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SECOND AUTUMN WORKSHOP ON MATHEMATICAL ECOLOGY

(2 - 20 November 1992)

"Persistence in Patchy Irregular Landscapes"

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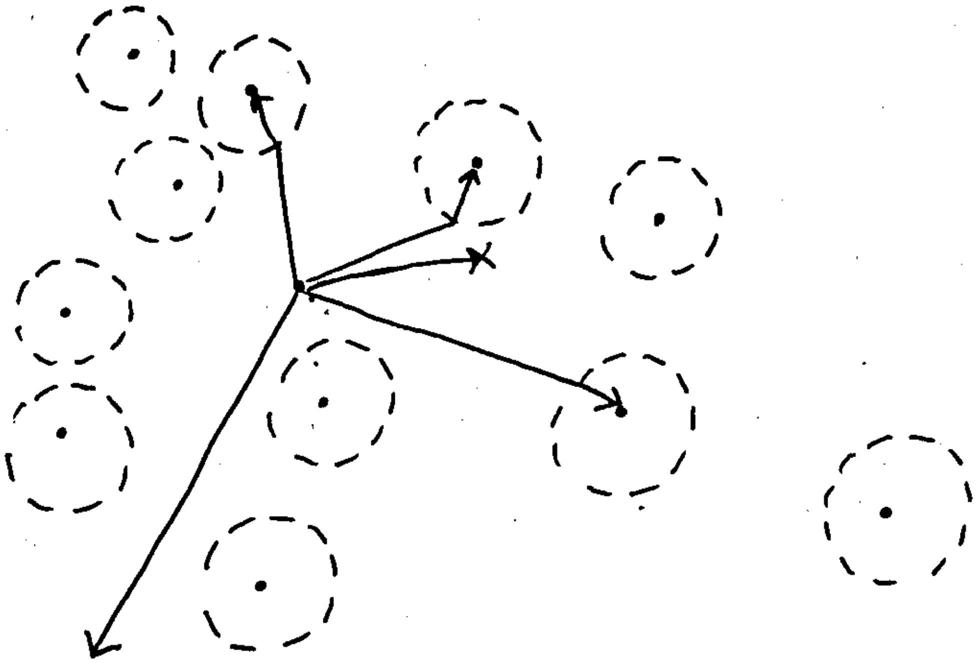
These are preliminary lecture notes, intended only for distribution to participants.

PERSISTENCE IN PATCHY IRREGULAR LANDSCAPES

Frederick R. Adler and Beate Nürnberger (submitted to TPB)

Movement Rules



Cost of Dispersal

$$a_{ij} = \left(\frac{1}{2}\right)^{D_{ij}/b}$$

D_{ij} - distance between patch i and patch j

b - movement range

a_{ij} - probability of successful arrival

def.: λ_{ij} - fraction of individuals leaving patch j which arrive successfully in patch i

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population size after dispersal:

$$N_{i,t+h} = (1-d)\,N_{i,t} + d \sum_{j=1}^{k} \lambda_{ij} N_{j,t}$$

population size after growth:

$$N_{i,t+1} = \frac{R\,N_{i,t+h}}{1 + (R-1)\,N_{i,t+h}/K}$$

R = finite rate of growth K = carrying capacity per patch

~~Population Growth~~

Parameter Values

dispersal range, b	low, medium, high
dispersal rate, α	0.03, 0.25, 0.5
R	1.5, 1.8
detection radius	const.
carrying capacity, K	200
extinction probability per patch per gen., x	0.05

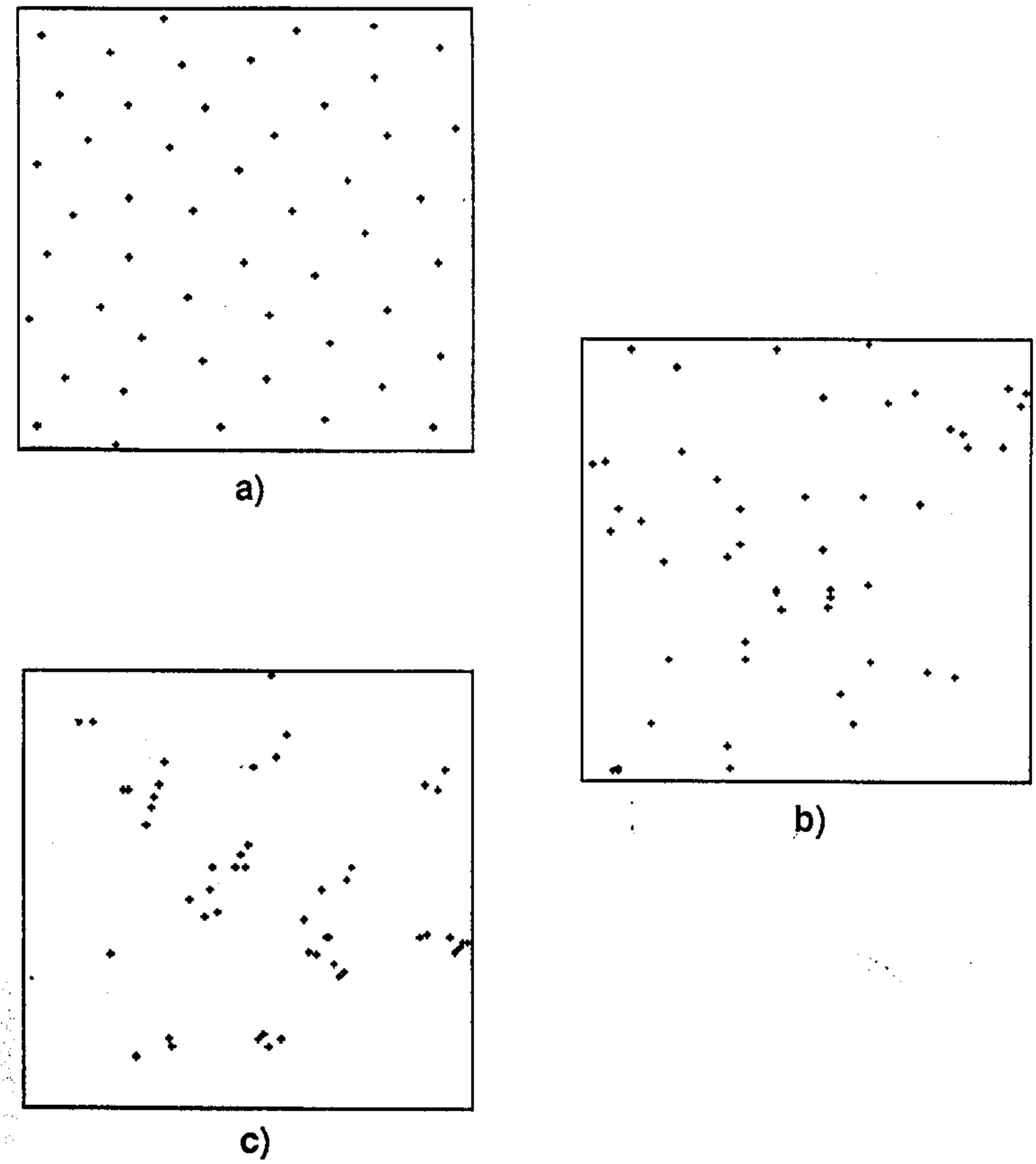


FIGURE 6.1 Three landscapes used in the simulation: a) regular, b) random, and c) clumped.

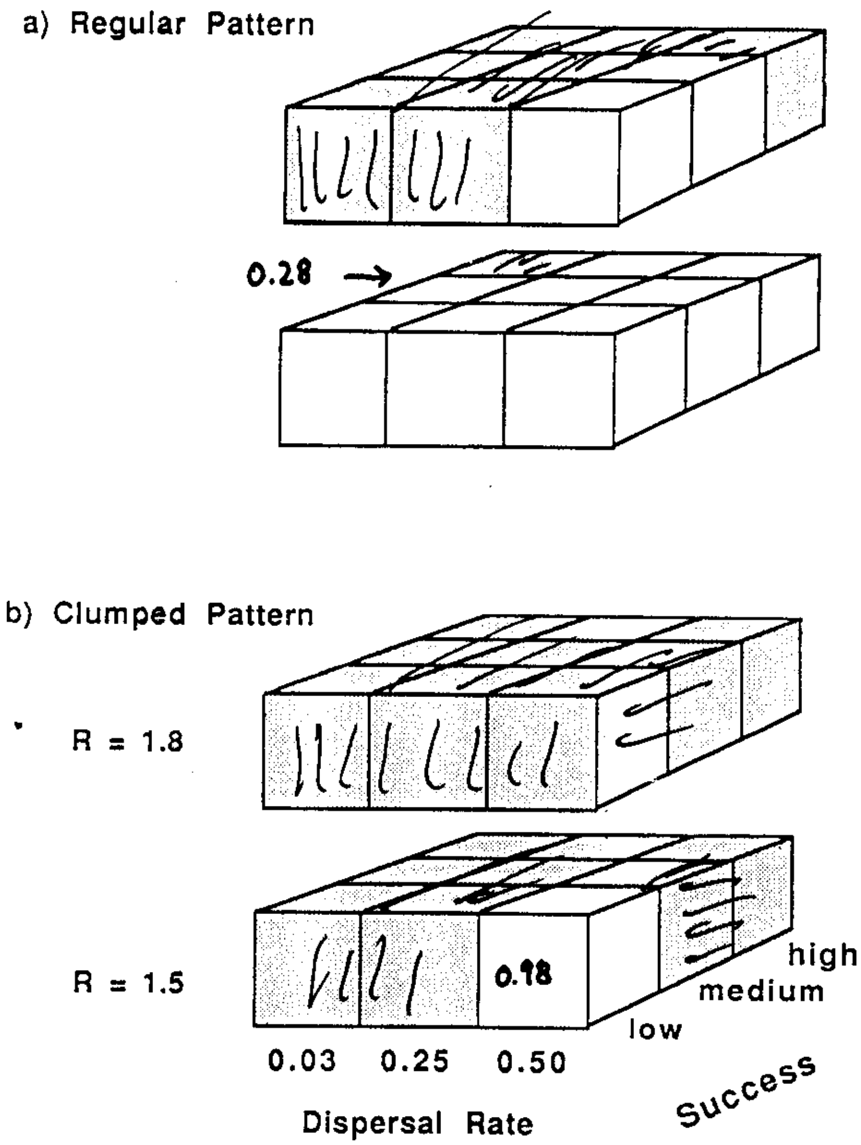


FIGURE 6.5 Species persistence as a function of the three life history variables for a regular and a clumped landscape (cf. Fig. 6.1a and c). Dark boxes indicate persistence over all 50 replicate runs. White boxes stand for parameter combinations that invariably lead to species extinction. The fraction of replicates in which the species persisted is given in those boxes in which the outcome was variable.

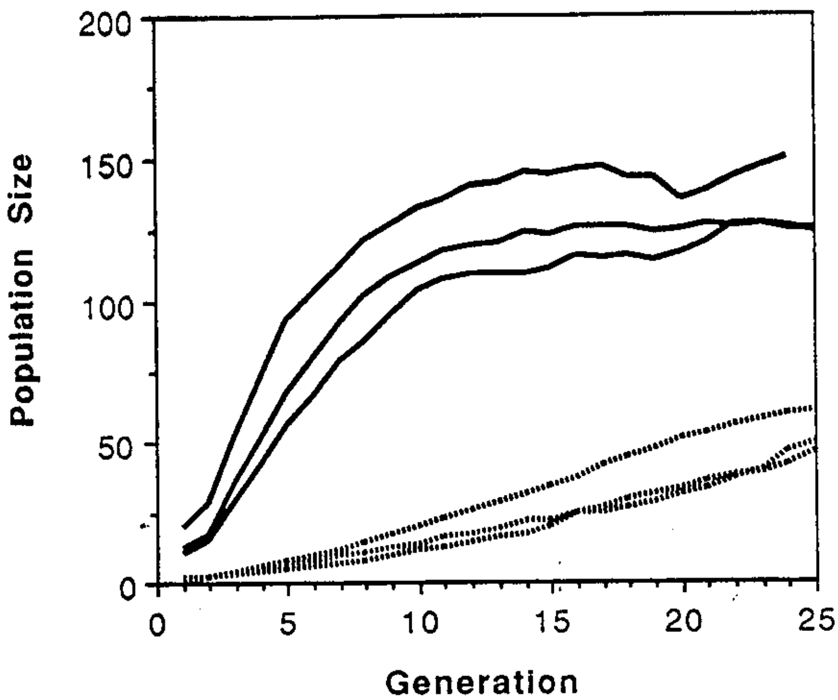
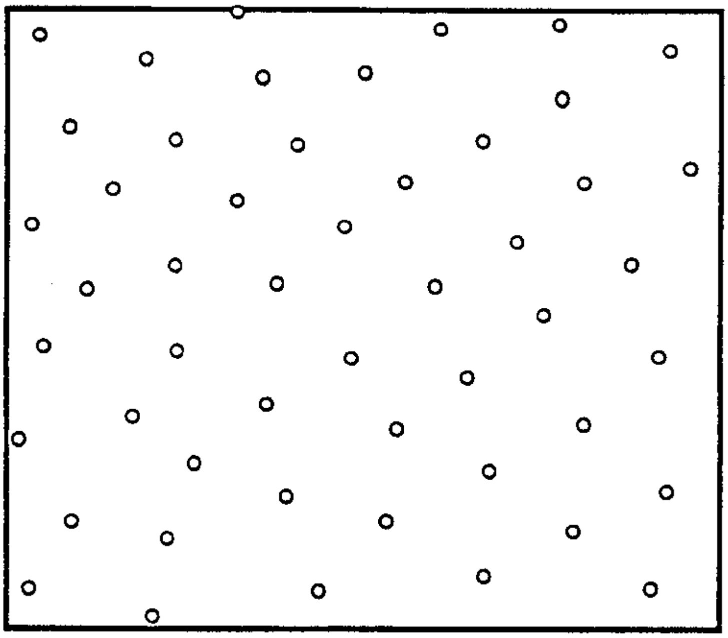


FIGURE 6.7 Mean growth trajectories of populations as a function of their location in the landscape. Each curve shows the average population size as a function of time since colonization in a particular patch taken from the clumped landscape (Fig. 6.1c). Solid curves: patches in clusters; broken curves: isolated patches. The data were compiled over three replicate runs from generation 500 to 1000 (R = 1.5, d = 0.25, b = 6). Note that the sample sizes decline with time because more and more populations are hit by catastrophes (minimum sample size = 5).

a)



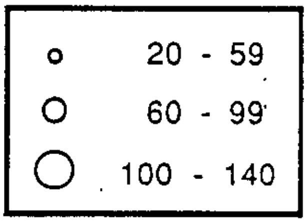
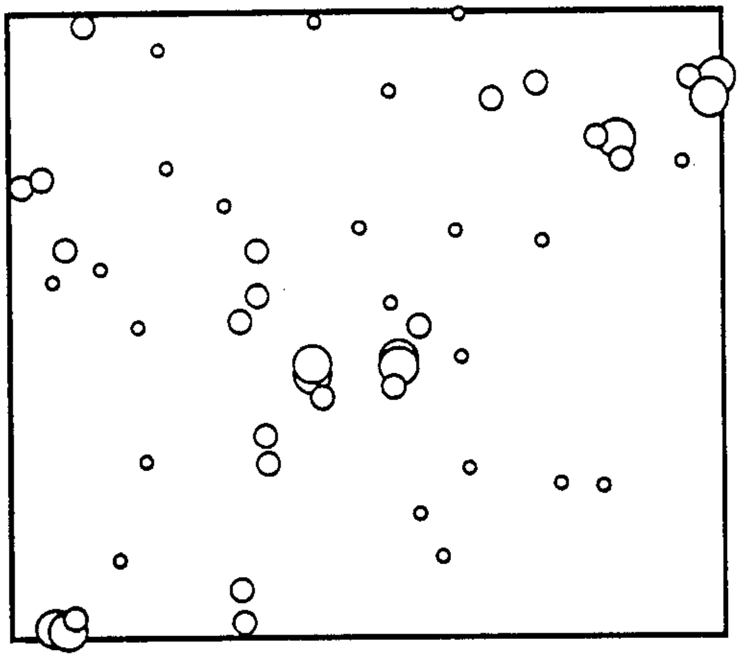


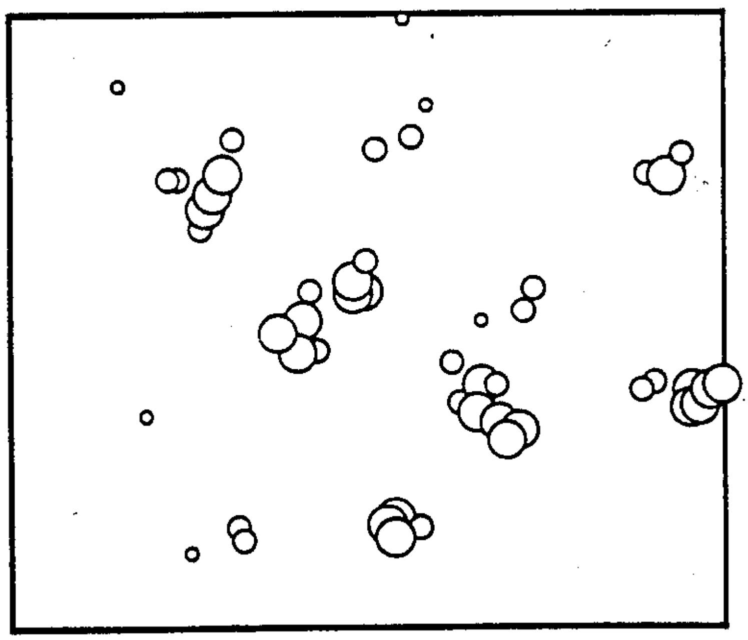
FIGURE 6.8 Spatial distribution of mean population sizes in different landscapes: a) random, b) regular, and c) clumped (cf. Fig. 6.1). Data were compiled from generation 500 to 1000 ($R = 1.5$, $d = 0.25$, $\beta = 6$). The population size categories are defined in the box above.

FIGURE 6.8 (Continued)

b)



c)



1. Full matrix approximation

q - mean ~~immigration rate~~ no. of immigrants

$\pi(q)$ - probability that a patch, when empty, is colonized by a disperser

Poisson distributed arrivals

$$\pi = 1 - e^{-q}$$

probability of at least one arrival

Probability of patch extinction : x

$$\rho_0 = \frac{x}{x + \pi}$$ fraction of time that a patch will, on average, be empty

ρ_t - probability that a patch has been colonized for exactly t generations

$$\rho_{t+1} = (1-x)\rho_t \quad \text{for } t \geq 1$$

$$1 - \rho_0 = \frac{\pi}{x + \pi}$$

$$= \sum_{t=1}^{\infty} \rho_t$$

$$= \sum_{t=1}^{\infty} (1-x)^{t-1} \rho_1$$

$$= \frac{\rho_1}{x}$$

$$\rho_t = (1-x)^{t-1} \frac{x\pi}{x + \pi}$$

n_t – expected population size t generations after successful colonization, no intervening extinctions

$$n_{t+1} \approx g((1-d)n_t + q)$$

$\nu(q)$ – expected population size of a given patch

$$\nu(q) = \sum_{t=1}^{\infty} p_t(q)\, n_t(q)$$

Consider patch i with immigration rate q_i:

$N_i = \nu(q_i)$ mean population size of patch i, $i = 1, \dots, k$

$$q_i = d \sum_{j=1}^{k} \lambda_{ij} N_j$$

$$= d \sum_{j=1}^{k} \lambda_{ij}\, \nu(q_j)$$

$$\vec{q} = d \Lambda \vec{N}$$

$$(\vec{\nu}(\vec{q}))_i = \nu(q_i)$$

$$\vec{N} = \vec{\nu}(\vec{q})$$

$$\vec{q} = d \Lambda \vec{\nu}(\vec{q})$$

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The Threshold

$$J = d\Lambda\nu'(0)$$

$$\nu'(q) = \sum_{t=1}^{\infty} \left(\rho_t'(q)\, n_t(q) + \rho_t(q)\, n'(q)\right)$$

Since $\rho_0 = 1$ when $q = 0$:

$$\nu'(0) = \sum_{t=1}^{\infty} \rho_t'(0)\, n_t(0)$$

$$\rho'(0) = (1-x)^{t-1}$$

$$\nu'(0) = \sum_{t=1}^{\infty} (1-x)^{t-1}\, n_t(0)$$

def: μ - leading eigenvalue of Λ

. Condition for persistence:

$$d\nu'(0)\mu > 1$$

An Approximation for the leading eigenvalue

def: immigration potential for patch i - s_i

$$s_i = \sum_{j=1}^{k} \lambda_{ij}$$

E - average of the immigration potentials

V - variance " " " " " "

$$\hat{\mu} = E + \frac{V}{E}$$

2. The averaged approximation

$$\nu(q_i) \approx \nu(q^*) + (q_i - q^*)\,\nu'(q^*)$$

$$\vec{\nu}(\vec{q}) \approx \nu(q^*)\vec{u} + (\vec{q} - q^*\vec{u})\,\nu'(q^*)$$

Substituting $\vec{q} = \alpha \Lambda \vec{\nu}(\vec{q})$:

$$\vec{q} \approx \alpha \Lambda \left(\nu(q^*) + (\vec{q} - q^*\vec{u})\,\nu'(q^*) \right)$$

$$= \alpha \nu(q^*)\,\vec{s} + \alpha \nu'(q^*)\left(\Lambda\vec{q} - q^*\vec{s}\right)$$

$$q^* = \alpha \hat{\mu}\, \nu(q^*)$$

applies to a landscape where each $s_i = \hat{\mu}$
with threshold $\alpha \hat{\mu}\, \nu'(0) > 1$

$$\hat{q}_i = \alpha \nu(q^*)\, s_i$$

$$\hat{N}_i = \nu(\hat{q}_i)$$

3. The "homogeneous connection" approximation

$$N^* = \nu(q^*)$$

Figure 3.1 The expected population size of a patch with constant immigration of q individuals per generation and finite rate of growth $R = 1.5$ for three values of the dispersal rate.

Figure 4.1 The three approximations as predictors of simulated regional average population size. Seven different patterns and eighteen parameter combinations were used. The diagonal lines indicate equality of simulation and prediction.

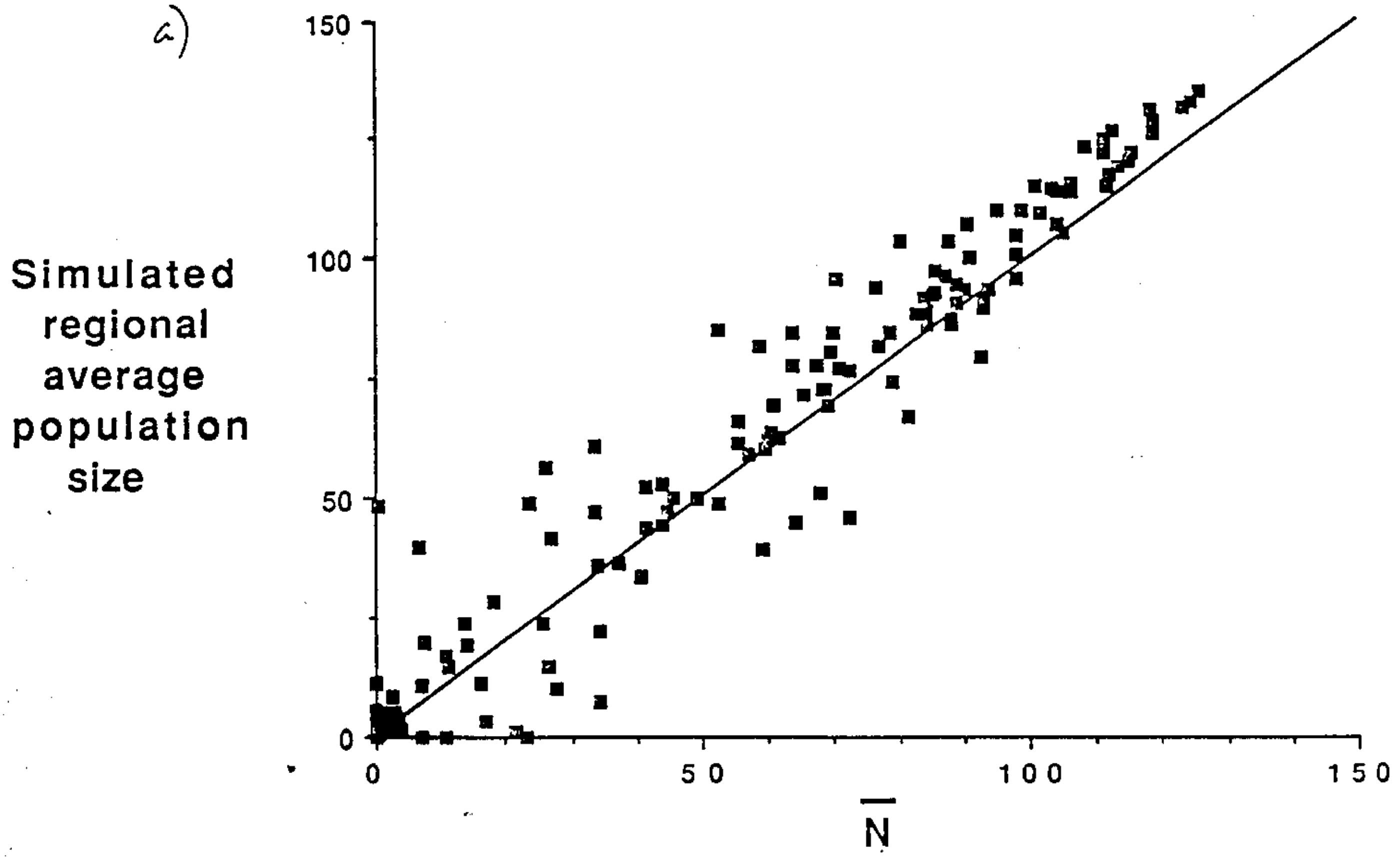
Figure 4.2 The survival coefficient $d\mu\nu'(0)$ (equation 3.13) as a predictor of simulated regional average population size. The lower figure blows up the upper figure near the threshold at 1.

Figure 4.3 The full matrix approximate average patch population sizes (N_i) as predictors of simulated average patch size for three different replicates of the simulation. Note the large variability among simulation results. each symbol stands for a simulation.

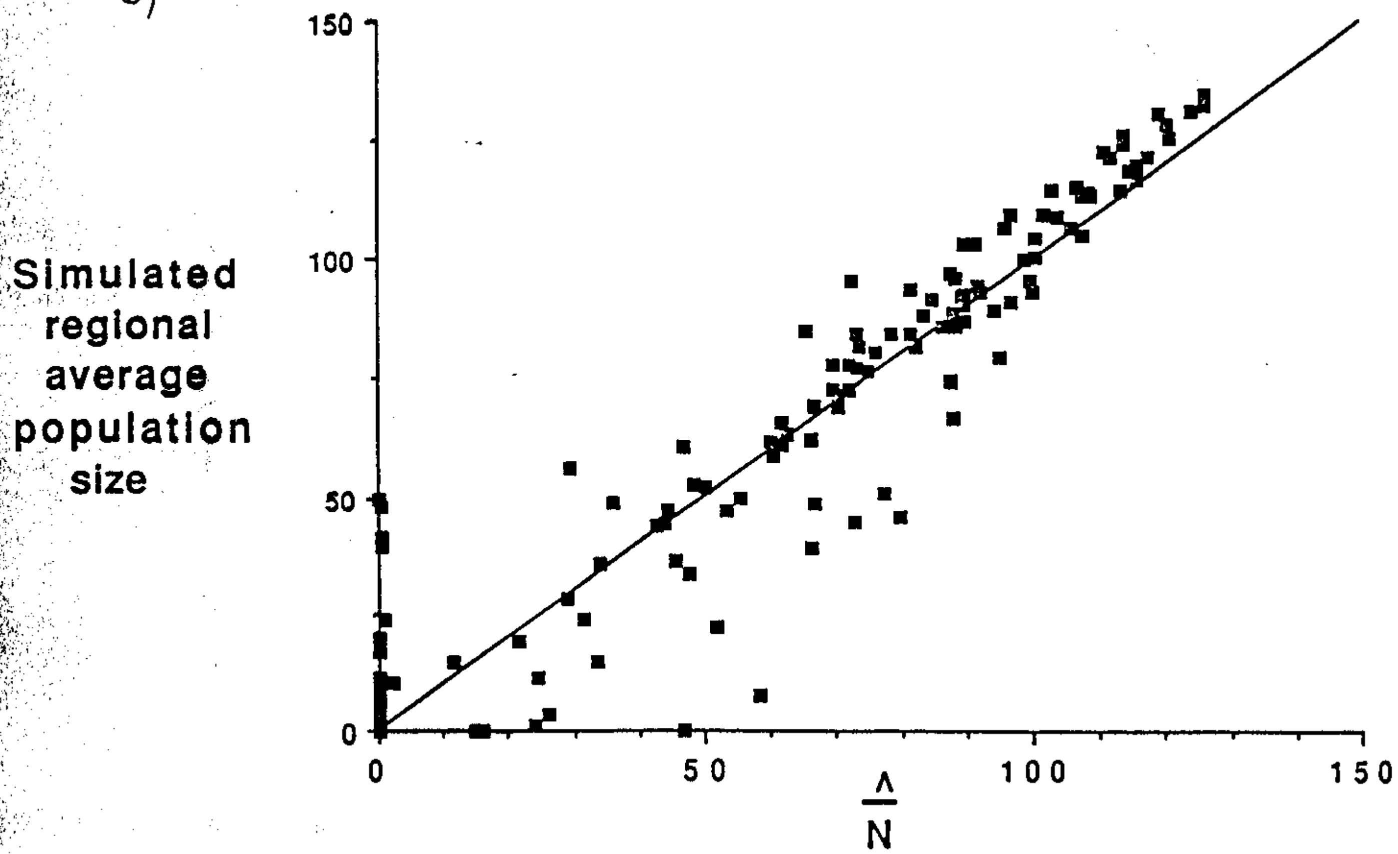
Figure 4.4 The average number of immigrants arriving in a patch per generation for two replicates of the simulation (crosses and open circles) and the average immigration rate q_i (black squares) predicted by the full matrix approximation plotted against the immigration potentials (s_i). In each case, the full matrix approximation lies along the line predicted by the averaged approximation (equation 3.21). With the more heterogeneous landscapes (note the different ranges of the immigration potentials), the simulations also follow this pattern.

Figure 4.5 The fraction of successful dispersers (dotted line) and the coefficient of variation (c.v.) of the average population sizes (dot-dashed line) predicted by the averaged approximation plotted against dispersal rate for a regular and a clumped pattern. The lower solid line is the average immigration potential E, and the upper solid line is the averaged approximate eigenvalue $\hat{\mu}$.

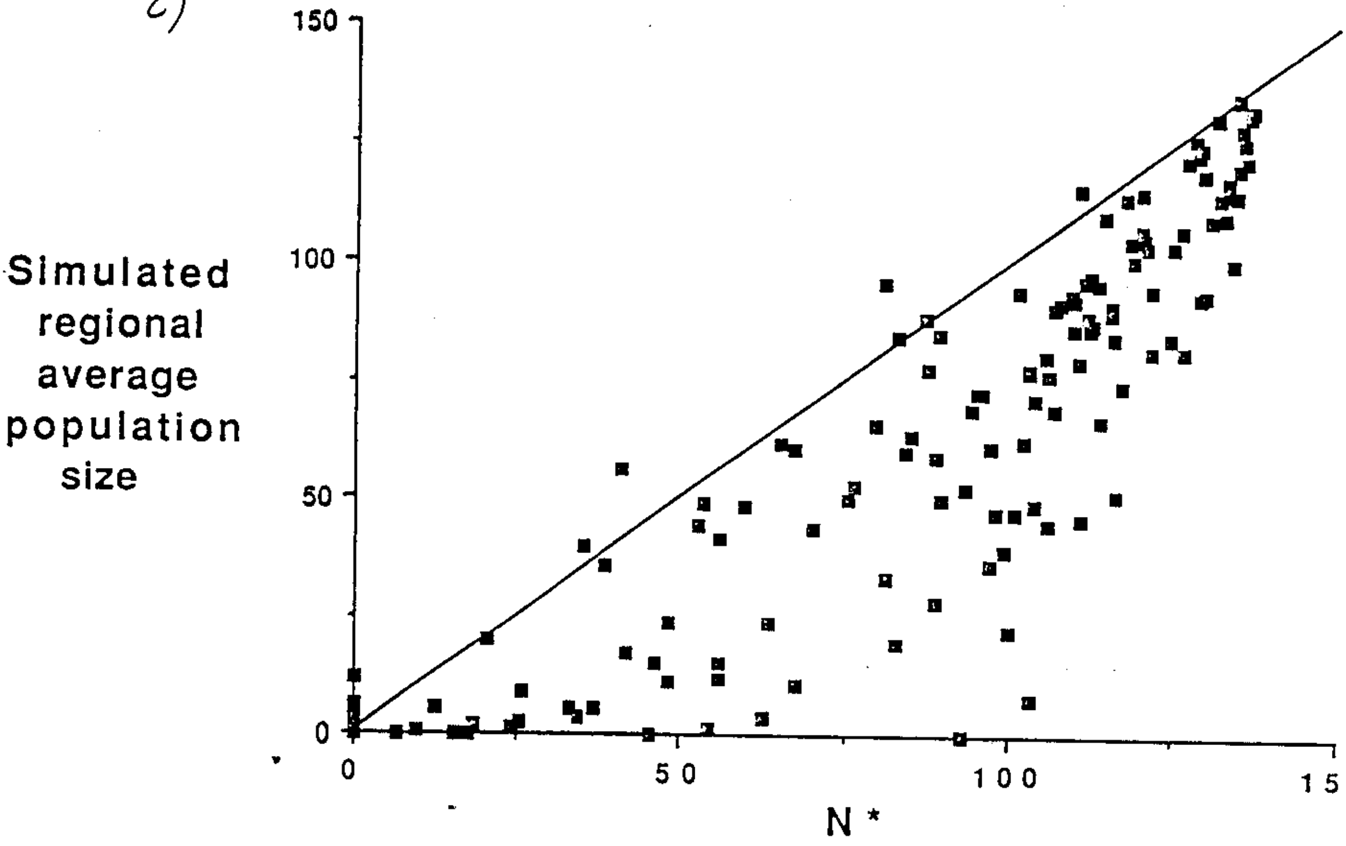
a)


Simulated regional average population size
150
100
50
0
0
50
100
150
$\overline{N}$

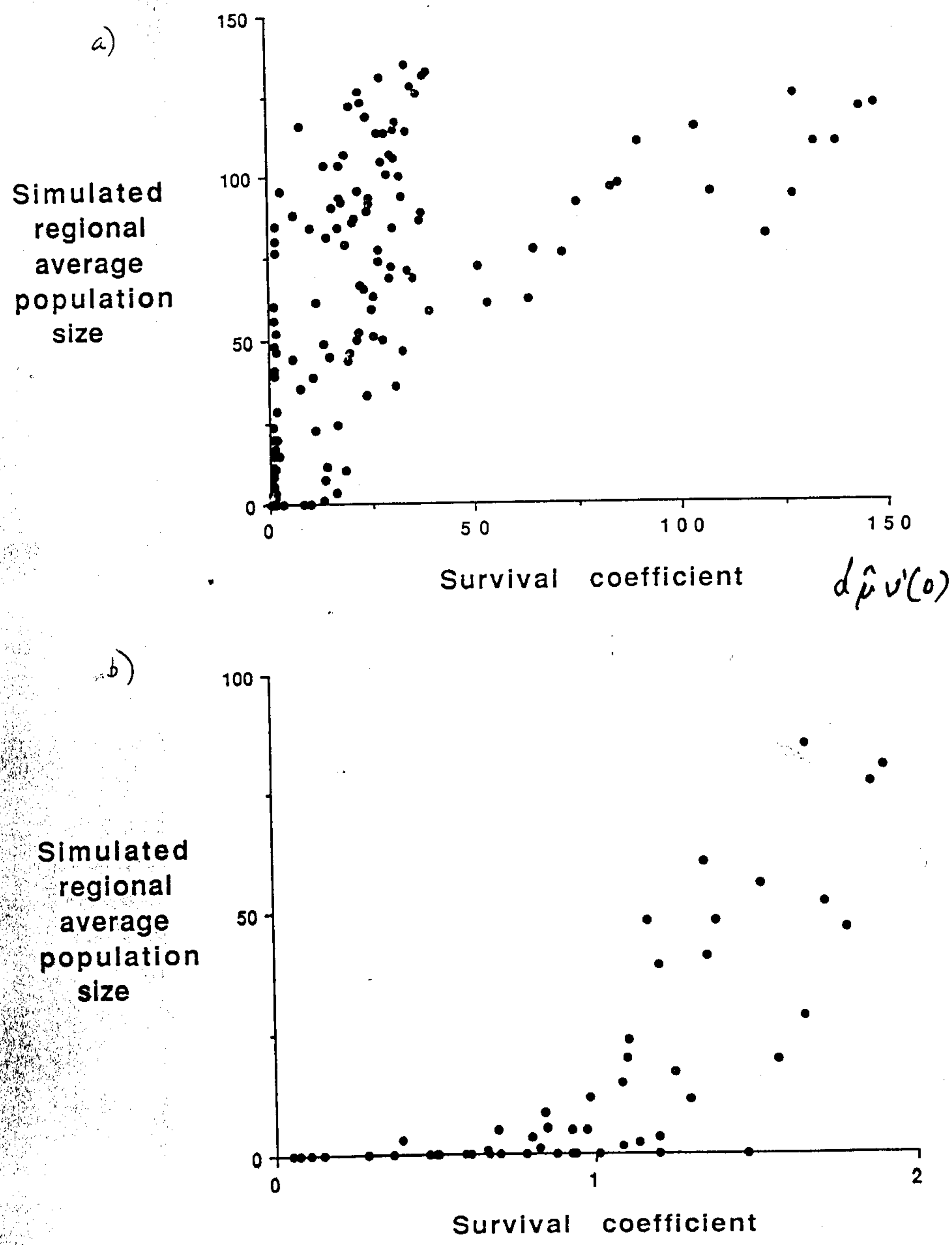
b)


Simulated regional average population size
150
100
50
0
0
50
100
150
$\hat{N}$

c)



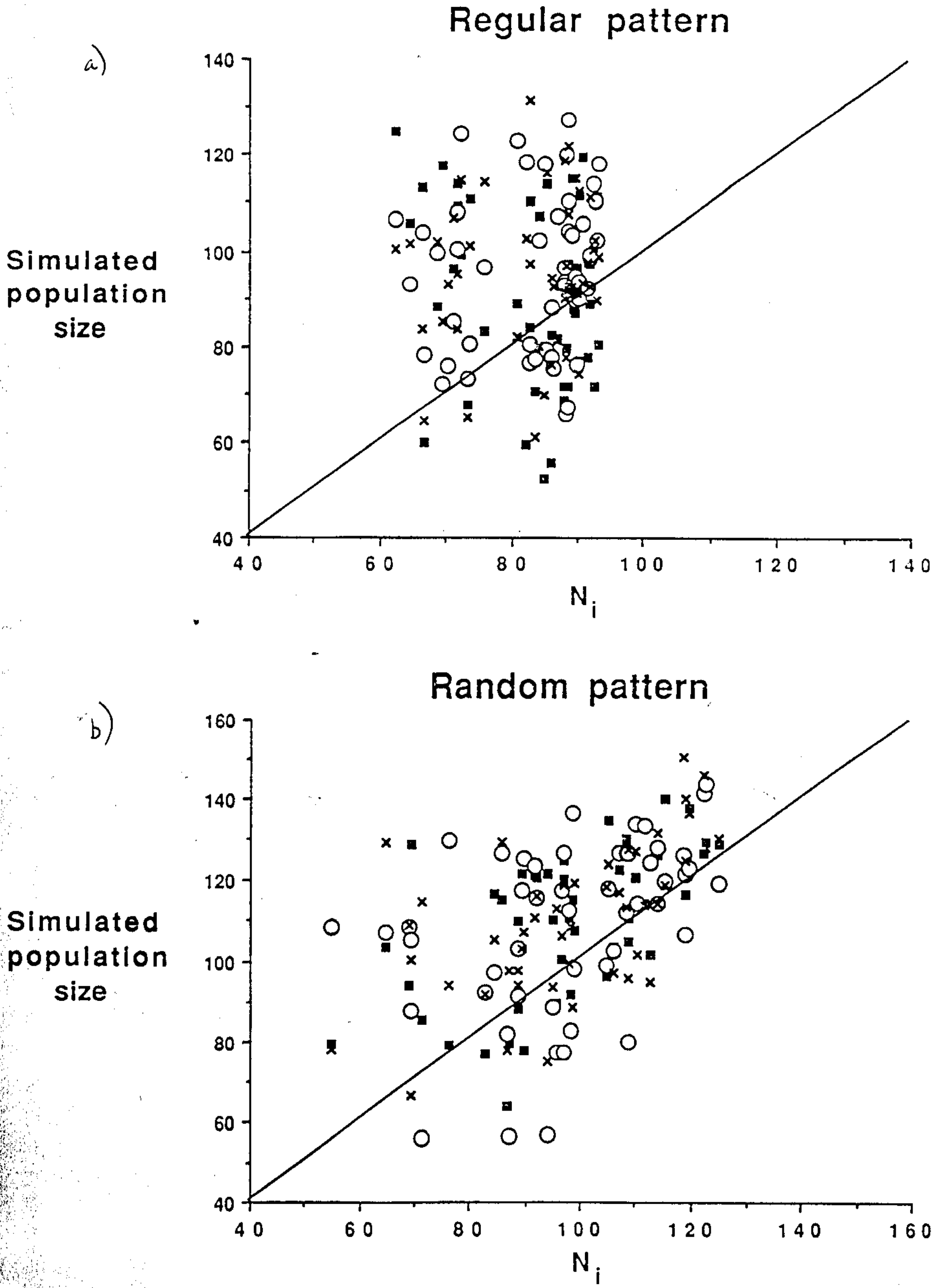
Simulated regional average population size
150
100
50
0
0
50
100
150
N*



a)
150
100
50
0
Simulated regional average population size
0
50
100
150
Survival coefficient
$d\hat{\mu}v'(0)$
b)
100
50
0
Simulated regional average population size
0
1
2
Survival coefficient

Figure 4.2

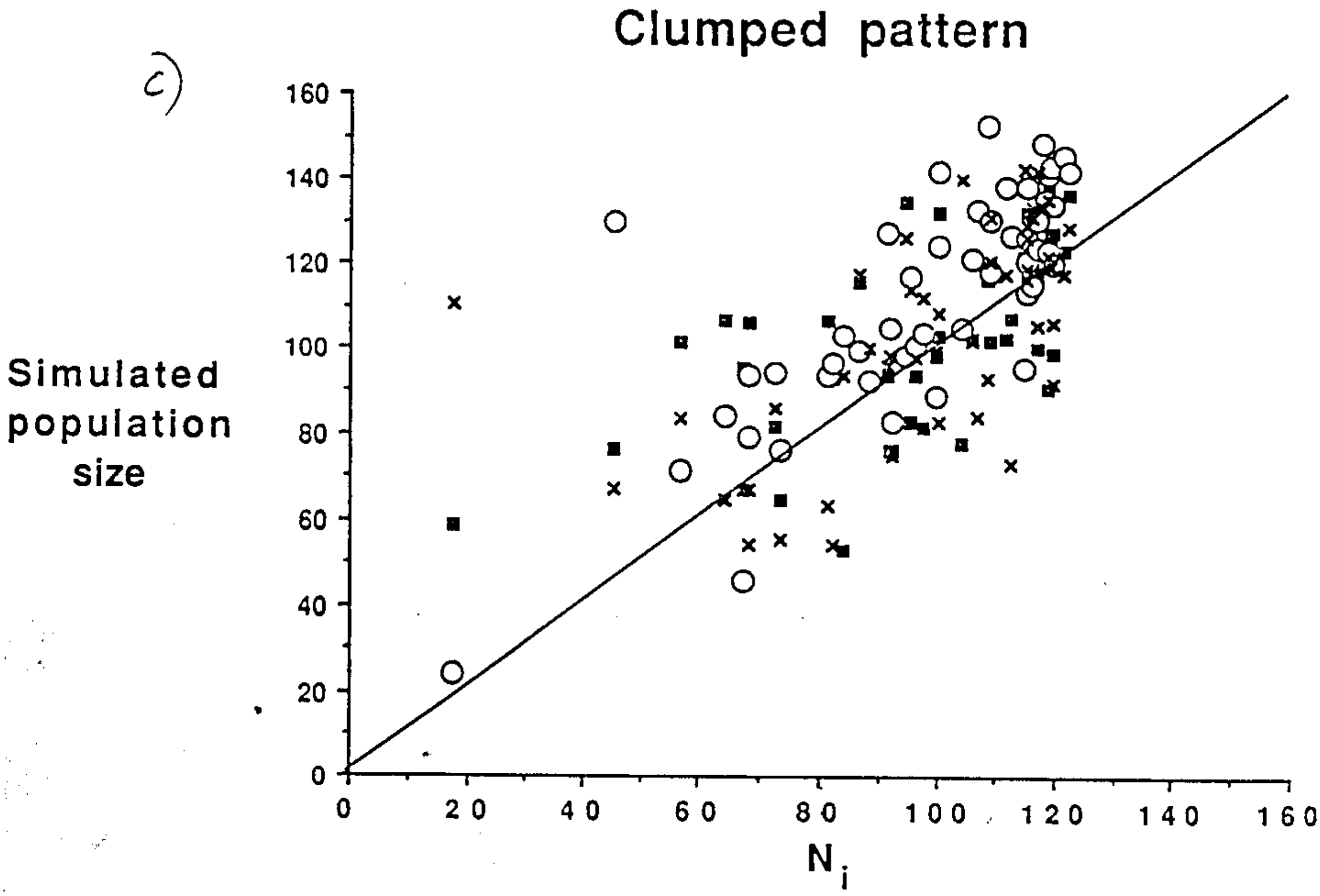
16



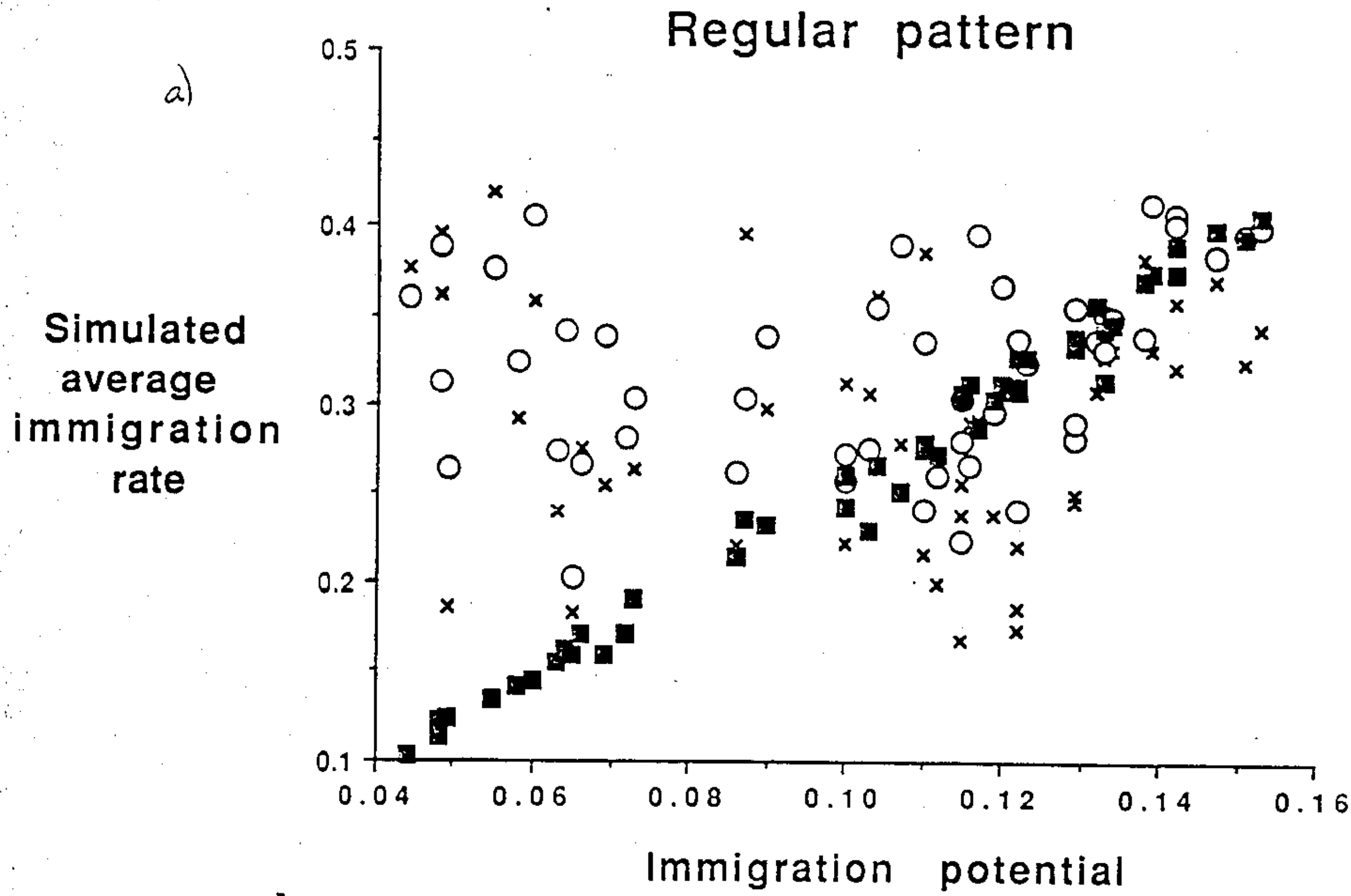
a)
Regular pattern
Simulated population size
140
120
100
80
60
40
40
60
80
100
120
140
N_i
b)
Random pattern
Simulated population size
160
140
120
100
80
60
40
40
60
80
100
120
140
160
N_i

Figure 4.3

c)



Clumped pattern
Simulated population size
160
140
120
100
80
60
40
20
0
0
20
40
60
80
100
120
140
160
N_i


a)
Regular pattern
Simulated average immigration rate
0.1
0.2
0.3
0.4
0.5
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Immigration potential

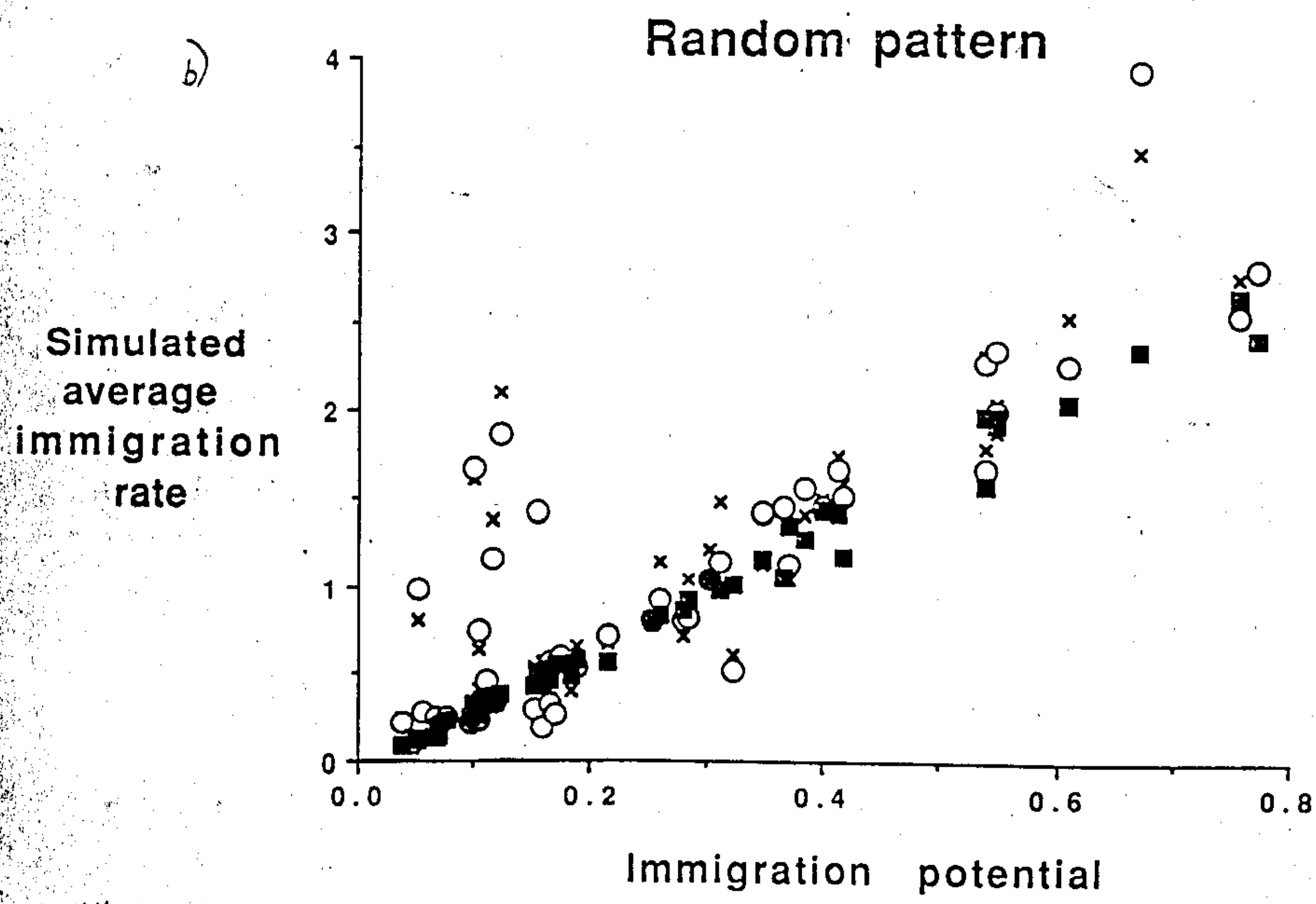
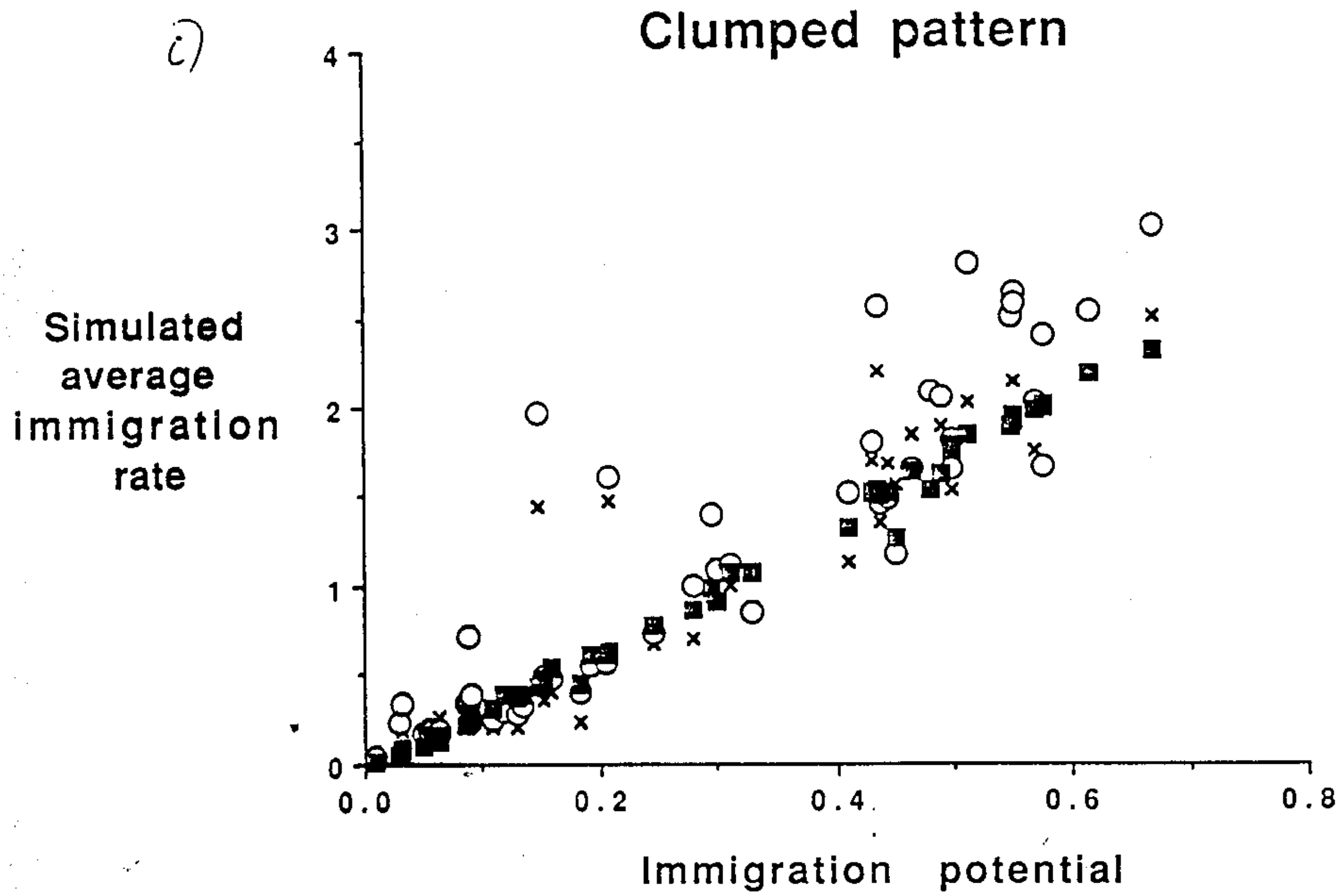

b)
Random pattern
Simulated average immigration rate
0
1
2
3
4
0.0
0.2
0.4
0.6
0.8
Immigration potential

Figure 4.4

i)


Clumped pattern
Simulated average immigration rate
Immigration potential
0
1
2
3
4
0.0
0.2
0.4
0.6
0.8