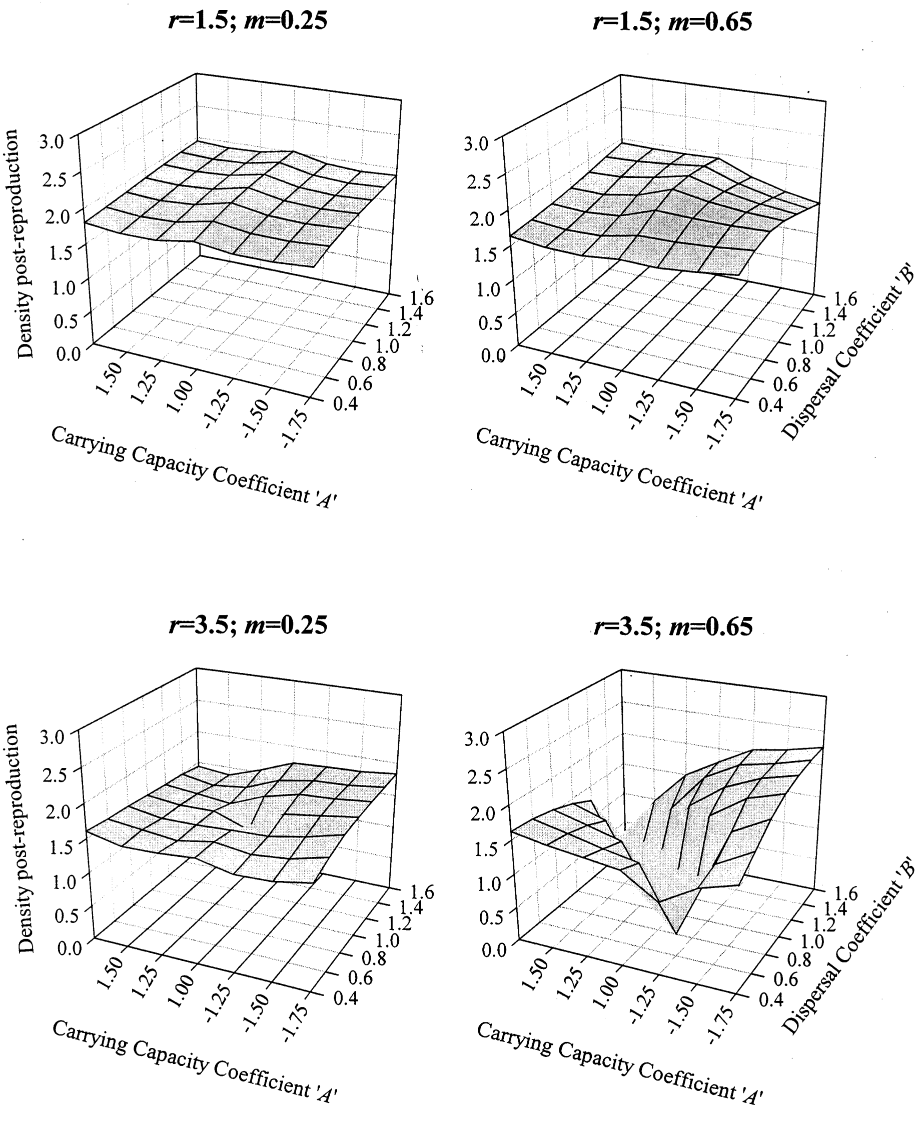


Fig. 7. The mean simulated ($n = 10$) density following reproduction for each dispersal coefficient (B) and carrying capacity coefficient (A) under four combinations of the rate of dispersal (m) and population growth (r).

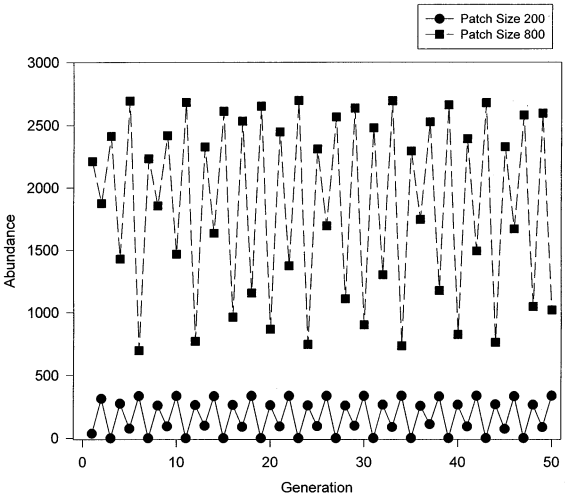


Fig. 8. A sample model run of 50 generations showing the dynamics of a size 200 and 800 patch. Carrying capacity for the size 200 patch was 253.0 and for the size 800 was 2023.9, $r = 3.00$, $m = 0.15$, $A = 1.50$ and $B = 0.60$.

the slope and the correlation of the density–area relationship. After reproduction, as expected from the effect size estimates, the slopes and correlations under all other parameter combinations were positive when the pattern of density at carrying capacity was increasing with patch size and negative when it was decreasing (Figs. 3 and 4). After dispersal the slope was less dependent on the carrying capacity with other factors and interactions playing a greater role (Fig. 5).

Following reproduction, spatial variation in density was most greatly affected by the carrying capacity pattern which accounted for 57% of the variation (Table 4). The proportion of the population dispersing had the next largest effect accounting for 26% of the variation. The dispersal pattern and population growth rate accounted for 13 and 4% of the variation, respectively. Highest variation tended to occur when the density at carrying capacity was toward small or large patches (Fig. 6). When both the dispersal and growth rates were high, spatial variation in density was greatest when the carrying capacity pattern and dispersal pattern were antagonistic, i.e. dispersal was directed toward small patches and the density at carrying capacity was greater for larger patches, or vice versa. Spatial variation in density following dispersal was most greatly affected by the pattern of dispersal, which accounted for 74% of the variation (Table 4). The rate of reproduction accounted for 24% of the spatial variation in density, followed by the carrying capacity pattern and the proportion of the population dispersing, which accounted for 4 and less than 1% of the variation, respectively.

Mean densities across the 100 patch landscape were lower, in some cases substantially, than the expected mean of 2.0 organisms per unit area. Mean densities as high as 2.0 only occurred when both the population growth and proportion dispersing were low and the carrying capacity coefficient was constant with patch size. Following reproduction, the proportion dispersing had the greatest effect on density, accounting for 57% of the variation, followed by the carrying capacity pattern which accounted for 27% (Table 5). The pattern of dispersal and the population growth rate had less influence on the mean density, accounting for 9 and 7% of the variation, respectively. Following reproduction densities tended to be greatest when dispersal was toward larger patches. When both the proportion dispersing and the population growth were high, densities were considerably lower when the patterns of density at carrying capacity and dispersal were complementary (Fig. 7). Following dispersal, the mean density across the landscape was most greatly influenced by dispersal, with the pattern of dispersal accounting for 43% of the variation and the proportion dispersing 30% of the variation in density (Table 5). The carrying capacity pattern and population growth rate accounted for 18 and 9% of the variation in mean density, respectively.

4. Discussion

The results of these simulations illustrate that a between-generation factor can affect density–area relationships and can be of greater importance than within-generation processes for long-term density–area patterns. This result does not diminish the importance of dispersal in creating within-generation density patterns which have been shown by numerous studies (e.g. Kareiva, 1985;

Turchin, 1986, 1987) and is also evident here. What these results do suggest is that between-generation processes are an important consideration and that solely focusing on within-generation mechanisms, such as dispersal, to explain density–area patterns is overly simplistic. A more comprehensive approach incorporating both within- and between-generation processes is needed.

Few empirical studies of density–area relationships have examined the relative contributions of within and between-generation effects, but those that have, have found between-generation processes be a substantial factor. A study of the density–area relationship for the red milkweed beetle, *Tetraopes tetraophthalmus*, found a pattern of increasing density with the size of patches of its host plant (Matter, 1997). This pattern resulted from disproportionately increasing reproductive success with patch size, not via directional movement from small to large patches. In fact, movement tended to be directed from larger to smaller patches. Dooley and Bowers (1996) investigated the effects of habitat fragmentation using patches of differing size for the meadow vole, *Microtus pennsylvanicus*. They found slightly higher mean densities on smaller than on larger patches that were set largely by within-patch recruitment.

These analyses produced several non-intuitive results and demonstrated that species with differing population growth or dispersal rates may show qualitatively different landscape-scale density patterns depending on the patterns of dispersal and carrying capacity with patch size. In situations where the carrying capacity was proportional to patch size ($A = 1$), the effect of dispersal following reproduction was opposite that expected, density–area correlations and slopes were more positive when dispersal was toward smaller patches and were more negative when dispersal was toward large patches. The magnitude of this trend varied with the population growth rate and proportion dispersing. These anomalous situations involve destabilizing interactions between dispersal and the carrying capacity (Vance, 1984). When the population growth rate is low ($r < 2.0$), without dispersal local populations experience damped oscillations about the carrying capacity. With dispersal, the effective population growth is altered to the point where local population dynamics can enter limit cycles or chaotic patterns and the type of dynamics may differ for different size patches (Fig. 8). Because the number of immigrants varies each generation based on total population size across the landscape, local population dynamics are more erratic than for single population dynamics. When dispersal is patterned with patch size in these situations, for example from large to small patches, emigration > immigration for larger patches and dispersal is a stabilizing factor, while emigration < immigration for smaller patches and is a destabilizing factor. This destabilization on smaller patches keeps their average density lower because of periodic population crashes.

This simulation also reveals an important procedural caveat—that it is important when in an organism's life-cycle density is estimated relative to a factor setting the pattern. If dispersal and reproduction occur discreetly in time there is generally a larger effect of the most recent factor, although effects of both within- and between-generation factors can 'carry-over' across generations. This result is in essence what was observed in the *Tetraopes–Asclepias* system, where beetle density strongly increased with the size of milkweed patches early in the season reflecting the pattern of in situ reproduction, but diminished as the season progressed due to movement of beetles out of larger and into smaller patches (Matter, 1997).

The results of this simulation also beg the question of how important or frequent are between generation, density-dependent factors. While the notion of a 'carrying capacity' is difficult to examine, examples of density-dependent mortality and survival abound in the insect literature, arising from top-down (Lessells, 1985; Walde and Murdoch, 1988) and bottom-up processes (McNeill, 1973; Dempster, 1975; Stubbs, 1977; Auerbach et al., 1995). Many of these factors can also vary with the size of host plant patches (Risch et al., 1982; Rothman and Darling, 1990). However, density dependent factors need not be patch size dependent to affect density patterns, as shown in the constant density at carrying capacity simulations ($A = 1$), as noted above, dispersal directed toward smaller patches resulted in positive post-reproduction correlations between density and area in some of these instances.

It is interesting to note that in two previous studies that examined both density–area relationships and the potential for density-dependence in that life stage, neither found evidence for any density-dependent mortality (Root and Kareiva, 1984; Capman et al., 1990). Both of these studies were examinations of Lepidoptera whose utilization of patches was more akin to the foraging scale, as both the sooty wing skipper, *Pholisora catullus* and the cabbage butterfly, *Pieris rapae*, are vagile species that leave patches of their host plant to forage for nectar on non-host plants and may oviposit in several patches (Root and Kareiva, 1984; Capman et al., 1990). The results of this simulation may be open to criticism because the between-generation factor was density-dependent, while dispersal was not. Because the carrying capacity alters both the number of individuals in the system and their distribution it may exert more influence than dispersal. I would argue that this is undoubtedly true and that density-dependent, patch size-dependent dispersal combined with a density-dependent, between-generation factor represents another potential scenario that merits investigation. Additionally, patch size dependent emigration rather than immigration may lead to differing results.

5. Conclusion

Several factors have been suggested to influence density–area patterns, such as dispersal, residence time, predation, scale of patch selection and a disproportionately varying resource base with patch size. My results suggest that of the two mechanisms investigated here, between-generation factors outweigh within-generation factors for long-term, density–area relationships. Within-generation mechanisms, such as the resource concentration hypothesis, may explain within-generation patterns, but are not sufficient to explain between-generation density–area patterns. More comprehensive approaches to understanding density–area relationships, incorporating both within- and between-generation processes are needed.

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References

Andrén, H., 1992. Corvid density and nest predation in relation to forest fragments. Ecology 73, 794–804.

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals with different proportions of suitable habitat: a review. Oikos 71, 355–366.

Auerbach, M.J., Connor, E.F., Mopper, S., 1995. Minor miners and major miners: population dynamics of leaf-mining insects. In: Cappuccino, N., Price, P.W. Jr. (Eds.), Population Dynamics. Academic Press, San Diego, pp. 83–105.

Bach, C.E., 1988. Effects of host plant patch size on herbivore density: patterns. Ecology 69, 1090–1102.

Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79, 517–533.

Bowers, M.A., Matter, S.F., 1997. Landscape ecology of mammals: relationships between density and patch size. J. Mammal. 78, 999–1013.

Capman, W.C., Batzli, G.O., Simms, L.E., 1990. Responses of the common sooty wing skipper to patches of host plants. Ecology 71, 1430–1440.

Connor, E.F., Courtney, A.C., Yoder, J., 1999. Individuals-area relationships: the relationship between animal population density and area. Ecology (in press).

Cornell, J.A., 1990. How to Apply Response Surface Methodology. American Society for Quality Control, Milwaukee, WI.

Cromartie, W.J. Jr., 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. J. Appl. Ecol. 12, 517–533.

Dempster, J.P., 1975. Animal Population Ecology. Academic Press, London.

Denno, R.F., Raupp, M.J., Tallamy, D.W., 1981. Organization of sap-feeding insects: equilibrium versus non-equilibrium coexistence. In: Denno, R.F., Dingle, H. (Eds.), Insect Life History Patterns: Habitat and Geographic Variation. Springer, New York, pp. 151–181.

Dooley, J.L., Bowers, M.A., 1996. Patch attributes and microhabitat as influences on the demography of two old-field rodents. Oikos 75, 453–462.

Fahrig, L., Merriam, G., 1985. Habitat patch connectivity and population survival. Ecology 66, 1762–1768.

Förare, J., Solbrek, C., 1997. Population structure of a monophagous moth in a patchy landscape. Ecol. Entomol. 22, 256–263.

Foster, J., Gaines, M.S., 1991. The effects of a succesional habitat on a small mammal community. Ecology 72, 1358–1373.

Funderburke, J.E., Soffes, A.R., Barnett, R.D., Herzog, D.C., Hinson, K., 1990. Plot shape and size in relation to soybean resistance to velvetbean caterpillar (Lepidoptera: Nocturidae). J. Econ. Entomol. 83, 2107–2110.

Gotelli, N.J., 1995. A Primer of Ecology. Sinauer Associates, Sunderland, MA, p. 206.

Hanski, I., 1991. Single-species metapopulation dynamics: concepts, models and observations. Biol. J. Linnean Soc. 42, 17–38.

Hanski, I., Thomas, C.D., 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biol. Conserv. 68, 167–180.

Hastings, A., Harrison, S., 1994. Metapopulation dynamics and genetics. Annu. Rev. Ecol. System. 25, 167–188.

Holt, R.D., 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theor. Popul. Biol. 28, 181–208.

Kareiva, P.M., 1981. Non-migratory movement and the distribution of herbivorous insects: experiments with plant spacing and the application of diffusion models to mark-recapture data. Ph.D. thesis. Cornell University, Ithaca, NY.

Kareiva, P.M., 1985. Finding and loosing host plants by *Phyllotreta*: patch size and surrounding habitat. Ecology 66, 1809–1816.

Kareiva, P.M., 1990. Population dynamics in spatially complex environments: theory and data. Philos. Trans. R. Soc. London. B 330, 175–190.

Khuri, A.I., Cornell, J.A., 1987. Response Surfaces Designs and Analyses. Marcel Dekker, New York.

Kindvall, O., Ahlen, I., 1982. Geometrical factors and metapopulation dynamics of the bush cricket, *Metrioptera bicolor*. Conserv. Biol. 6, 520–529.

Lessells, C.M., 1985. Parasitoid foraging: Should parasitism be density dependent? J. Anim. Ecol. 54, 27–41.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ, p. 203.

MacGarvin, M., 1982. Species-area relationships of insects on host-plants: herbivores of rosebay whillowherb. J. Anim. Ecol. 51, 207–223.

McNeill, S., 1973. The dynamics of a population of *Leptoterna dolabrata* (Heteroptera: Miridae) in relation to its food resources. J. Anim. Ecol. 42, 495–507.

Maguire, L.A., 1983. Influence of collard patch size on population densities of Lepidoperan pests (Lepidoptera: Pieridae, Plutellidae). Environ. Entomol. 12, 1415–1419.

Matter, S.F., 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. Oecologia 105, 447–453.

Matter, S.F., 1997. Population density and area: the role of within and between patch processes. Oecologia 110, 533–538.

Matter, S.F., Zawacki, J.F., Bowers, M.A., 1996. Habitat fragmentation and the perceived and actual risk of predation. Va. J. Sci. 47, 19–27.

May, R.M., 1974. Biological populations with non-overlapping generations: stable points, stable cycles and chaos. Science 186, 645–647.

Raupp, M.J., Denno, R.F., 1979. The influence of patch size on a guild of sap-feeding insects that inhabit the salt marsh grass *Spartina patens*. Environ. Entomol. 8, 412–417.

Risch, S.J., 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology 62, 1325–1340.

Risch, S.J., Wrubel, R., Andow, D., 1982. Foraging by a predaceous beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae), in a polyculture effects of plant density and diversity. Environ. Entomol. 11, 949–950.

Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. Ecol. Monogr. 43, 95–124.

Root, R.B., Kareiva, P.M., 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. Ecology 65, 147–165.

Rothman, L.D., Darling, D.C., 1990. Parasitoids of the goldenrod gall moth: effects of scale on spatial density dependence. Oecologia 83, 1–6.

Simberloff, D., 1988. The contribution of population and community biology to conservation science. Annu. Rev. Ecol. System. 19, 473–511.

Sokal, R.R., Rohlf, F.J., 1981. Biometry. W.H. Freeman, New York.

Stubbs, M., 1977. Density dependence in the life-cycles of animals and its importance in K- and r- strategies. J. Anim. Ecol. 46, 677–688.

Turchin, P.B., 1986. Modeling the effect of host plant patch size on Mexican bean beetle emigration. Ecology 67, 124–132.

Turchin, P.B., 1987. The role of aggregation in the response of Mexican bean beetles to host-plant density. Oecologia 71, 577–582.

Vance, R.R., 1984. The effect of dispersal on population stability in one-species, discrete-space population models. Am. Naturalist 123, 230–254.

Walde, S.J., Murdoch, W.W., 1988. Spatial density dependence in parasitoids. Annu. Rev. Entomol. 33, 441–466.