POPULATIONS GENETICS IN THE AMERICAN TROPICS XXVII. EXTINCTION AND RECOLONIZATION OF DEMES Vs. GENETIC VARIABILITY IN *DROSOPHILA PSEUDOOBSCURA* FROM COLOMBIA

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ABSTRACT

Drosophila pseudoobscura from the cundiboyacense Altiplano presents a populational structure consisting in small demes subjected to extinction, recolonization and migration. Whether or not population dynamics can be explained under a neutral frame is a matter of discussion in this paper. A mathematical model predicting the expected effective number of alleles under the neutral hypothesis is reviewed. The model does not present any variance calculations, and requires stochastic independence between the intrademe gene identity and the inverse of the effective population size.

INTRODUCTION

How to conserve genetic variability in various populational structures is one of the challenging problems of population genetics today. The Neutral Theory proposed by Kimura (Crow and Kimura, 1970) in its first version attempted to explain genetic variability by considering the effects of mutation and genetic drift, assuming that new mutations are always different from preexisting ones (Kimura and Crow's infinite allele model, 1964). The state variable considered to measure genetic variability is the effective number of alleles. This expected effective number of alleles for a large panmictic population is greater than for the same population subdivided in small demes, because drift is greater in small populations. Consequently, in addition to mutation and drift it became cogent to incorporate into the Neutral Theory effects of demification, extinction, recolonization, migration and bottlenecks (see, Ohta and Kimura, 1973; Maruyama and Kimura, 1980).

Bottleneck's effect on genetic variability are well characterized for a panmictic population: actually when a population goes through a small bottleneck genetic variability declines rapidly, but as it becomes large, variability increases again thanks to new mutations (Wright, 1931; Mayr, 1954; Nei, Maruyama and Chakraborty, 1975). In this paper the authors have considered the role played by a demificated populational structure subjected to extinction, recolonization and migration. Such a populational structure is similar to the populational structure of *Drosophila pseudoobscura* from the altiplano cundiboyacense; however our demes are small and therefore the expected effective number of alleles would have to have large variances which we have not calculated here.

AVERAGE HETEROZYGOSITY AND THE ISLAND MODEL

Following Maruyama and Kimura (1980) let us consider a large panmictic sexual diploid species with non-overlapping generations so that p_t be the probability that two randomly chosen homologous alleles of a locus at time t are identical by descent. Assuming the infinite allele model, let v be the mutation rate per diploid individual per generation and let N_t be the effective population size at time t. Migration is not considered until the second part. The probability of no mutation for one allele during the Δ t is $(1 - v\ \Delta t)$ and for any pair of homologous alleles is,

$$(1\text{-}v\,\Delta t)^2 = 1\text{-}2v\,\Delta t + v^2\,(\Delta t)^2 \simeq 1\text{-}2v\,\Delta t,$$

because $v^2\,(\Delta t)^2 \ll \Delta t$ as $\Delta t \to 0$.

Therefore, the probability of simultaneously sampling two alleles identical by descent is:

$$P_{t+\Delta t} = (1\text{-}2v\Delta t)\left\{\left(1 - \frac{\Delta t}{2N_t}\right) P_t + \frac{\Delta t}{2N_t}\right\} \cdots\cdots (1)$$

observe that we directly apply the Kimura and Crow's infinite allele model, because it is stated in (1) that mutation prohibits allelic identity.

From equation (1), taking $\Delta t \to 0$ – continuos time model, we get:

$$\frac{dp_t}{dt} = -\left(2v + \frac{1}{2N_t}\right) p_t + \frac{1}{2N_t} \cdots (2)$$

which is equation (6) in Maruyama and Kimura (1980). Equation (2) leads to equilibrium, which can be understood in two ways: one of which describes a closed system, without external "noise", and is defined by $\frac{dP_t}{dt} = 0$; the other one, in which external conditions randomly disturbs the equilibrium is described by

$$E\left(\frac{dP_t}{dt}\right) = 0,$$

where E is the operator "Expectatión", i.e., external "noise" leads the system to deviations around the mean value $\bar{P}$; the expected value of this small perturbation is zero.

Departing from Maruyama and Kimura (l.c., 1980) who do not explicitly work with a closed isolated system, we develop a steady state in which both sides of the equation contribute to the equilibrium,

$$\frac{dP_t}{dt} = 0 = -\left(2v + \frac{1}{2N}\right) P + \frac{1}{2N},$$

where P is the steady-state value of P_t, then

$$P = \frac{1}{1 + 4vN} \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots (3)$$

With $v = 0$ equation (3) gives $P = 1$; moreover, equation (2) turns to

$$\frac{dP_t}{dt} = -\frac{P_t}{2N_t} + \frac{1}{2N_t},$$ since $P_t \leq 1$, this gives

$$\frac{dP_t}{dt} \geq 0, \text{ with } v = 0, \cdots\cdots\cdots (4)$$

Inequality (4) and equation (3) tell us that if there is no mutation, P_t always increases to get its final value 1; with no mutation, any panmictic population tends to be identical and of course all their members will descend from a single parent. If there is mutation and the system is in steady-state, it will be defined by equation (3).

Equation (2) alone doesn't guarantee the steady-state: the absence of forces and pressures from the outside are indispensable. However, it is likely that in any case the population will show an average probability $\bar{P}$, and fluctuations around this arithmetic mean. Consequently, if we take the expectation $E\left(\frac{dP_t}{dt}\right)$ over a great number of generations in (2) we will have:

$$E\left(\frac{dP_t}{dt}\right) = 0 = E\left\{-\left(2v + \frac{1}{2N_t}\right) P_t + \frac{1}{2N_t}\right\}$$

$\frac{1}{2N_t}$ and P_t are dependent, but computer simulations show that by assuming independence the error is not misleading:

$$E\left\{-\left(2v + \frac{1}{2N_t}\right) P_t + \frac{1}{2N_t}\right\} = -E\left(2v + \frac{1}{2N_t}\right) \times$$

$$E(P_t) + E\left(\frac{1}{2N_t}\right) = -\left(2v + \frac{1}{2\tilde{N}}\right)\bar{P} + \frac{1}{2\tilde{N}} = 0$$

Where $\bar{P}$ is the arithmetic mean of P_t and $\tilde{N}$ is the harmonic mean of N_t

Hence:

$$\bar{P} = \frac{1}{1 + 4v\tilde{N}} \cdots\cdots\cdots\cdots\cdots\cdots\cdots (5)$$

which has the same form as (3).

For the island model the population must have n subpopulations which we refer to as demes. The state variables of this new system are:

P_t: genic identity coefficient within a deme at time t;

Q_t: genic identity coefficient between different demes at time t;

$\bar{H}_o$: equilibrium genic identity coefficient within the whole population;

v: mutation rate per gene per generation;

λ : extinction rate of each deme, with immediate recolonization from one of the other demes;

N_t: effective population size of each deme at time t.

$P_{t+\Delta t}$ as a function of P_t and Q_t is just the same as in the panmictic case that we already solved. Because demes' indistinguishableness, extinction and recolonization will not lead to any change in equation (1), because it is supposed that recolonization copies the parameters and present values of state variables of the colonizing deme.

The relationship between Q_t, P_t and $Q_{t+\Delta t}$ is expressed by

$$Q_{t+\Delta_t} = (1-v\Delta t)^2 \left[\left(1-\frac{2\lambda\Delta t}{n-1}\right)Q_t + \frac{2\lambda\Delta t}{n-1} \times P_t + \sigma(\Delta t)\right] \ldots\ldots\ldots\ldots (6)$$

In this equation each term has an appropiate interpretation: as before $(1-v\Delta t)^2$ is the probability of no mutation in any one of two genes under the infinite allele model.

The term $\frac{2\lambda\Delta t}{n-1} = \lambda \times \frac{1}{n-1}$ (stands for the probability of recolonization by one of the other (n-1) demes) X 2 (by symmetry) X Δt (the lineal effect of time). It follows that $\left(1-\frac{2\lambda\Delta t}{n-1}\right)$ means no extintion and no recolonization while $\sigma(\Delta t)$ stands for a neglectable term representing the effect of probability of extinction of two demes during Δt on $Q_{t+\Delta t}$. If the system is allowed to get an equilibrium it must be described by constant values of P_t and Q_t, $\bar{P}$ and $\bar{Q}$ respectively. As before we will have $(1-v\Delta t)^2 = 1-2v\,\Delta t$, from which equation (6) emerges to describe the genic identity coefficient between demes at time t+Δt. Now, taking expectations; by ignoring the higher order terms of Δt, we have,

$$\bar{Q}\left(\frac{2\lambda}{n-1}+2v\right) = \frac{2\lambda\bar{P}}{n-1} \text{ or}$$

$$\frac{\bar{Q}}{\bar{P}} = \frac{1}{1+\frac{v(n-1)}{\lambda}} \ldots\ldots\ldots\ldots (7)$$

which is equation (3) in Maruyama and Kimura (1980). Note that $\bar{Q}$, $\bar{P}$ have 3 interpretations:

(1) $\bar{Q}$ and $\bar{P}$ are steady-state equilibrium values; replacing in (6) $Q_{t+\Delta t}$ and Q_t by $\bar{Q}$ and $P_{t+\Delta t}$ by $\bar{P}$. This possibility may appear inconsistent with the meaning of λ in the present model, i.e, extinction rate, however probabilistic equations govern not the development of a single population, but the development of large samples of populations, i.e., the steady-state equilibrium values $\bar{Q}$ and $\bar{P}$ are really mean equilibrium values over a large number of populations.

(2) $\bar{Q}$ and $\bar{P}$ are arithmetic means over a large number of generations; taking expectations on equation (6) assuming that $E(Q_t+\Delta t) = E(Q_t)$, and time invariance of v and λ. This agrees with Maruyama-Kimura (1980).

(3) $\bar{Q}$ is the steady-state value of Q_t and $\bar{P}$ is the arithmetic means of P over a large number of generations; i.e., when λ is very small the whole system may reach a steady-state equilibrium in spite of fluctuations in P_t. This is so, because when $\lambda \simeq 0$, then $\frac{2\lambda\Delta t}{n-1} \approx 0$ and $\left(1-\frac{2\lambda\Delta t}{n-1}\right) \approx 1$ in (6).

Substituting the value of $\bar{P}$ according to (3) or (5) in (7), we have:

$$\bar{Q} = \frac{1}{1+\frac{(n-1)v}{\lambda}} \cdot \bar{P} = \frac{1}{(1+4\tilde{N}v)\left[1+(n-1)\frac{v}{\lambda}\right]} \ldots (8)$$

To calculate $\bar{H}_0$, the probability of getting two identical homologous alleles in random sampling from the whole population, we must note: (1) that they may be extracted from the same deme with probability $\frac{1}{n}$; and (2) from different demes with probability $(1-\frac{1}{n})$. In the first case genic identity is $\bar{P}$ and in the second it is $\bar{Q}$. So:

$$\bar{H}_0 = \left(1-\frac{1}{n}\right)\bar{Q} + \frac{1}{n}\bar{P} \ldots\ldots\ldots\ldots\ldots\ldots (9)$$

and picking up (8), and (3) or (5) we have:

$$\bar{H}_0 = \left(1-\frac{1}{n}\right)\frac{1}{(1+4\tilde{N}v)(1+(n-1)v/\lambda)} + \frac{1}{n}\,\frac{1}{1+4\tilde{N}v}$$

$$= \frac{1+(n-1/n)\,v/\lambda}{(1+4\tilde{N}v)(1+(n-1)v/\lambda)}$$

$\bar{H}_0$ is a measure of genic identity, therefore $1/\bar{H}_0$ is a measure of genic diversity. Crow and Kimura (1970) call it the effective number of alleles, and noted it by n_e.

So if we have n demes, each one with $\tilde{N}$ individuals

$$n_e = \frac{1}{\bar{H}_0} = \frac{(1+4\tilde{N}v)(1+(n-1)v/\lambda}{1+(n-1/n)v/\lambda} \ldots\ldots (10)$$

If n is large and $v/\lambda \ll 1$ then we have

$$n_e \simeq (1+4\tilde{N}v)(1+nv/\lambda) \qquad (11)$$

we can find the corresponding N_e (N_{e2} in Table 1) by equating n_e to $1+4N_ev$:

$$1+4N_ev = (1+4\tilde{N}v)(1+nv/\lambda) =$$
$$1+4\tilde{N}v+nv/\lambda + 4n\tilde{N}v^2/\lambda$$
$$N_e = \tilde{N}+n/4\lambda+n\tilde{N}v/\lambda$$

This N_e is the effective population size of a panmictic population which has the same variability (=the same n_e) as our demificated population. If all the $n\tilde{N}$ individuals are grouped in a panmictic population, we must apply equation (3) or (5) to get:

$$n_e = 1/P = 1+4n\tilde{N}v \ldots\ldots\ldots\ldots\ldots\ldots\ldots (12)$$

Where $\tilde{N}$ is the steady state value of N_t, else the harmonic mean of $N_e(t)$. To compare the situation in a panmictic population with a population grouped into isolated demes which are subject to extinction and replacement we tabulate (11) and (12) for some values, with n large and $v/\lambda \ll 1$ (see Table 1).

From our own work with *Drosophila pseudoobscura* from the altiplano cundiboyacense in Colombia (Dobzhansky an Hoenigsberg, 1974 unpublished work; Hoenigsberg, 1986, in press) we have selected as the most representatives values of mutation, migration, extinction rates and mean harmonic size ($\tilde{N}$) (Table 1).

From Table 1 we can infer that in general, if $\tilde{N}$ is relatively large and $v/\lambda \ll 1$ the effective number of alleles (n_e) for a panmictic population is about the same as for a population with about the same effective population size but grouped into isolated demes which are subject to extinction and recolonization from the other demes. Effective size appears everywhere in population genetics formulae, this implies that parameters will be different depending on connectiveness of the population. Ignoring demification of a population leads to sampling artefacts.

EFFECTS OF MIGRATION

In the preceeding analysis, we assumed that migration is allowed only for colonizational purposes. It is obviously desirable to extend that model to the presence of migration in spite of no extinction. In this case, every deme receives a fraction $m\Delta t$ of individuals from the entire population during a short time interval Δt. Using the same notations as before:

$$P_{t+\Delta t} = (1-v\,\Delta t)^2 \left\{ (1-2m\Delta t)\left[P_t + \left(\frac{1-P_t}{2N_t}\right)\Delta t\right] + 2m\Delta t Q_t \right\} + o\,(\Delta t);$$

$$P_{t+\Delta t} = (1\text{-}2v\Delta t-2m\Delta t)P_t + \left(\frac{1-P_t}{2N_t}\right)\Delta t + 2m\Delta t Q_t + o\,(\Delta t) \ldots\ldots\ldots\ldots\ldots\ldots (13)$$

Rearranging (13) and taking limit of $\Delta t \to 0$, leads to

$$\frac{dP_t}{dt} = -2(v+m)P_t + \frac{(1-P_t)}{2N_t} + 2mQ_t \qquad (14)$$

which correspond to equation (22) in Maryunama and Kimura's work (1.c., 1980).

TABLE 1

Case	V	m	λ	$\tilde{N}$	N_{e1} (n_{e2})	N_{e2}(n_{e2})	N_{e3} (n_{e3})
1	10^{-7}	0.001	0.1	35	69 (1.00)	65 (1.00)	420 (1.00)
2	10^{-4}	0.01	0.01	35	395 (1.15)	337 (1:13)	420 (1.16)
3	10^{-7}	0.001	0.01	225	795 (1.00)	525 (1.00)	2700 (1.00)
4	10^{-7}	0.001	0.05	225	339 (1.00)	290 (1.00)	2700 (1.00)
5	10^{-4}	0.1	0.01	1000	13030 (6.21)	1420 (1.56)	12000 (5.80)
6	10^{-4}	0.01	0.1	1000	2230 (1.89)	1042 (1.41)	12000 (5.80)
7	10^{-4}	0.01	0.01	35	395 (1.16)	39 (1.01)	420 (1.17)
8	10^{-4}	0.001	0.01	225	795 (1.21)	552 (1.22)	2700 (2.08)
9	10^{-7}	0.01	0.01	1000	7300 (1.00)	1300 (1.00)	12000 (1.00)
10	10^{-7}	0.001	0.001	1000	8500 (1.00)	4001 (1.00)	12000 (1.00)

Effective size (N_e) under three different populational situations. N_{e1} stands for effective size in separated but communicated populations, N_{e2} stands for effective size in totally isolated populations, N_{e3} stands for effective size in a panmictic population. Total extinction and inmediate recolonization according to the island model is assumed (see thetext). Mutation, migration and extinction rates (v, m and λ respectively), number of demes (=n), and harmonic means of population sizes (N, in Sewall Wright, 1931) were used following *Drosophila pseudoobscura's* parameters from the cundiboyacense altiplano of Colombia. In parenthesis the mean number of alleles in demes with migration (= n_{e1}) without migrations (n_{e2}) and in a population without demes (n_{e3}). The mean number of alleles are calculated from $n_{ei}=1+4N_{ei}v$.

Now for the study of the dynamics of Q_t we first consider the situation of no mutation:

(1) No extinction, no migration:

$$\left(1-\frac{2\lambda\Delta t}{n-1}\right)(1-2m\Delta t)Q_t$$

(2) Extinction, no migtation $\frac{2\lambda\Delta t}{n-1}(1-2m\Delta t)P_t$

considering that colonizing demes export their P_t

(3) No extinction, migration: $\left(1-\frac{2\lambda\Delta t}{n-1}\right)(2m\Delta t\, H_t)$

(4) Extintion and migration:

$$\sigma(\Delta t)=(2m\Delta t)\frac{2\lambda\Delta t}{n-1}H_t$$

Taking into account of mutation as before, we have,

$$Q_{t+\Delta t}=(1-v\Delta t)^2\left[\left(1-\frac{2\lambda\Delta t}{n-1}\right)(1-2m\Delta t)Q_t+\right.$$
$$(1\text{-}2m\Delta t)\left(\frac{2\lambda\Delta t}{n-1}p_t\right)+$$
$$\left.\left(1-\frac{2\lambda\Delta t}{n-1}\right)2m\Delta tH_t+\sigma(\Delta t)\right]$$

and the continuous time version becomes;

$$\frac{dQ_t}{dt}=-2\left(v+\frac{\lambda}{n-1}+m\right)Q_t+\left(\frac{2\lambda}{n-1}p_t\right)+2m\,H_t$$

Recalling that $H_t=\frac{p_t}{n}+\left(1-\frac{1}{n}\right)Q_t=\frac{p_t}{n}+\left(\frac{n-1}{n}\right)Q_t$ we have

$$\frac{dQ_t}{dt}=-2(v+\lambda+m)Q_t+2(\lambda+\hat{n})\left[\frac{1}{n}p_t+\frac{n-1}{n}Q_t\right]$$

.... (15)

which is equation (23) in Maruyama and Kimura (1980) work.

From equation (14) and (15) we have the equilibrium equations of P and Q as:

$$\left[-2(v+m)-\frac{1}{2\tilde{N}}\right]\bar{P}+2m\bar{Q}=-\frac{1}{2\tilde{N}}\quad\ldots.\ (16)\text{ and}$$

$$\left[-2(v+\lambda+m)+\frac{2(\lambda+m)(n-1)}{n}\right]\bar{Q}+$$

$$2\frac{(\lambda+m)}{n}\bar{P}=0\quad\ldots\ldots\ldots\ldots\ldots\ (17)$$

The equilibrium value of $\bar{P}$ is:

$$\bar{P}=\frac{1}{1+4v\tilde{N}+\dfrac{4m\tilde{N}nv}{nv+\lambda+m}}\quad\ldots\ldots\ (18)$$

and

$$\frac{\bar{Q}}{\bar{P}}=\frac{1}{1+vn/(\lambda+m)}\quad\ldots\ldots\ldots\ldots\ldots\ldots\ (19)$$

The effective size N_e, for this entire population can be defined such

that $1+4N_ev=\frac{n}{\bar{P}+(n-1)\bar{Q}}$ and then it becomes,

$$Ne=1/4v\left[\frac{n/\bar{p}}{1+(n-1)\bar{Q}/\bar{P}}-1\right]$$

Substituting $\bar{P}$ from equation (18) and $\bar{Q}/\bar{P}$ in (19) leads to

$$Ne=1/4\,\frac{n+4\tilde{N}nv+4\tilde{N}\lambda+4\tilde{N}m+4n\tilde{N}m-1}{v+\lambda+m}$$

or,

$$Ne=1/4\,\frac{n+4\tilde{N}nv+4\tilde{N}(\lambda+m)+4n\tilde{N}m}{v+\lambda+m}\quad\ldots..(20)$$

for $n \gg 1$. Furthermore if $v \ll \lambda$, (20) becomes,

$$Ne=\tilde{N}+\frac{n}{4(\lambda+m+v)}+\frac{n\tilde{N})(v+m)}{(\lambda+m+v)}\quad\ldots\ldots..(21)$$

On the other hand, if $m \gg \lambda, v$

$$Ne=(n+1)N+\frac{n}{4m}>nN$$

this last inequality shows that by keeping $m \gg \lambda, v$ and letting $m \rightarrow 0$, the effective size of a population can be increased as much as desired.

DISCUSSION

Maruyama and Kimura (1980) analyzed how genetic variability and effective population size can be affected by frequent extinctions and recolonizations of demes. Since we have accumulated data about the frequent colonizing attempts of local subpopulations of *Drosophila pseudoobscura* from seventeen different localities in the altiplano cundiboyacense of Colombia, we have found curselves with an appropiate mathematical model (Wright's island model) with which effective population sizes can be calculated. The state variables of the formulated populational system include genic identity coefficient within each deme at time t ($=P_t$); genic identy coefficient between demes at time t ($=Q_t$); equilibrium genic identity coefficient within the whole population ($= H_0$); mutation ($=$ v) and extinction (λ) rates per diploid generation in each deme, as long as immediate recolonization from one of the demes take place; and finally, effective population size ($=$ Ne) of any of the demes at time t.

Drosophila pseudoobscura from the cundiboyacense altiplano presents a populational structure amenable to Maruyama and Kimura's recolonization model. When Dobzhansky and Hoenigsberg initiated the study of colonizing attempts of *Drosophila pseudoobscura* in 1970 it was evident that the attempts were frequent and that rates of local extinctions varied according to the place. In some places (Aguas Calientes, Tenjo, Santillana and Potosi) colonizing attempts of new areas within the experimental reticulate (16 kms^2) were totally abscent. In those places the initial colonizers (see Hoenigsberg, 1986 in press) simply disappeared from view after their first attempt in 1971. In other localities (Recreo, Torobarroso, Cajicá, Chía, Sochagota, Tota, Lanceros, etc. in l.c. Hoenigsberg, 1986 in press) several attempts at colonizations in various areas and within the same area of the local reticulate were made. These frequent attempts of recolonization were similar to the theoretical pattern suggested by Maruyama and Kimura (l.c., 1980). Our studies revealed overall migration rate (=m) of 0.01 and extinction rates around 0.05. Nevertheless, since a few isolated experimental trials gave $m = 0.0009$ in Sochagota and Lanceros and $m = 0.003$ in Tota, Table 1 presents a realistic range for migration and extinction rates that include reasonable approximations of what was found in nature.

From Table 1 it is clear that if $\tilde{N}$ (harmonic mean) is relatively large ($\sim$ 1000) and if $v/\lambda \ll 1$, the effective number of alleles (n_e) in a panmictic population is about the same as in a divided but communicated (by migration) population with about the same effective population size whose isolated demes are subject to extinction and recolonization from other demes (case 5 Table 1). Populations with relatively small harmonic means (35 or 225 frequent in Torobarroso, Aguas Calientes, Sochagota, etc.) have little genic variability throughout (cases 1, 2, 3, 4) although they may have substantial differences in mean effective sizes. Panmictic populations with smal harmonic sizes always have larger effective sizes than subdivided populations with/without migrations. Our experiences with *Drosophila pseudoobscura* from Colombia force us to consider much smaller but realistic subpopulations (see Hoenigsberg, 1986 in press) with frequent bottlenecks. It must not surprise that with appropriate adjustment of parameters ($v, m, \lambda, \tilde{N}$) the effective size of a population could be enlarged as desired! When extinction and mutation rates are too low compared with migration rate, and this last one is also low, genetic drift drives each deme to homozygosity, but in different demes the kind of homozygosity will be different with a relevant probability, because migration is low. So immigrants will enreach genetic variability at all demes without attempting agains the predominant allele.

When mutation rate is small relative to extinction and migration rates, the effective population size ($=$ Ne) becomes independent of the mutation rate. Therefore, this extinction /recolonization neutral model can be applied to get a rough idea about how effective population size behaves when lethal mutations are considered. Moreover, as long as N is small, n_e ($=$ the effective number of alleles) is 1 if neutral mutation rate ($= v = 10^{-7}$) is present.

For a panmictic population the finite allele model gives an effective allele size smaller than the one given by the infinite allele model of Kimura and Crow (1964). Therefore, we expect that the island extinction/recolonization model furnished with the finite allele model must give an effective allele size smaller than the one give by the Maruyama and Kimura model here considered, i.e., furnished with the infinite allele model. From Table 1, for small populations both allele models are expected to be equivalent.

ACKNOWLEDGMENTS

We are grateful to Professors M. Kimura and M. Nei for comments and corrections. M. Kimura extended his courtesy by sending us this important contributions to Mathematical population genetics theory. This work was profitted by Grant No. 1204-05-41-84 of COLCIENCIAS.

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