EXACTLY SOLVABLE MODEL FOR A GENETICALLY INDUCED GEOGRAPHICAL DISTRIBUTION OF A POPULATION

by

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ABSTRACT

We consider a population with bi-parental procreation which genetically transmits, through a specific blending-like mechanism, a combination of two characters, namely a *nomadic* and a *sedentary* ones. Consequently, as time goes on, the population spreads out geographically, space distribution thus reflecting genetic distribution. The model is exactly tractable, and we calculate the relevant quantities. We finally present and calculate a generalized version of the model.

Key-words: Genetical evolution; Sedentary/Nomadic characters; Populational geographic distribution; Population evolution.

1 INTRODUCTION

Either because of its high intrinsic interest, or because of its analogy with spin glasses (see, for instance, Ref. [1]), Evolutionary Genetics is actively studied nowadays (for updated reviews see Refs. [2,3]). The current basic model for genetic evolution of populations relies on the Mendelian picture. More precisely, a given macroscopic observable (say the individual size or the individual colour) of a given species is genetically transmitted through a genotype n-sized "strip" of practically independent binary (or more general) variables. All the individuals of all generations of a given species share basically the same set of n's for the various macroscopic observables (n $\simeq$ 1 for say the sex or the overall colour of the eyes; n >> 1 for say the size or the weight; in this case n could achieve, in real species, values up to 10^3 - 10^4). This mechanism for the transmission of genetic information has clearly proved its biological efficiency. However, on evolutionary grounds, it can be considered as relatively sophisticated, and has presumably been achieved through a slow optimization along successive generations. For primitive populations (ancestors of the present species, or new species still under relatively strong evolution) a simpler mechanism, blending-like, seems more plausible. Within this picture, the value of n could probably increase (up to a relatively high limit) along successive generations. An extreme type of increase one can think of is the *geometric* one; for instance, in the case of bi-parental procreation, n would become 2n at the next generation. A more moderate increase would be the *arithmetic* one; for instance, n would become

n + 1 at the next generation. Such hypothesis lies, in what time evolution of n concerns, in between the geometric and the basic Mendelian one (for which n is *stationary*). In any of these cases, the particular type of increase (stationary, arithmetic, geometric or any other type) of n should somehow be included in the genetic information to be transmitted. The three types of increase under consideration are illustrated in Fig. 1.

We formulate here, for a population with (unisex) bi-parental procreation, a mathematically tractable model of the arithmetic type by assuming a binary variable which takes the values A (*sedentary* character) or B (*nomadic* character). If we were focusing bacteries, the presence of B could determine the appearence of say a flagellum (vibrating tail), which would greatly enhance the translational motion. For this population, the associated genetic strip of each individual contains, at each generation, a certain amount of A's and B's. The tendency of any individual to move away is assumed to increase, in a blending-like manner to be specified later on, with increasing proportion of B's in its strip (for example, in the picture of the bacteries, the proportion of B's could somehow determine, through its size and/or strength or anything similar, the migratory efficiency of the flagellum). Consequently, a geographic spread out of the population will emerge along subsequent generations. In particular, the individuals with BBB... strips will be found at positions further and further away from the initial one, whereas the individuals with AAA... strips will be found on the same place for all generations. Consequently, space distribution will intimately reflect genetic distribution and can be used as a tool for genetic

studies.

The model and some relevant quantities are presented in Section 2; we generalize it in Section 3; we finally conclude in Section 4.

2 MODEL

For simplicity we assume that the population can travel only *one*-dimensionally, say along a natural "valley" (x axis). Furthermore, we assume that only the *positive* x axis is accessible; for instance, a very high natural obstacle exists at x = 0 which forbiddens the passage to the negative x region. This second assumption is adopted for definiteness, and could be released with no further mathematical complexities. To each individual strip we associate a number ν ($0 \leq \nu \leq 1$) defined as its proportion of B's (e.g., ν equals 1/2 and 2/3 for AB and ABB respectively). Next we define, for an arbitrarily given individual, its *migratory strength* ρ as the space expansion rate which will drive him, during his life, along the positive x-axis starting from the point where he was born: more precisely, if he was born in a space interval whose width is Δx, he will die in a space interval whose width is $(1 + \rho)$Δx and which is shifted along the positive x-axis in a way we shall detail later on. We now assume the *basic hypothesis* of the present model, namely the following blending-like law relating ν and ρ:

$$\rho(\nu) = \rho_B \nu^\gamma \tag{1}$$

where $\rho_B \gtrsim 0$ and $\gamma \gtrsim 0$ are genetic characteristics of the species (see Fig. 2). Furthermore, we assume discrete time, the unit step corresponding to one generation; also, all individuals of one generation die simultaneously and, at precisely that moment, start living (and migrating) all the individuals of the next generation (whose genetic strips will have one unit more than those of the preceding generation: arithmetic growth). This is a good moment for claryfing that, although we shall, for simplicity, keep talking of n increasing arithmetically (by one) at every new generation, the time unit step could, in fact, as well refer to a certain *set of successive generations*; all the generations of the same set would maintain the same value of n, which would become (n + 1) for the next set of generations (in this case – indeed more realistic – the increase of n would be due to say a mutation rather than to a genetic prescription).

At time t = 0 we have, in the region $0 < x < r_A$ (in the region $r_A < x < r_A + r_B$), N_A (N_B) individuals whose one-locus strip has the value A (B). The total number of individuals then is $N = N_A + N_B$, and we define the probabilities $p_A \equiv N_A/N$ and $p_B \equiv N_B/N$. The N_A (N_B) individuals are uniformly distributed in the interval with width r_A (r_B), the populational density thus being $\lambda_A \equiv N_A/r_A = Np_A r_A$ ($\lambda_B \equiv N_B/r_B = Np_B/r_B$). As frequently done in theory of multifractals (see [4,5] and references therein) let us introduce a measure defined through the momenta of the probabilities, i.e., let us introduce p_A^q, p_B^q and $p_0 \equiv p_A^q + p_B^q$, where q is any fixed real number. The parameter q will be used to characterize the growth (or decrease) of the population: q = 1 (hence $p_0 = 1$), q > 1 (hence $p_0 < 1$) and q < 1 (hence $p_0 > 1$) will respectively imply *stationary*, *decreasing* and *increasing*

populations. The space occupancy as a function of time t follows a deterministic dynamics which is indicated in Fig. 3 (where, for future convenience, we have introduced $\rho(0)$ which, at the present stage, equals zero). At any time t - 0 (with t = 1,2,...) we have 2^t regions (along the x axis) characterized by $i = 1,2,...,2^t$, and univocally associated with t-locus strip sequences; for instance, for $i = 1$ we have $\overbrace{AAA...A}^{t}$, for $i = 2$ we have $\overbrace{AAA...B}^{t}$, and for $i = 2^t$ we have $\overbrace{BBB...B}^{t}$. The width of each region is directly related to the particular sequence. For instance for t = 1 - 0, we have

$$r_A^{(1)} = r_A[1 + \rho(0)] \tag{2.a}$$

and

$$r_B^{(1)} = r_B[1 + \rho(1)] \; ; \tag{2.b}$$

for t = 1 + 0, we have

$$r_{AA} = r_A^{(1)} p_A^q / p_0 = r_A[1 + \rho(0)]p_A^q / p_0 \; , \tag{3.a}$$

$$r_{AB} = r_A^{(1)} p_B^q / p_0 = r_A[1 + \rho(0)]p_B^q / p_0 \; , \tag{3.b}$$

$$r_{BA} = r_B^{(1)} p_A^q / p_0 = r_B[1 + \rho(1)]p_A^q / p_0 \; , \tag{3.c}$$

and

$$r_{BB} = r_B^{(1)} p_B^q/p_0 = r_B[1 + \rho(1)]p_B^q/p_0 \; ; \qquad (3.d)$$

for $t = 2 - 0$, we have

$$r_{AA}^{(2)} = r_{AA}[1 + \rho(0)] = r_A[1 + \rho(0)]^2 p_A^q/p_0 \; , \qquad (4.a)$$

$$r_{AB}^{(2)} = r_{AB}[1 + \rho(1/2)] = r_A[1 + \rho(0)][1 + \rho(1/2)]p_B^q/p_0 \; , \qquad (4.b)$$

$$r_{BA}^{(2)} = r_{BA}[1 + \rho(1/2)] = r_B[1 + \rho(1)][1 + \rho(1/2)]p_A^q/p_0 \qquad (4.c)$$

and

$$r_{BB}^{(2)} = r_{BB}[1 + \rho(1)] = r_B[1 + \rho(1)]^2 p_B^q/p_0 \; ; \qquad (4.d)$$

for $t = 2 + 0$, we have

$$r_{AAA} = r_{AA}^{(2)} p_A^q/p_0 = r_A[1 + \rho(0)]^2 p_A^{2q}/p_0^2 \; , \qquad (5.a)$$

$$r_{AAB} = r_{AA}^{(2)} p_B^q/p_0 = r_A[1 + \rho(0)]^2 p_A^q p_B^q/p_0^2 \; , \qquad (5.b)$$

$$r_{ABA} = r_{AB}^{(2)} p_A^q/p_0 = r_A[1 + \rho(0)][1 + \rho(1/2)]p_A^q p_B^q/p_0^2 \; , \qquad (5.c)$$

$$r_{ABB} = r_{AB}^{(2)} p_B^q/p_0 = r_A [1 + \rho(0)][1 + \rho(1/2)] p_B^{2q}/p_0^2 , \qquad (5.d)$$

$$r_{BAA} = r_{BA}^{(2)} p_A^q/p_0 = r_B [1 + \rho(1)][1 + \rho(1/2)] p_A^{2q}/p_0^2 , \qquad (5.e)$$

$$r_{BAB} = r_{BA}^{(2)} p_B^q/p_0 = r_B [1 + \rho(1)][1 + \rho(1/2)] p_A^q p_B^q/p_0^2 , \qquad (5.f)$$

$$r_{BBA} = r_{BB}^{(2)} p_A^q/p_0 = r_B [1 + \rho(1)]^2 p_A^q p_B^q/p_0^2 \qquad (5.g)$$

and

$$r_{BBB} = r_{BB}^{(2)} p_B^q/p_0 = r_B [1 + \rho(1)]^2 p_B^{2q}/p_0^2 . \qquad (5.h)$$

In general, for an arbitrary sequence Σ containing a A's and b B's $(a + b = t)$ we have:

(i) at time $t - 0$

$$r_\Sigma^{(t)} = \begin{cases} \Gamma_A \left\{ \prod_{j=1}^{t} \left[1 + \rho\left(\nu_j^{(\Sigma)} \right) \right] \right\} p_A^{(a-1)q} p_B^{bq}/p_0^{a+b-1} & \text{if } \Sigma \text{ starts with A,} \\[4mm] \Gamma_B \left\{ \prod_{j=1}^{t} \left[1 + \rho\left(\nu_j^{(\Sigma)} \right) \right] \right\} p_A^{aq} p_B^{(b-1)q}/p_0^{a+b-1} & \text{if } \Sigma \text{ starts with B,} \end{cases} \qquad (6)$$

where the set $\left\{ \nu_j^{(\Sigma)} \right\}$ depends on the particular sequence (e.g., AABA, ABAB and

BBAA respectively yield $\left\{\nu_j^{(\Sigma)}\right\}$ = (0,0,1/3,1/4), (0,1/2,1/3,2/4) and

(1,1,2/3,2/4);

(ii) at time t + 0

$$r_{\Sigma A} = r_{\Sigma}^{(t)} p_A^q / P_0 \qquad (7.a)$$

and

$$r_{\Sigma B} = r_{\Sigma}^{(t)} p_B^q / P_0 \qquad (7.b)$$

As we see, at times between (t - 1 + 0) and (t - 0), the population is constituted by $N_{total}^{(t-1)} = Np_0^{t-1}$ individuals. Then the entire generation dies and, at time (t + 0), $N_{total}^{(t)} = Np_0^t$ individuals appear distributed in 2^{t+1} regions (i = 1,2,...,2^{t+1}). Each region at time (t - 0) provides, at time (t + 0), two new regions, the left (right) one of which is associated with a (t + 1)-locus strip sequence which reproduces the generating sequence and adds, at the last locus, the value A (B).

Let us now focus the values $\nu_j^{(t)}$ and the associated occurrence probabilities $g\left(\nu_j^{(t)}\right)$ at times between [(t - 1) + 0] and (t - 0). For times between t = 0 and t = 1 - 0 we have $\nu^{(1)}$ = 0,1 and $g\left(\nu^{(1)}\right)$ = p_A, p_B; for times between t = 1 + 0 and t = 2 - 0 we have $\nu^{(2)}$ = 0,1/2,1 and $g\left(\nu^{(2)}\right)$ = p_A^{2q}/p_0^2, $2p_A^q p_B^q/p_0^2$, p_B^{2q}/p_0^2. In general we have $\nu^{(t)}$ = 0,1/t,2/t,...,1 and $g\left(\nu^{(t)}\right)$ = p_A^{tq}/p_0^t, $tp_A^{(t-1)q}p_B^q/p_0^t$,...,p_B^{tq}/p_0^t, i.e.,

$$\nu_j^{(t)} = j/t \qquad\qquad (j = 0,1,2,\dots,t) \qquad\qquad (8.a)$$

and

$$g\left(\nu_j^{(t)}\right) = \binom{t}{j} P_A^{(t-j)q} P_B^{jq}/P_0^t \qquad\qquad (8.b)$$

With this binominal probability law we can easily calculate, for any real λ,

$$\langle e^{\lambda\nu^{(t)}} \rangle = \sum_{j=0}^{t} e^{j\lambda/t} \binom{t}{j} P_A^{(t-j)q} P_B^{jq}/P_0^t$$

and we obtain

$$\langle e^{\lambda\nu^{(t)}} \rangle = \left[\frac{P_A^q + P_B^q e^{\lambda/t}}{P_0}\right]^t \qquad\qquad (9)$$

Through this generating function we can easily calculate any average momentum of $\nu^{(t)}$ just by using Eq. (9) into

$$\langle \left[\nu^{(t)}\right]^r \rangle = \frac{d^r}{d\lambda^r} \langle e^{\lambda\nu^{(t)}} \rangle \Big|_{\lambda=0} \qquad\qquad (r = 0,1,2,\dots) \qquad\qquad (10)$$

In particular we have

$$\langle \nu^{(t)} \rangle = \frac{p_B^q}{p_0} \tag{11}$$

and

$$\sigma^2 \equiv \left\langle \left[\nu^{(t)} \right]^2 \right\rangle - \left[\langle \nu^{(t)} \rangle \right]^2 = \frac{p_A^q p_B^q}{p_0^2} \frac{1}{t} \tag{12}$$

Consequently we recover the well known binominal result

$$\frac{\sigma}{\langle \nu^{(t)} \rangle} = \left(\frac{p_A}{p_B} \right)^{q/2} \frac{1}{\sqrt{t}} \qquad (t = 1,2,\dots) \tag{13}$$

For $t \gg 1$, the distribution $g\left(\nu^{(t)} \right)$ becomes a Gaussian one, centered in $\langle \nu^{(t)} \rangle$ given by Eq. (11) and with an increasingly narrow width given by Eq. (12).

At time $t = 0$ the population spreads from $x = 0$ to $x = r_A + r_B$; the baricenter $x_A^{(0)}$ $\left(x_B^{(0)} \right)$ of the A-subpopulation (B-subpopulation) is given by $x_A^{(0)} = r_A/2$ $\left(x_B^{(0)} = r_A + r_B/2 \right)$; the overall baricenter $R^{(0)}$ is given by

$$R^{(0)} = p_A x_A^{(0)} + p_B x_B^{(0)}$$

$$= \frac{r_A}{2} + p_B \frac{r_A + r_B}{2} \tag{14}$$

At time t = 1 - 0 the population spreads from x = 0 to x = $r_A[1 + \rho(0)]$ + $r_B[1 + \rho(1)]$; the $x_A^{(1-0)}$ and $x_B^{(1-0)}$ baricenters are respectively given by $r_A[1 + \rho(0)]/2$ and $r_A[1 + \rho(0)]$ + $r_B[1 + \rho(1)]/2$; the overall baricenter $R^{(1-0)}$ is given by

$$R^{(1-0)} = P_A x_A^{(1-0)} + P_B x_B^{(1-0)}$$

$$\frac{r_A[1+\rho(0)]}{2} + P_B \frac{r_A[1+\rho(0)] + r_B[1+\rho(1)]}{2} \qquad (15)$$

At time t = 1 + 0 the population still spreads from x = 0 to x = $r_A[1 + \rho(0)]$ + $r_B[1 + \rho(1)]$ in the following way: the $x_{AA}^{(1+0)}$, $x_{AB}^{(1+0)}$, $x_{BA}^{(1+0)}$ and $x_{BB}^{(1+0)}$ baricenters are respectively given by $r_{AA}/2$, $r_{AA} + r_{AB}/2$, $r_{AA} + r_{AB} + r_{BA}/2$ and $r_{AA} + r_{AB} + r_{BA} + r_{BB}/2$. The overall baricenter $R^{(1+0)}$ is given by

$$R^{(1+0)} = \left(p_A^{2q}/p_0^2\right) r_{AA}/2 + \left(p_A^q p_B^q /p_0^2\right)(r_{AA} + r_{AB}/2)$$

$$+ \left(p_B^q p_A^q /p_0^2\right)(r_{AA} + r_{AB} + r_{BA}/2) + \left(p_B^{2q}/p_0^2\right)(r_{AA} + r_{AB} + r_{BA} + r_{BB}/2)$$

$$(16)$$

This equation yields (by using Eqs. (3))

$$R^{(1+0)} = \frac{r_A[1+\rho(0)]}{2} + \frac{p_B^q}{p_0} \frac{r_A[1+\rho(0)] + r_B[1+\rho(1)]}{2} \qquad (17)$$

By comparing this equation with Eq. (15) we verify that $q = 1$ implies $R^{(1+0)} = R^{(1-0)}$.

Generally speaking $R^{(t-0)}$ and $R^{(t+0)}$ ($t = 2,3,...$) are complex functions of $\left(r_A, r_B, \left\{ \rho\left(v_j^{(t)} \right) \right\}, p_B, q \right)$. However, for the particular case for which $\rho\left(v_j^{(t)} \right) = 0$ ($\forall j$) we have

$$R^{(t-0)} = R^{(t+0)} = \frac{r_A}{2} + \frac{p_B^q}{p_0} \frac{r_A + r_B}{2} \qquad (t = 2,3,...) \qquad (18)$$

The result is also simple for another (and very relevant) particular case, namely when $t \gg 1$. Indeed, because of Eq. (13), we have

$$R^{(t+0)} \sim \left[\frac{r_A}{2} + \frac{p_B^q}{p_0} \frac{r_A + r_B}{2} \right] \left[1 + \rho\left(<v^{(t)}> \right) \right]^t \qquad (19)$$

or equivalently

$$R^{(t+0)} \sim \left[\frac{r_A}{2} + \frac{p_B^q}{p_0} \frac{r_A + r_B}{2} \right] e^{t/\tau_R} \qquad (20)$$

with the following *geographic spreading characteristic time*

$$\tau_R \equiv \frac{1}{\ln\left[1 + \rho\left(<v^{(t)}> \right) \right]} \qquad (21)$$

Finally, by using Eqs. (1) and (11), we obtain

$$\tau_R = \frac{1}{\ln\left\{1 + \dfrac{\rho_B}{\left[\left(\dfrac{p_A}{p_B}\right)^q + 1\right]^q}\right\}} \tag{22}$$

We can verify, $\forall(q,p_A,p_B = 1 - p_A)$

$$\tau_R(q,p_A,p_B) = \tau_R(-q,p_B,p_A) \tag{23}$$

The q-dependence of τ_R is shown in Fig. 4.

Let us now turn back to the population growth. We have seen that $N_{total}^{(t)} = p_0^t N$, hence

$$\frac{N_{total}^{(t)}}{N} = e^{t/\tau_N} \tag{24}$$

with the following *populational growth characteristic time*

$$\tau_N \equiv \frac{1}{\ln p_0} = \frac{1}{\ln\left(p_A^q + p_B^q\right)} \tag{25}$$

Its q-dependence is shown in Fig. 5. Furthermore, Eqs. (22) and (25)

parametrically provide τ_R as a function of τ_N, q being the parameter. We have exhibited this dependence in Fig. 6. This is a very interesting figure. Indeed, macroscopically observable quantities (τ_N and τ_R) are intimately related, the parameters of the relationship being genetic quantities (ρ_B and γ) and initial conditions (p_B).

3 GENERALIZED MODEL

We have until now considered genetic characters A and B respectively associated with sedentary and nomadic tendencies. Let us now extend this situation by associating to A a nomadic tendency towards the *negative* x axis, whereas B still refers to a nomadic tendency towards the *positive* x axis. This is an interesting possibility since it is precisely what occurs with the fascinating "north-seeking" and "south-seeking" magnetotactic bacteries (see [6,7] and references therein). To cover this possibility we generalize Fig. 2 into Fig. 7. Accordingly, the law proposed in Eq. (1) can be generalized into

$$\rho(\nu) = \begin{cases} \rho_A \left(\dfrac{\nu_0 - \nu}{\nu_0} \right)^{\gamma_A} & \text{if} \quad \nu \leq \nu_0 \\[4mm] \rho_B \left(\dfrac{\nu - \nu_0}{1 - \nu_0} \right)^{\gamma_B} & \text{if} \quad \nu \geq \nu_0 \end{cases} \tag{26}$$

The model discussed in Section 2 is recovered here as the $\nu_0 = 0$ particular case. In this extended version we have five genetic parameters

$(\rho_A, \rho_B, \gamma_A, \gamma_B, \nu_0)$ instead of the previous two (ρ_B, γ). In particular, ν_0 could be independent or dependent from $(\rho_A, \rho_B, \gamma_A, \gamma_B)$. To illustrate the possibility of dependency, let us consider the case of arbitrary (ρ_A, ρ_B) but $\gamma_A = \gamma_B \equiv \gamma$ (in fact, this particular situation might be more than an academic possibility since it seems biologically reasonable that the γ's have a degree of universality higher than the ρ's in analogy with what occurs in standard Critical Phenomena). We could have the following law:

$$\rho(\nu) = \left| \rho_B^{1/\gamma} \nu - \rho_A^{1/\gamma}(1 - \nu) \right|^\gamma \qquad (27)$$

This law is more general than Eq. (1) and less general than Eq. (26). Indeed, it precisely satisfies Eq. (26) with $\gamma_A = \gamma_B \equiv \gamma$ and

$$\nu_0 = \frac{\rho_A^{1/\gamma}}{\rho_A^{1/\gamma} + \rho_B^{1/\gamma}} \qquad (28)$$

We see that ν_0 increases from 0 to 1 while (ρ_A/ρ_B) increases from 0 to infinity. In particular, Eq. (27) (with Eq. (28)) recovers Eq. (1) in the $\rho_A/\rho_B \to 0$ limit. Also, the case $\rho_A = \rho_B$ yields $\nu_0 = 1/2$ and

$$\rho(\nu) = \rho_B |2\nu - 1|^\gamma \qquad (29)$$

which could be an interesting proposal for species such as the above

mentioned magnetotatic bacteries (indeed, it has been found [6,7] that, near the geomagnetic Equator line, about half of them are "north seeking" and half are "south-seeking").

The time evolution of the genetical (hence geographical) spreadings associated with Eq. (26) still is qualitatively well represented by Fig. 3 just by assuming that the $x = 0$ position is no more that of the (time-invariant) extreme left of the figure, but rather would conveniently be chosen as precisely the point which, at $t = 0$, separates the A from the B subpopulations. Let us be more explicit about this point. Eqs. (11) and (21) remain as they stand for the present general case, $\rho(<\nu^{(t)}>)$ being now calculated through Eq. (26). Therefore we have to consider now three cases, namely $p_B^q/p_0 > \nu_0$ (Section 2 belongs to this category since $\nu_0 = 0$), $p_B^q/p_0 < \nu_0$, and $p_B^q/p_0 = \nu_0$. If $p_B^q/p_0 > \nu_0$, the population spreads, in average, along the *positive* x axis (i.e., the bulk of the stationary, increasing or decreasing population travels, as time goes on, further and further away to the *right* of the point separating, at $t = 0$, the A and B subpopulations). If $p_B^q/p_0 < \nu_0$, the population spreads, in average, along the *negative* x axis. Finally, if $p_B^q/p_0 = \nu_0$, then $\rho\left(<\nu^{(t)}>\right) = \rho(\nu_0) = 0$ and consequently the bulk of the population behaves in a *sedentary* manner, basically remaining at the same place (confined in the initial $(r_A + r_B)$ region and shrinking, as time goes on, onto the point separating, at $t = 0$, the A and B subpopulations). The associated phase diagram is depicted in Fig. 8 which eloquently exhibits the relevance of the initial conditions (i.e., p_B).

As a final and further generalization we can easily take into account a trivial spatial expansion (or contraction) due to demographic pressure. Let us first discuss the case for which $\rho(\nu) = 0$ for all values of ν. Even in this case, the populational growth or decrease (controlled by the parameter q) could result in a space expansion or contraction according to whether we want to maintain or vary, along successive generations, the populational densities. This effect is independent of the genetic strips of the individuales, and can be easily taken into account by introducing, at every birth of a new generation, a spatial expansion factor p_0^α common to all distances of the model (the *demographic pressure index* α can be any real number). Let us be more precise and illustrate the situation at $t = 1 + 0$ for instance: distances r_{AA}, r_{AB}, r_{BA} and r_{BB} given by Eqs. (3) will respectively become $p_0^\alpha r_{AA}$, $p_0^\alpha r_{AB}$, $p_0^\alpha r_{BA}$ and $p_0^\alpha r_{BB}$. Analogously, at $t = 2 + 0$, the distances r_{AAA}, r_{AAB},..., and r_{BBB} (given by Eqs. (5)) will become $p_0^\alpha r_{AAA}$, $p_0^\alpha r_{AAB}$,..., and $p_0^\alpha r_{BBB}$. The populational densities $\delta_{AA} \equiv N_{AA}/r_{AA}$, $\delta_{AB} \equiv N_{AB}/r_{AB}$, $\delta_{BA} \equiv N_{BA}/r_{BA}$ and $\delta_{BB} \equiv N_{BB}/r_{BB}$ will be given, at $t = 1 + 0$, by

$$\delta_{AA} = \delta_{AB} = \frac{p_A^{q-1}}{p_0^\alpha} \delta_A \qquad (30.a)$$

$$\delta_{BA} = \delta_{BB} = \frac{p_B^{q-1}}{p_0^\alpha} \delta_B \qquad (30.b)$$

In general at time $(t + 0)$ with $t = 1,2,...,$ we will have

$$\delta_\Sigma = \begin{cases} p_0^{(1-\alpha)t}\left(p_A^{q-1}/p_0\right)\delta_A & \text{if } \Sigma \text{ starts with A,} \\[3em] p_0^{(1-\alpha)t}\left(p_B^{q-1}/p_0\right)\delta_B & \text{if } \Sigma \text{ starts with B.} \end{cases} \qquad (31)$$

If α vanishes we recover the situation basically considered in this and preceding Sections, i.e., $q = 1$, $q < 1$ and $q > 1$ respectively correspond to stationary, increasing and decreasing populational densities (we recall we are now analysing the case $\rho(\nu) = 0$, $\forall\nu$). If $\alpha = 1$, the densities remain stationary for all values of q; the same occurs, for all values of α, if $q = 1$. Summarizing, the densities are stationary, increase or decrease according to whether $p_0^{(1-\alpha)} \gtrless 1$, or equivalently to whether $(1 - \alpha)(1 - q)$ is respectively zero, positive or negative.

The above discussion becomes more complex if the ν-dependence of ρ is taken into account. However, in the particular case for which only ν's close to $\langle\nu^{(t)}\rangle$ are relevant (i.e., $t \gg 1$), the entire theory remains essentially unchanged, Eq. (19) is generalized into

$$R^{(t+0)} \sim \left[\frac{r_A}{2} + \frac{p_B^q}{p_0}\frac{r_A + r_B}{2}\right]\left\{p_0^\alpha\left[1 + \rho\left(\langle\nu^{(t)}\rangle\right)\right]\right\}^t \qquad (32)$$

and Eq. (21) is generalized into

$$\tau_R = \frac{1}{\alpha \ln p_0 + \ln[1 + \rho(\langle\nu^{(t)}\rangle)]} \qquad (33)$$

Consequently, two different contributions appear in $1/\tau_R$, one of them is intimately related to the genetic evolution of the population and is always positive, whereas the other contribution is related to demographic pressure and its sign depends on whether $p_0^\alpha \gtrless 1$ (i.e., it is positive, zero or negative if $\alpha(1 - q)$ is positive, zero or negative respectively); Fig. 6 remains as it is excepting for an additive term α/τ_N.

4 CONCLUSION

We have presented a biparental procreation model exhibiting the possibility of using geographical spreading of populations as a tool for genetical studies.

The model presents several simplifications (maybe even over-simplifications!). Among them let us mention: (i) there is no coexistence of generations, since all the individuals of one generation die simultaneously, and all the individuals of the next generation appear simultaneously; (ii) no discussion has been undertaken of the case in which procreation is possible only among individuals of *different* sex; (iii) time is discrete; (iv) the model is not Mendelian in what concerns the size of the relevant genetic strips since it is not fixed, but rather increases (without fluctuations) arithmetically along time; (v) no fluctuations are permitted for the space occupancy of different genetic strips since it follows a strictly deterministic dynamics (depicted in Fig. 3). On the other hand, the model

presents some advantages. Let us mention: (i) it is *exactly* solvable, and enables consequently a careful analysis of the connections between macroscopically observable quantities (such as τ_N and τ_R) and genetic quantities (such as ρ_B and γ) as well as initial conditions (such as p_B); (ii) it presents some plausibility for primitive populations, for which the full Mendelian-like genetic mechanism could have not yet been achieved (after all, since various real genotypes of living species are associated to strips whose length is $10^3 - 10^4$ units, place is left, at least as a relatively long transient, for a philogenetic mechanism like the one assumed herein); (iii) the overall dynamics of geographical spreading strongly reminds that of existing magnetotactic bacteries[6,7]; (iv) it appears as a possible prototype for other types of spreadings (not necessarily the geographical one, but say the spreading of sizes or weights or any other one related to long-sized genetic strips); (v) it enables, in a very simple way, to take into account demographic pressure effects.

Let us finally add that microscopic genetic justification for the (blending-like) law proposed in Eq. (1) (or Eq. (26) in its generalized version), as well as identification of specific real biological examples (either living nowadays or having lived at some primitive stage) presenting some similarity with the present theoretical model would be very welcome. Also, the mathematical formulation and solution, along the present lines, of a Mendelian-like populational model would be of great interest.

CAPTION FOR FIGURES AND TABLES

Fig. 1 - Typical examples of possible genetic strip growth for n = 2 bi-parental procreation; A and B are the possible values for binary variables. (a) The possible genotypes of the next generation are constructed by associating with each locus a value randomly chosen among the actual values of the parents *at the same locus*; (b) Among the various possible types of arithmetic growth we assume here the following one: the possible genotypes of the next generation are constructed by *adding at the right* of the genotype of one of the parents a single value randomly chosen among the values appearing at any locus of the other parent; (c) Among the various possible types of geometric growth we assume here the following one: the possible genotypes of the next generation are constructed by just *puting side by side* the genotypes of the parents (hence, if the parents have the same genotype, only one genotype is possible for their "child"; if the parents have different genotypes, only two genotypes are possible for their "child").

Fig. 2 - Migratory strength ρ as a function of ν (proportion of B's in the strip sequence): basic model.

Fig. 3 - Time evolution of the genetic strip sequences and their spatial distribution along the positive x axis for

a typical case ($r_B/r_A = 4/3$, $\gamma = 1$, $\rho(0) = 0$, $\rho(1) = \rho_B = 0.5$, $q = 1$, $\alpha = 0$ and $p_A = p_B = 0.5$); $p_0 \equiv p_A^q + p_B^q$.

Fig. 4 – q-dependence of the geographic spreading characteristic time τ_R (q = 1, q < 1 and q > 1 respectively correspond to stationary, increasing and decreasing population). For this particular example we have used $\rho_B = 0.25$, $\gamma = 1$, $\alpha = 0$, $p_B = 1/4$ (for $p_A > p_B$) and $p_B = 3/4$ (for $p_A < p_B$).

Fig. 5 – q-dependence of the populational growth characteristic time τ_N (q = 1, q < 1 and q > 1 respectively correspond to stationary increasing and decreasing population). For this particular example we have used $p_B = 1/4$ (for $p_A > p_B$) and $p_B = 3/4$ (for $p_A < p_B$).

Fig. 6 – Inverse geographical spread characteristic time as a function of the inverse populational growth characteristic time. $1/\tau_N$ zero, positive and negative respectively correspond to stationary, growing and decreasing population; $1/\tau_R$ zero and much larger than unity respectively correspond to no geographical spread and quickly spreading population. For this particular example we have used $\rho_B = 0.25$, $\gamma = 1$, $\alpha = 0$, $p_B = 1/4$ (for $p_A > p_B$) and $p_B = 3/4$ (for $p_A < p_B$).

Fig. 7 – Migratory strength ρ as a function of ν (proportion of B's in the strip sequence): generalized model.

Fig. 8 – Phase diagram in the $(\nu_0, p_B^q/p_0)$ space for $\alpha = 0$. If $\nu_0 = 0$ ($\nu_0 = 1$) the extreme left (right) position of the entire population remains *fixed for all values of* t: see Fig. 3. If

$\nu_0 = p_B^q/p_0$, the frontier separating the A-starting strip and the B-starting strip subpopulations remains *fixed for all values of t*.

Table 1 - Relevant values of τ_R as a function of q.

Table 2 - Relevant values of τ_N as a function of q.

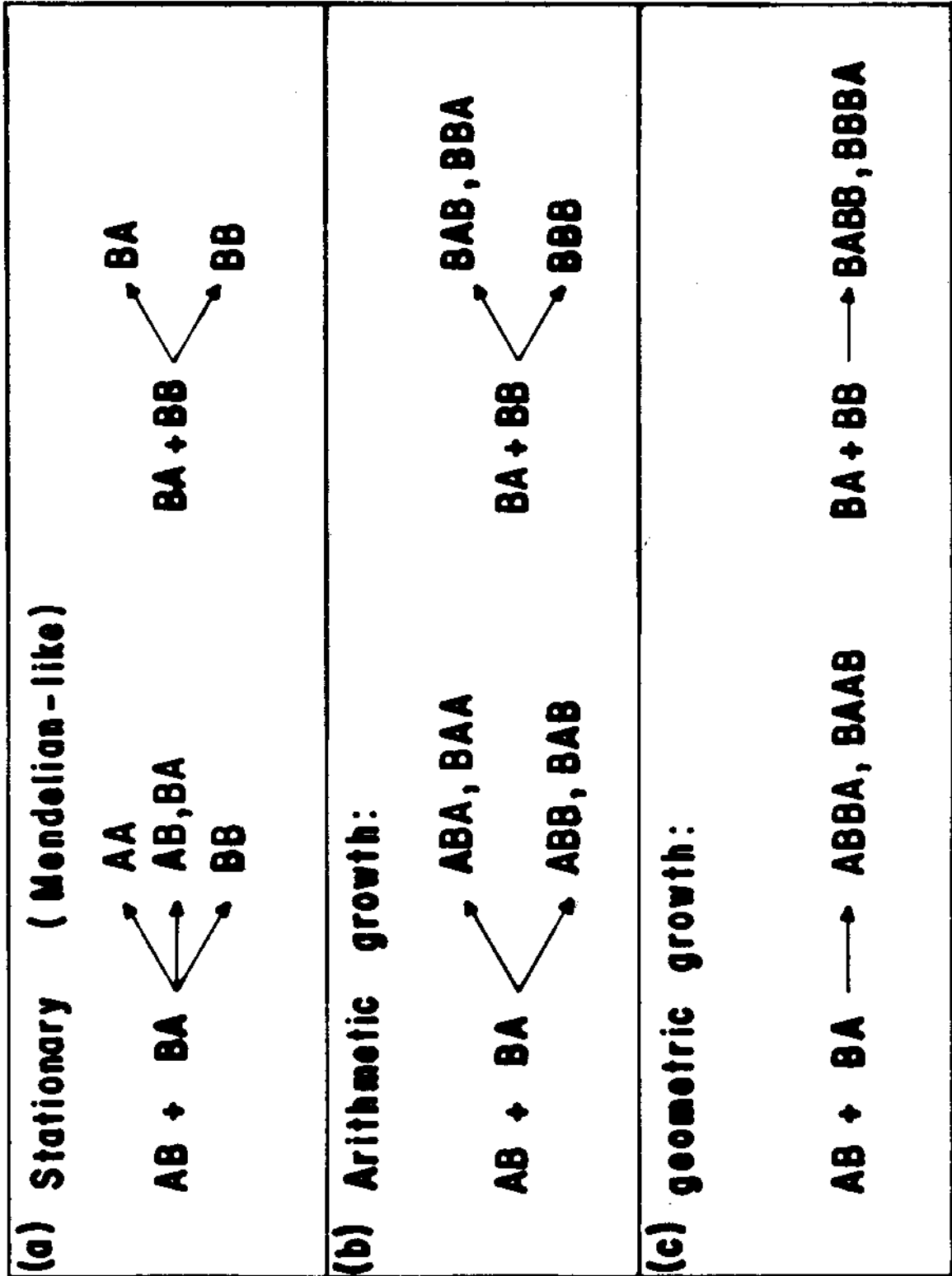Table 3 - Relevant values of $1/\tau_R$ as a function of $1/\tau_N$.

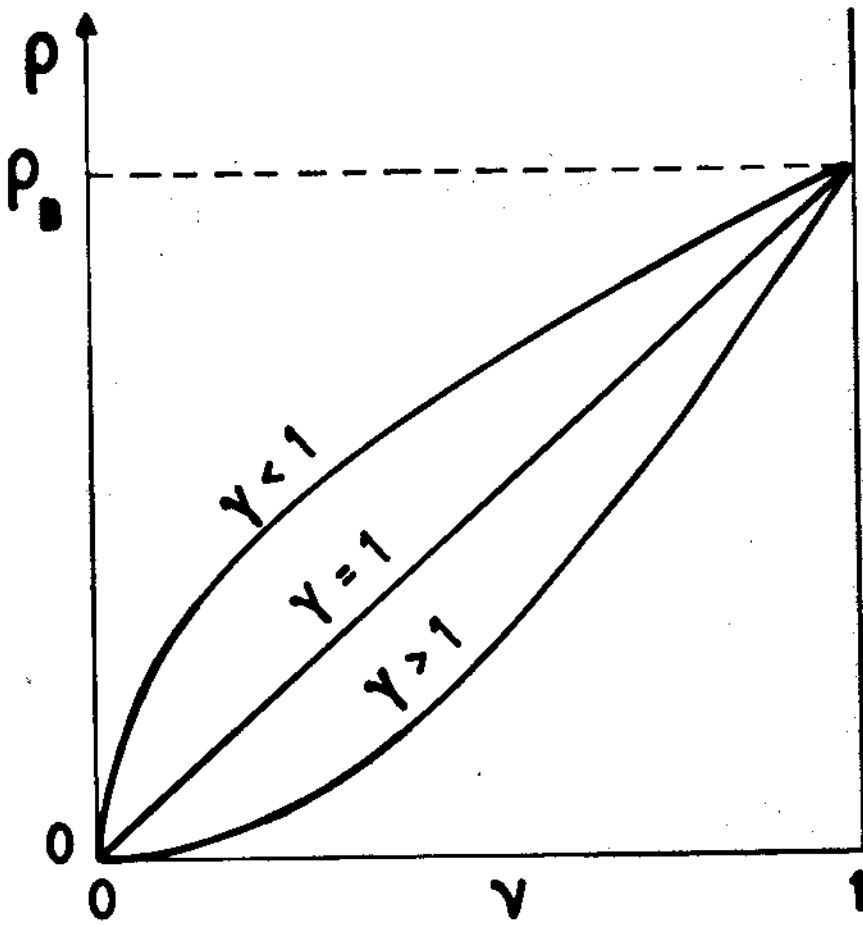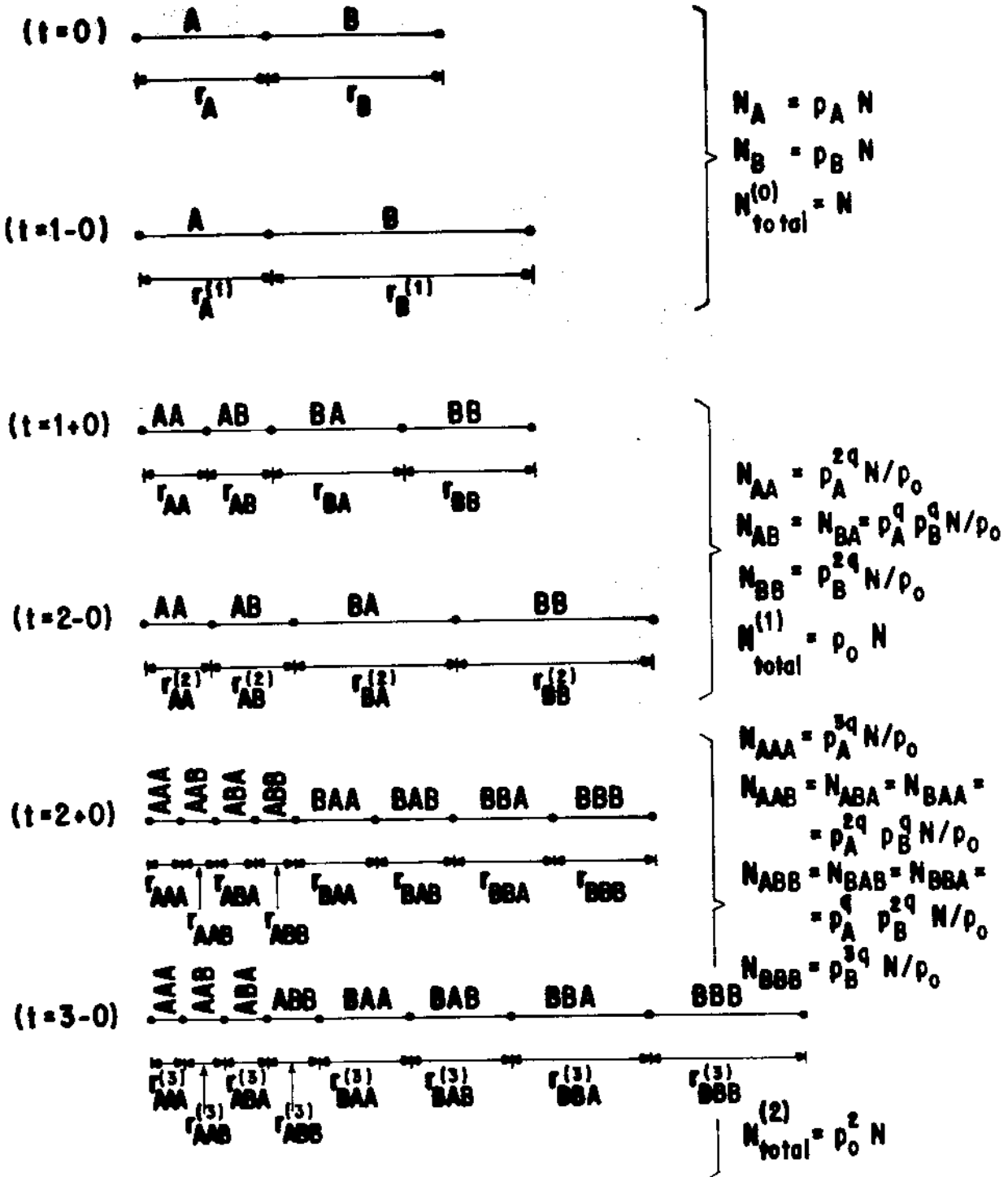**(a) Stationary (Mendelian-like)**

AB + BA

AA
AB, BA
BB

BA + BB

BA
BB

(b) Arithmetic growth:

AB + BA

ABA, BAA
ABB, BAB

BA + BB

BAB, BBA
BBB

(c) geometric growth:

AB + BA $\longrightarrow$ ABBA, BAAB

BA + BB $\longrightarrow$ BABB, BBBA

FIG.1

FIG.2

FIG.3

FIG. 4

FIG. 5

FIG. 6

FIG.7

FIG.8

		$1/\tau_R$
$p_A = p_B = \frac{1}{2}$	$\forall q$	$\ell n(1 + \rho_B/2^\gamma)$
$p_A > p_B$	$q \to -\infty$	$\ell n(1 + \rho_B)$
	$q = 0$	$\ell n(1 + \rho_B/2^\gamma)$
	$q = 1$	$\ell n(1 + \rho_B p_B^\gamma)$
	$q \to \infty$	$\sim \rho_B(p_B/p_A)^{q\gamma}$
$p_A < p_B$	$q \to -\infty$	$\sim \rho_B(p_A/p_B)^{|q|\gamma}$
	$q = 0$	$\ell n(1 + \rho_B/2^\gamma)$
	$q = 1$	$\ell n(1 + \rho_B p_A^\gamma)$
	$q \to \infty$	$\ell n(1 + \rho_B)$

TABLE 1

		$1/\tau_{_B}$
$P_A = P_B = \frac{1}{2}$	$\forall q$	$(1 - q)\ell n 2$
$P_A \neq P_B$	$q \to -\infty$	$\sim q \; \ell n \; [\inf\{p_A, p_B\}]$
	$q = 0$	$\ell n \; 2$
	$q = 1$	$\sim (q-1)(p_A \ell n \; p_A + p_B \ell n \; p_B)$
	$q \to \infty$	$\sim q \; \ell n \; [\sup\{p_A, p_B\}]$

TABLE 2

		$1/\tau_R$
$p_A = p_B = 1/2$	$\forall 1/\tau_N$	$\ell n(1 + \rho_B/2^\gamma)$
$p_A > p_B$	$\dfrac{1}{\tau_N} \to -\infty$	$\sim\rho_B \exp\left[\dfrac{\gamma \ell n\ p_B/p_A)}{\ell n\ p_A} \dfrac{1}{\tau_N}\right]$
	$\dfrac{1}{\tau_N} = 0$	$\ell n(1 + \rho_B p_B^\gamma)$
	$\dfrac{1}{\tau_N} = \ell n\ 2$	$\ell n(1 + \rho_B/2^\gamma)$
	$\dfrac{1}{\tau_N} \to \infty$	$\ell n(1 + \rho_B)$
$p_B < p_B$	$\dfrac{1}{\tau_N} \to -\infty$	$\ell n(1 + \rho_B)$
	$\dfrac{1}{\tau_N} = 0$	$\ell n(1 + \rho_B p_B^\gamma)$
	$\dfrac{1}{\tau_N} = \ell n\ 2$	$\ell n(1 + \rho_B/2^\gamma)$
	$\dfrac{1}{\tau_N} \to \infty$	$\sim\rho_B \exp\left[\dfrac{\gamma \ell n(p_B/p_A)}{\ell n\ p_A} \dfrac{1}{\tau_N}\right]$

TABLE 3

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