

## ON PENNA MODEL OF POPULATION EVOLUTION

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**Abstract:** Computer studies of population evolution are presented. Numerical calculations are based on the Penna model. This model accounts for mutation load of individuals resulting in non-trivial age ( $a$ ) dependence of the mortality rate  $q(a)$  which may be compared with empirical data. The Penna model is also very flexible for suitable modifications of the population evolution process such as hunting, genetic death, migration etc. Here we present some examples of the population growth for different evolution rules. Calculations require about 100 MB memory for  $10^6$  population which is necessary to get reliable statistics. Typical running time for 3000 iteration steps is several hours for HP S2000 machine.

**Keywords:** population evolution, biological ageing, Penna model, bad mutations, migration process, logistic equation, Gompertz law

### 1. Evolution and Logistic Equation

Population evolution is often described in terms of the number of individuals  $n(t)$  at time ( $t$ ). The simplest old fashioned model is based on a concept of birth rate ( $b$ ) against the death rate ( $d$ ) balance. Then the population ( $n$ ) in the next time step ( $t + 1$ ) is:

$$n(t + 1) = n(t) + (b - d) \cdot n(t). \quad (1)$$

This is just a geometrical series:

$$n(t + 1) = n(t) + B \cdot n(t), \quad (2)$$

with  $B = b - d$  as the reproduction rate. It is easy to see that this recipe leads to either the trivial case of extinction (if  $B \leq 0$ ) or to an unlimited growth (for  $B > 0$ ). That's why it is necessary to include additional factors to properly describe the evolution. One of them is the Verhulst factor ( $p$ ) [1], which is just a probability of

eliminating an individual from the population as a result of limited environmental capacity. The probability ( $p$ ) of elimination, before entering a new time step ( $t + 1$ ), is assumed to be proportional to the actual population  $n(t)$ ,  $p = n(t)/N$ , where ( $N$ ) is the model parameter known as environmental capacity. Note that for ( $n$ ) approaching ( $N$ ), the death ratio is one and so all population dies. With the Verhulst factor ( $p$ ) added we modify the evolution equation (2) by replacing  $n(t) \rightarrow n(t) - p \cdot n(t)$ . Then:

$$n(t + 1) = (n(t) - p \cdot n(t)) + B \cdot (n(t) - p \cdot n(t)), \quad (3)$$

since we first apply the Verhulst elimination (see also [2]) and then allow the remaining population  $(n(t) - p \cdot n(t)) = n(t) \cdot (1 - n(t)/N)$  to grow with rate ( $B$ ). This leads to the well known logistic equation:

$$x(t + 1) = (1 + B) \cdot x(1 - x), \quad (4)$$

where the right-hand-side  $x = n/N$  is at time ( $t$ ).

It should be mentioned that the logistic equation serves its purpose mostly as a test for computer simulations of population evolution. This is so since the number of analytical properties of this simple equation are known, and therefore may support our claim for quality of our programs used in simulations. The evolution rule for  $t \rightarrow t + 1$  transition, with  $n(t) \rightarrow n(t + 1)$  thus reads:

- step 1: eliminate fraction  $x = n(t)/N$  of the population;
- step 2: create a new fraction ( $B$ ) of the remaining  $(1 - x) \cdot N$  individuals.

This equation predicts a single stable solution  $x^* = B/(B + 1)$  for  $0 < B < 2$ , followed by cyclic solutions for higher growth rates up to  $B \approx 2.6$ , and chaotic region for still larger  $B \gg 2.6$ . For example, for  $B = 2.44$  we have solution of cycle 2,  $x^* = 0.442, 0.849$ . However, in computer implementation we get one single value around  $x = 0.7$ . This is so since we apply a probabilistic rule in steps 1 and 2, while scanning the whole population at time ( $t$ ), demanding death or birth with probabilities ( $x$ ) and ( $B$ ) instead of the fully deterministic version which is the *logistic* equation. Therefore, when comparing simulation results with logistic equation predictions, we need to be careful. It may be worth to realize that the deterministic version of the logistic equation with some noise admixture ( $r$ ):

$$x(t + 1) = (1 + B) \cdot x(1 - x) + r, \quad (5)$$

can be interpreted as an equivalent of our probabilistic approach.

The Penna model [3, 4] which we discuss in the next section introduces two more variables, the age ( $a$ ) of an individual number ( $\mu$ ) of active mutations (or perhaps diseases already developed in this individual), which serves for better description of the population. Then we may study not only time evolution  $n(t)$  of the whole population, but also its more detailed characteristics  $n(t, a, \mu)$ , or perhaps its stationary limit  $n(a, \mu) = n(t \rightarrow \infty, a, \mu)$ . Out of the  $n(a, \mu)$  statistics we may extract  $n(a)$ , the population at a chosen age ( $a$ ), or average number  $m(a)$  of mutations in sub-population of a given age ( $a$ ) etc.

## 2. Penna Model of Evolution

In the standard Penna model each individual gets an inherited *genome* which is a computer word (integer *genome*), storing information in each bit position on presence (bit '1') or lack (bit '0') of bad mutation, a disease. Each bit position is interpreted as either active or not, and only the active mutations play role in the life game rules. Actually, the model assumes simple time sequence for disclosing and activating the bad mutations, and so at age ( $a$ ) we account only for the portion of *genome* from bit position zero to bit position ( $a$ ). When getting older in one time step, the individual goes from age ( $a$ ) to ( $a + 1$ ) and the next bit is disclosed. If it is '1', we increment number ( $\mu$ ) of the active mutations by one. Thus essentially the numbers  $\mu(a)$  are pre-determined at birth time, when the offspring gets a copy of *genome* from its parent, in this simplest asexual model when cloning is the only way to pass genetic information to offsprings.

With this concept, we incorporate a new elimination mechanism into the first step of logistic version, where only the Verhulst factor was the death cause. Now, we scan over all members of population and eliminate some of them for the limited environmental capacity (the Verhulst factor), or having too many *active* mutations (above a threshold ( $T$ )), or perhaps for other reasons as it is in some extended versions of the Penna model. Then the second step is the growth of population, same as before, if the individual survives in the first step. The individual gives birth with probability ( $B$ ) if the reproduction age ( $R$ ) is reached. The offspring is then offered a copy of *genome* from the parent, enriched by ( $M$ ) additional mutations randomly picked over its whole lifespan. The role of these extra mutations is seen as accumulation of bad mutations at older ages in the population at equilibrium after long time  $t \rightarrow \infty$ .

Thus Penna model has 5 input parameters ( $N, B, R, M, T$ ) that control population structure  $n(t, a, \mu)$ , the number of members at time ( $t$ ), of age ( $a$ ) and number of active mutations ( $\mu$ ). Note that  $\mu = 0, 1, \dots, T - 1$  since all members with higher ( $\mu$ ) had been eliminated. For younger members we may restrict ourselves to  $\mu = 0, 1, \dots, a$  as we may activate one mutation per time step only. We get  $n(t, a, \mu)$  from simulation. The total population is then:

$$n(t) = \sum_{a, \mu} n(t, a, \mu). \quad (6)$$

As it was mentioned earlier, we are interested at equilibrium reached after a long time:

$$n(a, \mu) = n(t \rightarrow \infty, a, \mu), \quad (7)$$

from which:

$$n(a) = \sum_{\mu} n(a, \mu), \quad (8)$$



is the age structure of the population. Another quantity we may extract from the data is the survival rate:

$$s(a) = n(a + 1)/n(a), \quad (9)$$

the fraction of those at age ( $a$ ) which survived for the next time step. The logistic case is recovered for  $(N, B, R, M, T) = (N, B, 0, 0, \infty)$  and following analytical results from equation (4):

$$x(t \rightarrow \infty) = n(t \rightarrow \infty)/N = B/(1 + B), \quad (10)$$

$$s(a) = 1/(1 + B), \quad (11)$$

may be confronted with computer experiment.

Alternatively, we may use mortality rate  $q(a)$ :

$$q(a) + s(a) = 1, \quad (12)$$

and so:

$$q(a) = B/(1 + B), \quad (13)$$

for the logistic case, a trivial  $q(a)$  dependence. Actually, the observed  $q(a)$  follows the exponential Gompertz law for age ( $a$ ) above the reproduction threshold ( $R$ ):

$$q(a) \sim e^{g^a}, \quad (14)$$

where  $g$  is constant. Then we may compare  $q(a)$  from simulations against (14).

The Penna model is very much an open structure, rich in numerous possible modifications which are simple for implementation, and may correspond to important new ingredients in the evolution rules. This allows us to study the role of different factors such as influence of sexual selection [5, 6], parental care [7], overfishing or hunting [8] etc., on population dynamics. We may also study effects of migration between locations with different evolution parameters  $(N, B, R, M, T)$  as dependence of such variables as environmental capacity, living space still available etc. Some examples of the population evolution based on Penna model are presented in the next sections.

### 3. Fluctuations in Threshold for Bad Mutations

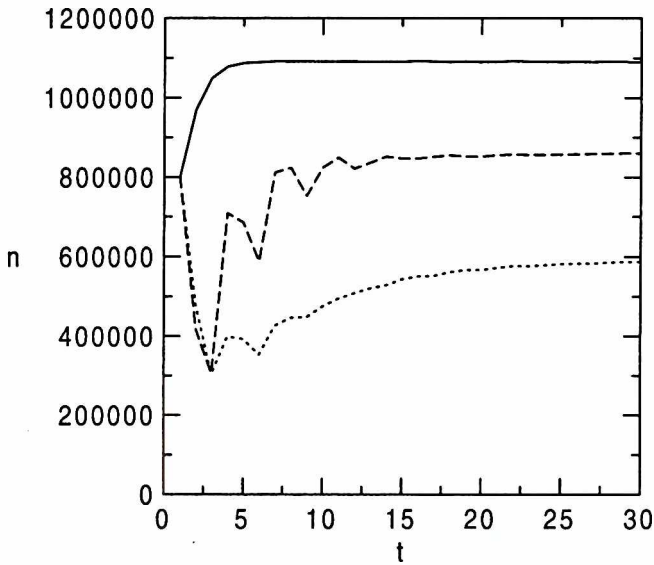
In the Penna model it is assumed that the offspring gets its *genome* from the parent at the birth time. However this is not true and the copying takes place at an earlier moment. We may account for this by suitably adjusting the counter of bad mutations for the already activated mutations before the birth. It means that the counter, which was reset to zero at birth time, needs to be set to a different value.

For example, let us consider three individuals  $i = 0, 1, 2$  with bad mutation threshold  $T = 3$ , which is the standard Penna model. Instead  $T = 3$ , we may propose threshold  $T = 7$  as a common value for all items in population and assume  $\mu = 4$  bad mutations already activated at age  $a = 0$  for first item at the birth time. In other words, there are still 3 bad mutation limit ahead, before this item would eventually be eliminated. This is the same as the previous limit  $T = 3$  with initial counter of active

'bads' equal to zero. However, it is easy to accept that another item is born with different ( $\mu$ ) if we apply the Penna rule of summing up all bad mutations in inherited *genome*, from the beginning to the age given, here to the birth time. Therefore we may accept  $\mu = 5$  and  $\mu = 2$  for another two items. This means that an effective limit after the birth for bad mutations is  $T(i) = 3, 2$  and  $5$  for items  $i = 0, 1$  and  $2$ , respectively.

With such arguments, we claim possible variations in threshold  $T(i)$  which may fluctuate from one individual to another, and does not change with time. For simplicity we assume a uniform distribution of  $T(i)$  ranging from 0 to 6 for the born ones, to recover the average  $T = 3$  for comparison with the standard Penna model where  $T = 3$ .

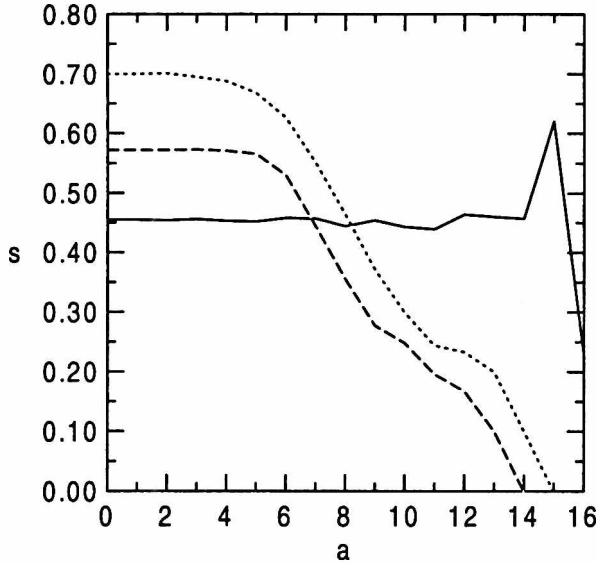
We need several hundreds iteration steps to reach the equilibrium. In Figure 1 the equilibrium population  $n(t \rightarrow \infty) = N \cdot B/(1+B) = 1\,090\,000$  is obtained for the logistic case.



**Figure 1.** Population evolution  $n(t)$ . Solid line corresponds to the logistic case, Penna model is represented by dotted line and dashed line is the Penna model with fluctuations in  $(T)$ , see text

Smaller value for the Penna model, the dotted line, is expected since additional deaths due to mutations may take place. The dip at time  $t = 3$  is a result of no birth for the initial population which is still below the reproduction age  $R = 4$ , while the Verhulst elimination is already switched on. Our minimum is not as deep as in paper [5] since in their paper the minimum reproduction age  $R = 8$  and so twice longer was the initial period of only the elimination by the Verhulst factor. Then some oscillations follow when the system is catching up balance between death and birth rates, until the equilibrium is reached. Both the minimum and oscillations do not correspond to reality since we merely would accept the very assumption underlying that behavior of the world being created momentarily at  $t = 0$  with all items at age  $a = 0$ .

The proposed modification (c) with fluctuations in threshold ( $T$ ) leads to a population nearly twice as high. We may interpret this as a result of presence in population of a fraction of quite high resistance  $T$  to mutations, the effect of the allowed variations in  $T = 0.6$ , as compared with  $T = 3$  in standard Penna model. Figure 2 shows the survival rate  $s(a) = n(t + 1, a + 1)/n(t, a)$ , the fraction of those at age  $a$  which survived for the next era, in the stationary limit of  $t \rightarrow \infty$ .



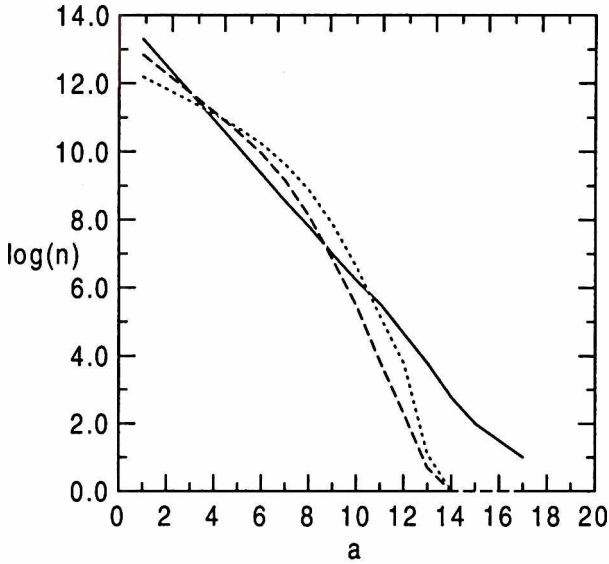
**Figure 2.** Survival rate  $s = n(a + 1)/n(a)$ . Solid line is the logistic case, dotted line is the Penna model and dashed line is the model with fluctuations in threshold ( $T$ )

Age structure is important — it may be compared with data obtainable from institutions, unlike the numbers for population ( $n$ ) itself normalized to the capacity ( $N$ ),  $n \propto N$ , with rather unknown ( $N$ ). The age-independent value  $s = 1/(1 + B) = 0.455$  for the logistic case (a) is confirmed, with some strong alterations close to advanced age when the statistics is very poor since only few do reach that age of roughly half the lifespan, here the lifespan is 32 for the 32–bits machine. If mutations are also included in cases (b) or (c), the survival rate for younger ones is larger than in (a) as the best fit individuals (with only a small number of bad mutations) are dominant in the population. This, however, does not mean that *genomes* with plenty of mutations are not present in the older-age when they may still stay inactive. On the contrary, the effect of accumulation of the defected gens, which are pumped into the newly born ones at rate ( $M$ ), must lead to accumulation of these mutations at old age. Therefore  $s(a)$  drops significantly for old ones. The Penna model cuts the oldest at age  $a = 15$ , and fluctuations reduce the age limit further on to  $a = 14$ . Generally, the survival rate is lower if fluctuations in ( $T$ ) are included. This may be accounted for the fraction of items with smaller threshold ( $T$ ). They are eliminated sooner and so the survival rate ( $s$ ) is then smaller.

Figure 3 is another way to analyze the age structure of the population. In logistic model (a),  $n(a) = n(0) \cdot e^{-sa}$  with same survival rate ( $s$ ) as defined before. This exponential dependence is known as the biologically observed Gompertz law. From simulation we get the fitted  $s_{\text{logistic}} = 0.454$ , very close indeed to 0.455 from the analytical model. For Penna cases (b) and (c) we observe systematic deviations from the Gompertz law and characteristic  $s$ -slope is always larger at younger age than at old age. For young individuals below the reproduction age  $a < R = 4$  we get  $s = 0.70$  for the Penna case (b). This is very close indeed to the predicted value  $s = 0.703$  from equation:

$$s(a) = 1 - n/N, a < R, \quad (15)$$

which may be proved for the Penna scenario for the pre-mature age  $a < R$ , and with population ( $n$ ) to environmental capacity ( $N$ ) ratio taken from the simulation.

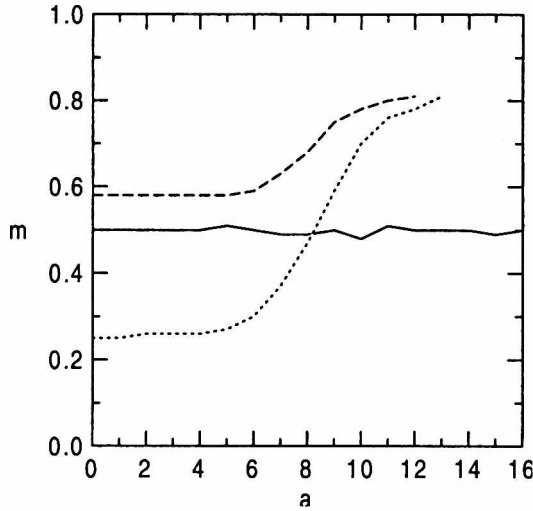


**Figure 3.** Population structure versus age. For logistic case, a straight solid line is expected following the Gompertz law  $\log(n) \propto a$ . Dotted and dashed lines correspond to cases (b) — Penna model and (c) — the model with fluctuations in threshold ( $T$ ), respectively

The corresponding value ( $s$ ) from the simulation for young individuals for case (c) with fluctuations is  $s = 0.59$ . For both cases (b) and (c), ( $s$ ) is *greater* than for logistic case (a), as we have already indicated. It was also discussed that we get  $s(a)$  *smaller* than logistic value at old ages, say for ( $a$ ) from 10 to 12. This time the fluctuations in  $T(i)$  do not play a dominant role and it is the accumulated mutations which cut population sharply. At old age, we are already close to the terminating  $T$ 's and there are plenty of accumulated bad mutations ahead. We get same  $s = 0.20$  from computer simulation for cases (b) and (c).

Figure 4 shows some simple statistics in terms of percentage  $m(a)$  of bad mutations against bit position ( $a$ ). This is just information on how many mutations would be active at age ( $a$ ), if we sum up all ( $m$ ) for bit positions from zero to ( $a$ ).





**Figure 4.** Percentage of bad mutations versus bit position for logistic case (solid line), Penna model (dotted line) and model with variations in threshold ( $T$ ) (dashed line)

If mutations are randomly distributed over all bits positions,  $m(a) = 0.5$ . This is the logistic case (a) when initial population was created with random *genome* composition. This is a *very* arbitrary choice, yet it belongs to the Penna model and the initial population choice is totally unimportant after only first several iteration steps. For the Penna model we expect fewer mutations at a younger age (the best ones survive in evolution process), and an increase at old age (effect of bad mutation accumulation). This can be seen in the picture. Higher mutations concentration for case (c) with dispersion in ( $T$ ) indicates presence of less healthy individuals that exist as a result of more tolerant higher threshold ( $T$ ) for some of them. They pass the elimination process when cutting down all items with number of active mutations ( $\mu$ ) above ( $T$ ).

We conclude that fluctuation in threshold  $T(i)$  is important and may influence the age structure of population and its health condition.

#### 4. Migration Process

In this section we consider a number of locations labeled by  $i$ , each with its own set of evolution parameters. One iteration step leading from the normalized population  $x_i(t) = n_i/N_i$  at time ( $t$ ) to  $x_i(t+1)$  is the result of a scan over the whole population. For each item in the population we consider:

- ... start from  $x_i(t)$  ...
- virtual elimination due to the Verhulst factor or for other reasons, then
- giving birth
- ... finish at  $x_i(t+1)$ .

This is the Penna model which we apply for ( $k$ ) iteration steps. This yields the new population  $y_i = x_i(t+k)$ . Then after a given number ( $k$ ) of evolutionary steps,



we allow each individual for a migration from location  $i$  to location  $j$  with probability  $p(i, j)$ . The probability  $p(i, j)$  is negotiated according to a variety of scenarios. After all migration moves are carried out, the full iteration cycle is then complete:

- ... from  $x_i(t)$ , by elimination followed by growth,  $k$ -times, to  $y_i = x_i(t + k)$ ...
- ... from  $y_i$ , by migration, to  $x_i(t + k)$ .

Obviously, for  $p(i, j) = 0$  the game describes independent sub-populations and the standard Penna model applies to each location. However, when migration is allowed a new equilibrium is established which may be different from the isolated islands case. The individual picked out with a probability  $p(i, j)$  from  $i$ -th location, and of destination  $j$ , is placed in a buffer matrix  $(i, j)$ . As we said before, this action takes place after each  $(k)$  iteration steps with the evolution game independent at each location and according to the Penna model rules. The buffer concept is convenient since we intend to determine the  $p(i, j)$  on the basis of actual state of the population in each location. Therefore we freeze evolution until all migrating items are collected in the buffer, and then they are transferred to their destinations. This completes one evolution cycle of  $(k)$  independent iterations at each location, and followed by the migration controlled by current characteristics of the populations at each location.

For simplicity, we assume later on that the probability  $p(i, j)$  is a product,  $p(i, j) = q(i) \cdot p(j)$  of initial location  $q(i)$  mobility factor and probability  $p(j)$  of picking out  $j$ -th location as the destination. In this case, the decision-making-process splits into two independent steps:

- decision of moving out-of- $i$ -th location into a buffer (a transition camp), with probability  $q(i)$ , then
- picking out  $j$ -th location as destination with probability  $p(j)$ , and no memory of the past  $i$ -th location.

Then *random migration* takes place if  $q(i) = q$ , location independent mobility of any strength, and  $p(j) \propto y_j N_j$ , the actual population in  $j$ -th location, just before the migration. This random migration takes place only if overall characteristics for each location is the same and the locations differ only by their environmental capacity ( $N_i$ ). To see this, let us consider a more analytical approach to the limiting case of the logistic equation  $R = 0$ ,  $M = 0$  and large threshold ( $T$ ). Then the population ( $y_i$ ) after elimination and growth is expected to be:

$$y_i = k_i \cdot x_i (1 - x_i), \quad (16)$$

where  $k_i = 1 + B_i$ . The migration process alters ( $y_i$ ) to the new value  $x_i(t + k)$ :

$$x_i(t + k) = y_i + \frac{N}{N_i} \cdot \sum_j T_{i,j}, \quad (17)$$

where:

$$N = \sum_i N_i, \quad (18)$$

and the anti-symmetrical transfer matrix  $T_{ij} = -T_{ji}$  is:

$$T_{ij} = (N_j/N) \cdot y_j p(j, i) - (N_i/N) \cdot y_i p(i, j). \quad (19)$$

The first term represents the inflow of population into  $i$ -th location from any location  $j$ , while the other term is the opposite. As we said,  $p(i, j)$  stands for the probability of an individual to migrate from location  $i$  to location  $j$ . In the following we confined ourselves to the uncorrelated version when:

$$p(i, j) = q(i) \cdot p(j), \quad (20)$$

and so:

$$T_{ij} = (N_j/N) \cdot y_j q(j) p(i) - (N_i/N) \cdot y_i q(i) p(j). \quad (21)$$

It is easily seen for the case  $q(i) = q$  and  $p(j) \propto y_j N_j/N$ , for the actual population at time  $(t + k)$ , just before migration, that the transfer matrix vanishes and so we get the claimed *random migration* for which  $x_i(t + k) = y_i$ , according to the Penna scheme. (We may choose different  $q(i)$  and  $p(j)$  also leading to the neutral migration.) Thus for random migration we have:

$$q(i) = q, \quad p(j) \propto y_j N_j/N. \quad (22)$$

For non-random migration we choose probabilities for the migration different from the ones leading to the random moves. For example, for:

$$q(i) = q/(y_i N_i/N), \quad (23)$$

where  $q$  is a proportionality constant and the total number of the 'move-out-of' individuals is same for each location, and independent of the actual population there. This is a resemblance of a 'quota' limit policy for migrating people and the same for all locations, which may lead to the faster escape of individuals from already deserted areas. As a result we expect a new equilibrium between locations with a tendency toward clustering. Perhaps it is illustrative to consider the stability of two identical locations, coupled by migration process, in the simple logistic case. Obviously  $y_i = y_j$  is the solution. However, if a small fluctuation  $\varepsilon(t)$  is allowed, then one of the locations has a surplus population,  $x_i + \varepsilon$ , at the cost of the other location population,  $x_j - \varepsilon$ , then the system response after one full cycle with  $\varepsilon(t + k) = r \cdot \varepsilon(t)$ . The ratio ( $r$ ) may be obtained for pure logistic equation as:

$$r = (1 - B) + (1 - B)(q/q_{max}), \quad q_{max} = 2B/(1 + B), \quad (24)$$

with maximum ( $q$ ) coefficient so that probability is less than one. The system becomes unstable for the mobility parameter ( $q$ ) larger than a minimum  $q_{min}$  value when ( $r$ ) exceeds one. This yields the instability regime for ( $q$ ):

$$0 < B^2/(1 - B^2) < 2q < B/(1 + B), \quad 0 < B < 0.5. \quad (25)$$

Let us summarize the main concept. In the above example we claimed modification of the migration probability, as compared to the reference random transfers, according to some environmental factors such as actual population  $y_i N_i$ . In fact we may propose:

$$q(i) = q \cdot (y_i N_i / N)^{-1}, \quad (26)$$

$$q(i) = q \cdot (y_i N_i / N)^0, \quad (27)$$

$$q(i) = q \cdot (y_i N_i / N)^{+1}, \quad (28)$$

for the discussed clustering tendency ( $c$ ), random migration and for tendency towards equal population at each location ( $u$ ), respectively. Alternatively, we may alter probability  $p(j)$  in a similar fashion by a multiplication factor  $(y_j N_j / N)^d$ , where  $d = -1, 0, 1$ . We may account for some typical environmental factors to modify the probability  $q(i)$ , such as:

- $(y_i N_i / N)^{-n_i}$ , ... actual population;
- $(N_i / N)^{-e_i}$ , ... environmental capacity;
- $[(N_i / N) - (y_i N_i / N)]^{-v_i}$ , ... living space still available;

and adjust the power coefficients  $d = n_i, e_i, v_i$  to get the assumed tendency for clusterization ( $c$ ) with positive exponent coefficients, neutral (random) migration for zero exponent coefficients, or the opposite tendency for negative ones. Then we may apply similar modification not only to the out-coming population  $q(i)$ , but to the incoming one  $p(j)$ . In each case we may discuss stability, at least for the logistic case.

The proposed form for  $q(i)$  is then:

$$q(i) = q_i \cdot (y_i N_i / N)^{-n_i} \cdot (N_i / N)^{-e_i} \cdot [(N_i / N) - (y_i N_i / N)]^{-v_i}, \quad (29)$$

where  $(q_i)$  is the mobility coefficient which shows the degree of determination to start moving. Similarly we modify  $p(j)$  to the form:

$$p(j) = C \cdot (y_j N_j / N)^{+n_j} \cdot (N_j / N)^{+e_j} \cdot [(N_j / N) - (y_j N_j / N)]^{+v_j}, \quad (30)$$

and all zero power coefficients correspond to random migration, positive ones indicate preferences towards clusterization and the negative ones show the opposite tendency. In other words, for example similar tendency toward clustering causes by the population factor may be produced by an increase in  $q(i)$  for smaller ( $n_i$ ) (tendency for more intensive escape from smaller populations), or by increase in  $p(j)$  for higher  $n_j$  (more likely destination of the migrants to densely populated locations).

The model is then controlled by the three parameters ( $n_i, e_i$  and  $v_i$ ) for the outgoing population and another three parameters ( $n_j, e_j$  and  $v_j$ ) for the in-flowing population. The set  $(n_i, e_i, v_i, n_j, e_j, v_j) = (0, 0, 0, 0, 0, 0)$  serves as the random migration reference only. In each case we use population of order of  $10^6$  or so on a 32 bit machine. The number of iterations necessary to get an equilibrium is about a couple of hundreds iteration steps.

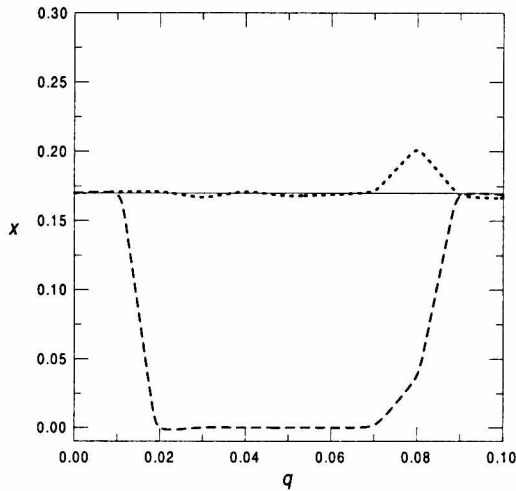
For example we may consider  $(n_i, e_i, v_i, n_j, e_j, v_j) = (1, 0, 0, 0, 0, 0)$  for two identical locations. This causes a preference towards clustering as individuals are forced to go by increasing ( $q$ ), they are still reluctant to move out of more crowded locations. Analytical results for logistic case show instability above critical



$q_c = 0.5 \cdot B^2/(1 - B^2)$ , and only for  $B < 0.5$ , which yields  $q_c = 0.021$ . So we expect population  $x(q) = n/N$  to stay stable at same level for both locations at the value  $x = B/(1 + B) = 0.17$  predicted by the logistic equation until about (remember non-deterministic implementation of deterministic logistic rules)  $q = 0.021$ , and then followed by perhaps a sharp decrease in population in one of the location as a result of instability. This is illustrated in Figure 5. It should be noticed that for still larger ( $q$ ), when migration is forced to become very intensive, the deserted location may become re-occupied again.

Similar behavior is seen in Figure 6 for three locations. In this case capacity ratio 1 : 2 : 3 was used in calculations.

However, more detailed analysis shows that, with increasing ( $q$ ), we observe a sharp transition from 3 occupied locations to 2 non-empty sites, followed by  $2 \rightarrow 1$



**Figure 5.** Normalized population  $x_i = n_i/N_i$  at 2 locations versus mobility ( $q$ ). Population capacities  $N_i$  are same on both locations. Penna case for set of the model parameters  $(n_i, e_i, v_i, n_j, e_j, v_j) = (1, 0, 0, 0, 0, 0)$

site transition and reentry  $1 \rightarrow 3$  occupied sites for intensive migration.

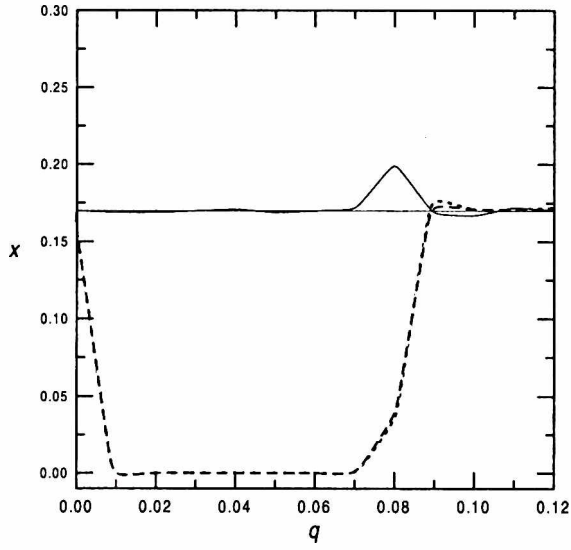
An opposite tendency towards avoiding overcrowded locations is demonstrated in Figure 7 and caused by mechanism: avoiding large territories. In this cases locations of larger capacities are less densely packed.

Our conclusion is that migration also alters the population growth.

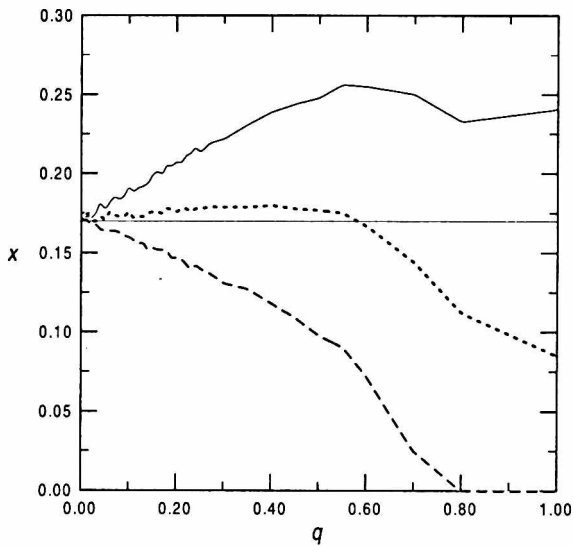
### Acknowledgments

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**Figure 6.** Normalized population  $x_i = n_i/N_i$  at 3 locations with capacity ratio 1 : 2 : 3 versus mobility ( $q$ ). Penna case for set of the model parameters  $(n_i, e_i, v_i, n_j, e_j, v_j) = (1, 0, 0, 0, 0, 0)$



**Figure 7.** Normalized population  $x_i = n_i/N_i$  at 3 locations with capacity ratio 1 : 2 : 3 versus mobility ( $q$ ). Penna case for set of the model parameters  $(n_i, e_i, v_i, n_j, e_j, v_j) = (0, -1, 0, 0, 0, 0)$

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