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A population genetic study on the transition from Jomon people to Yayoi people

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In the study on the origin of Japanese, one of main unsolved problems is the transition from the Jomon people to the Yayoi people. The main difficulty in solving this problem has been the lack of suitable skeletal materials belonging to the time between the two periods, i.e. the final Jomon and the early Yayoi Periods. Therefore, we know few details of the transition period. It is important to know who carried out a drastic change of the Yayoi culture during this transitional period, i.e. the native Jomon people or the immigrant people. By introducing population genetic models, we show that a view that the immigrant people had a significant genetic contribution to the origin of Japanese is compatible with results from anthropological and archeological studies. This result implies that the immigrant people were mainly responsible for the drastic cultural change during the transitional period.

INTRODUCTION

In the study on the origin of the Japanese, various morphological and genetic researches have demonstrated that the people who migrated from the Asian Continent between the end of the Jomon Period and the Yayoi Period (see Fig. 1) had a significant influence on the formation of the Japanese and the Japanese culture (Kanaseki, 1976; Omoto, 1978; Brace and Nagai, 1982; Mizoguchi, 1988; Dodo and Ishida, 1990; Nakahashi, 1993a). The human skeletal remains excavated from Northern Kyushu and Yamaguchi region located closest to the Korean Peninsula, recently referred to as “the Yayoi colonists”, have played an important role in this controversial topic. They possessed a differential suite of physical characteristics in comparison with those of the Jomon people (see Fig. 2) and also, they show clear physical resemblances to the people of ancient China and Korea (Kim *et al.*, 1993; Han and Matsushita, 1997; Nakahashi and Li, 2002). According to these researches, it would be reasonable to support the so-called “Hybridization theory” of Kanaseki (1976) who suggested that the

immigrant people played a significant role in the formation of the Japanese.

Several important questions, however, remain to be solved concerning the transition from the Jomon to the Yayoi people, especially during the early stages of immigration into Northern Kyushu. Human remains from the early stage of the Yayoi Period or the final stage of the Jomon Period are totally lacking and most of the Yayoi skeletons unearthed from this region so far are from the middle Yayoi Period. Therefore, we know few details about the transitional period. For example, who were the first wet rice agriculturalists in Japan, or which group of people is responsible for the “Yayoi revolution” (the drastic cultural changes in the Yayoi Period), the native Jomon people or a new immigrant group?

Although some archaeologists have insisted that the native people in Northern Kyushu introduced the new culture of the Asian Continent such as wet rice cultivation and reformed their society by themselves, we showed that their hypothesis does not agree with the results of the morphological analysis of the Yayoi skeletons in Northern Kyushu (Nakahashi and Iizuka, 1998). Using paleodemographical and population genetic analysis, we also proposed the interpretations that the immigrant people are mainly responsible for the transition from the

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Fig. 1. The Jomon Period and the Yayoi Period.

Fig. 2. Jomon skull (Yamaga site, late Jomon Period, male, left) and Yayoi skull (Kanenokura site, middle Yayoi Period, right) in Fukuoka prefecture.

Jomon to Yayoi Period.

Since the model used in our previous study (Nakahashi and Iizuka, 1998) may be too simple, we will reconsider the problem by introducing more general models. The first point of the generalization is the treatment of hybrid individuals. In our previous study, we assumed that the phenotype of hybrid individuals who are the children of a Jomon individual and an immigrant individual is the same as that of the immigrant individual. In other words, hybrid individuals are assumed to belong to the immigrant group when each individual is classified to either the immigrant type or the Jomon type using discriminant function analysis, since the discriminant coefficients of the Yayoi skeletons, which were supposed to contain the hybrid people and the Jomon skeletons. It is not clear, however, whether all of the hybrid individuals can

be classified as the immigrant people. In this paper, we introduce a ratio p in which the phenotype of hybrid individuals is the same as that of the immigrant people (the ratio $1-p$ of the phenotype of hybrid individuals is the same as that of the Jomon people). Then we will investigate the effect of the ratio p on the results.

The second point of the generalization is the growth rate of the Jomon individuals in a population formed by the immigrant people. In our previous study (Nakahashi and Iizuka, 1998), it is assumed that all the individuals in this population have the same growth rate. The motivation of this assumption is that all the individuals in this population are subject to the same environmental and social conditions such as rich and steady food supply. The growth rate of the Jomon people in this hybrid population, however, may be smaller than that of the immigrant people. The reason of this possibility is

as follows. It is known that infectious diseases introduced by the immigrant people may give damage to the native people who have no immunity for these diseases (Kaplan, 1988). It is also known that the native people may be discriminated socially because of cultural differences between the native people and the immigrant people. We will investigate the effect of the difference of growth rates between the immigrant people and the Jomon people in the hybrid population.

THE MODEL

Morphological characters may be polygenic traits. For simplicity, however, we assume that a major gene is responsible for the morphological difference between the Yayoi and the Jomon phenotypes. We consider a locus with two alleles A_1 and A_2 . An individual who is an immigrant from the Asian Continent has genotype A_1A_1 and that who is a direct descendant of Jomon people has genotype A_2A_2 . Three genotypes A_1A_1 , A_2A_2 and A_1A_2 are called the immigrant-type, the Jomon-type and the hybrid-type, respectively.

We consider two populations. The first population was formed recently by the immigrant people with or without addition of some fraction of the Jomon-type people. The second population has existed for a long time through the Jomon Period and all individuals in this population are the Jomon-type. To simplify mathematical analysis, we assume that there is no migration between the first and the second populations after the formation of the first population and mating is random in the first population.

The numbers of the immigrant-type, the hybrid-type and the Jomon-type individuals at generation n in the first population are denoted by $N_{11}(n)$, $N_{12}(n)$ and $N_{22}(n)$, respectively. The total number of individuals in the first population at generation n is denoted by $N_1(n)$. Let

$$y_{ij}(n) = \frac{N_{ij}(n)}{N_1(n)} \quad (1)$$

and

$$X(n) = y_{11}(n) + \frac{y_{12}(n)}{2} \quad (2)$$

be the relative frequency of A_iA_j and the gene frequency of A_1 at generation n in the first population. Let $n = 0$ be the first time when random mating ratios

$$\begin{cases} y_{11}(n) = X(n)^2 \\ y_{12}(n) = 2X(n)\{1 - X(n)\} \\ y_{22}(n) = \{1 - X(n)\}^2 \end{cases} \quad (3)$$

are attained. Then we have

$$X(n+1) = \frac{W_{11}y_{11}(n) + \frac{1}{2}W_{12}y_{12}(n)}{\bar{W}(n)}, \quad (4)$$

where W_{ij} is the fitness of A_iA_j in the first population and

$$\bar{W}(n) = W_{11}y_{11}(n) + W_{12}y_{12}(n) + W_{22}y_{22}(n) \quad (5)$$

is the mean fitness of the first population at generation n . Note that

$$N_1(n) = N_1(0) \prod_{k=0}^{n-1} \bar{W}(k) \quad (6)$$

holds.

Let $N_2(n)$ be the number of individuals at generation n in the second population. Then we have

$$N_2(n) = w^n N_2(0), \quad (7)$$

where w is the fitness of A_2A_2 in the second population. We denote the total number of individuals in both populations at generation n by $N(n)$, and call it the total population.

The phenotypes of A_1A_1 and A_2A_2 are referred to as the Yayoi-phenotype and the Jomon-phenotype, respectively. As we stated in Introduction, we assume that the ratio p of phenotype of A_1A_2 is the same as that of A_1A_1 and the ratio $1-p$ of phenotype of A_1A_2 is the same as that of A_2A_2 ($p \geq 0.5$). Let

$$Y(n) = \frac{N_{11}(n) + pN_{12}(n)}{N(n)} \quad (8)$$

be the relative frequency of the Yayoi-phenotype at generation n in the total population. Note that $Y(n)$ is a morphologically observable quantity, though $X(n)$ is not observable.

We introduce two quantities α and β at the initial stage of the formation of the first population. Let

$$\alpha = \frac{N_1(0)}{N(0)} \quad (9)$$

be the relative size of the first population at generation 0. Note that

$$\alpha \geq Y(0) \quad (10)$$

holds by definition. On the other hand, we denote the relative frequency of the Jomon-phenotype at generation 0 in the first population by

$$\beta = \frac{(1-p)N_{12}(0) + N_{22}(0)}{N_1(0)}. \quad (11)$$

Note that

$$\beta = 1 - \frac{Y(0)}{\alpha} \quad (12)$$

holds. Then we have

$$\beta = (2p-1)X(0)^2 - 2pX(0) + 1 \quad (13)$$

and

$$X(0) = \frac{1-\beta}{p + \sqrt{p^2 - (2p-1)(1-\beta)}} \quad (14)$$

(See Appendix 1).

We remark on the relation between the fitness and the growth rate of population per year since the latter is an observable quantity. Let g be the generation time and define R_{ij} and r by

$$W_{ij} = (1 + R_{ij})^g \quad (15)$$

and

$$w = (1 + r)^g, \quad (16)$$

respectively. Then r is the growth rate of the second population per year and R_{ij} is that of the first population when all the members are A_iA_j . We call R_{ij} the growth rate of A_iA_j in the first population. From now on, we use a time unit

$$t = gn \quad (17)$$

and denote $Y(0)$, $Y(n)$, $X(0)$ and $X(n)$ by Y_0 , Y_t , X_0 and X_t , respectively. In other words, we measure time by year instead of generation. Let

$$\Delta_s Y_t = Y_{t+s} - Y_t \quad (18)$$

be the increment of frequency of the Yayoi-phenotype in s years from time t in the total population.

Estimation of the value of Y_t for some t (about 200 ~ 300 years after $t = 0$ and we denote this time t by τ) and the value of the growth rate in the first population are given by paleo-anthropological studies on the number of graves of the Yayoi people (Nakahashi, 1993b). We are interested in the following two problems.

- 1) By assuming the values of τ , r , Y_0 and Y_τ , we will obtain the values of R_{ij} that guarantee the increase of frequency of the Yayoi-phenotype $\Delta_\tau Y_0$ in τ years from $t = 0$. Then we will see whether these values are consistent with those obtained by anthropological studies.
- 2) By assuming the values of τ , r , R_{ij} , Y_0 and Y_τ , we will obtain the values of α and β .

We consider the following two selection schemes which are referred to as the model I and the model II, respectively.

Model I: The case where fitness is determined by the environmental state We consider the case where fitness is determined by the environmental state. In other words, A_1A_1 , A_1A_2 and A_2A_2 have the same fitness in the first population, that is

$$R = R_{11} = R_{12} = R_{22} \quad (19)$$

since all the members are subject to the same environmental and social conditions such as rich and steady food supply in the first population regardless of their genotypes. On the other hand, the food supply of the second population is not steady and it may be poor since this population has a culture of hunter-gatherer. Then we can assume that

$$R > r \quad (20)$$

since the first population has higher culture such as agriculture than that of the second population. In this case, A_1 and A_2 are selectively neutral (Kimura, 1968, 1983) in the first population and it is easy to show that

$$Y_t = \frac{Y_0}{\alpha + (1-\alpha)D^t}, \quad (21)$$

where we put

$$D = \frac{1+r}{1+R}. \quad (22)$$

By solving (21) for α , we have

$$\alpha = \frac{\frac{Y_0}{Y_t} - D^t}{1 - D^t}. \quad (23)$$

By (12) and (23), α and β are increasing functions of Y_0 and R . On the other hand, they are decreasing functions of Y_t and r . By solving (21) for R we have

$$R = (1+r) \left(\frac{\frac{1-\alpha}{Y_0} - \alpha}{\frac{Y_0}{Y_t} - \alpha} \right)^{1/t} - 1. \quad (24)$$

By (12) and (24), R is an increasing function of Y_t , r , α and β . On the other hand, it is a decreasing function of Y_0 . Note that

$$Y_0 \leq \alpha < \frac{Y_0}{Y_t} \quad (25)$$

must be satisfied by (10) and (24). The inequality (25) is equivalent to

$$0 \leq \beta < 1 - Y_t. \quad (26)$$

We can expect the inequality (26) under the model I since the frequency of the Jomon-phenotype at time t in the total population ($1-Y_t$) is larger than that at time t in the first population which is the same as β by the assumption of the selective neutrality of A_1 and A_2 in the first population. Note also that

$$R \geq (1+r) \left(\frac{\frac{1}{Y_0} - 1}{\frac{1}{Y_t} - 1} \right)^{1/t} - 1 \quad (27)$$

must be satisfied since $\alpha \geq Y_0$ (see (23)).

Model II: The case where fitness is determined by the environmental and genetic states We consider the case where fitness is determined by the environmental and genetic states. Infectious diseases might be introduced with the immigrant people into the first population. The immigrant people may have immunity to these diseases though the Jomon-type people may not have the immunity. In such a case, the fitness of A_2A_2 in the first population is smaller than that of A_1A_1 and that of A_1A_2 is between these values. The fitness of A_2A_2 in the first population may not be smaller than that of A_2A_2 in the second population by the same reason as in the model I. In this situation, we can put

$$R_{11} = R, R_{22} = qr. \quad (28)$$

Note that $1 \leq q < R/r$ since $r \leq R_{22} < R_{11}$. Note that the case of $q = 1$ ($R_{22} = r$) is that fitness is determined by genetic state only and the case of $q = R/r$ is nothing but the model I. For R_{12} , we consider the case of no-dominance in the sense that

$$W_{12} = \sqrt{W_{11} W_{22}} \quad (29)$$

Hence, we have

$$X_t = \frac{X_0}{X_0 + (1 - X_0)C^t}, \quad (30)$$

where we put

$$C = \sqrt{\frac{1+qr}{1+R}}. \quad (31)$$

(see Appendix 2). Then X_0 is a solution to the quadratic equation

$$F(X_0) = 0 \quad (32)$$

with $0 < X_0 < 1$, where

$$F(x) = \left\{ (1 - C^t)^2 Y_t - 1 + 2pC^t + (1 - 2p)D^t \frac{Y_t}{Y_0} \right\} x^2 - 2 \left\{ pC^t - C^t(1 - C^t)Y_t - pD^t \frac{Y_t}{Y_0} \right\} x + (C^{2t} - D^t)Y_t \quad (33)$$

(see Appendix 2). By substituting X_0 to (13), we can determine β as a function of t, Y_0, Y_t, R, r, p and q . Note that α and β are not expressed by simple formulas such as (23) and they depend in complicated manners on Y_0, Y_t, r and R .

By

$$D = \frac{(1+r)C^2}{1+qr}, \quad (34)$$

(15), (16) and (59) in Appendix, C is given by

$$C = \lambda^{1/t}, \quad (35)$$

where λ is a solution to the quadratic equation

$$\left\{ (1 - X_0)^2 + \left(\frac{1+r}{1+qr} \right) \left[\frac{X_0(1-2p)X_0 + 2p}{Y_0} - 1 \right] \right\} Y_t \lambda^2 - 2X_0(1 - X_0)(p - Y_t)\lambda - X_0^2(1 - Y_t) = 0 \quad (36)$$

with $0 < \lambda \leq 1$. By (31), we have

$$R = \frac{1+qr}{\lambda^{2/t}} - 1. \quad (37)$$

Note that λ can be expressed as a function of t, Y_0, Y_t, α, p and q by (14) and (35). Note that R is not expressed by a simple formula such as (24) and it depends in a complicated manner on Y_0, Y_t, r, α and β .

RESULTS AND DISCUSSION

We assign the value of parameters as follows. We put the generation time being $g = 20$. Since the available data Y_t is about 200 ~ 300 years after the formation of the first population judging from the results of archaeological survey, we put $\tau = 200$ and $\tau = 300$. The value of Y_t is $Y_t = 0.8$ and $Y_t = 0.9$ based on the discriminant functional analysis of the human skeletons belonging to the middle Yayoi Period. Some archeologists consider that the ratio of the Yayoi-phenotype in the early stage of the Yayoi Period is between 0.3 and 0.4 by the ratio of potteries of Jomon type and that of the continental type (Yane, 1993). We put, however, $Y_0 = 0.001, 0.01$ and 0.1 . Note that the smaller the value of Y_0 is, the more difficult it becomes to attain fixed value of Y_t (the larger the value of R is necessary). So these values are not in favor of the increase of the Yayoi-phenotype. Nakahashi (1993b) reported by using changes in the number of graves that the growth rate per year of Yayoi populations at the middle stage of the Yayoi Period in Northern Kyushu is more than 0.01. On the other hand, Ando (1995) pointed out that the growth rate of Yayoi populations in Kanto area of Japan can be as large as 0.03 or 0.04. Here we put $R = 0.005, 0.01, 0.02$ and 0.03 for the growth rate per year for A_1A_1 in the first population. For the growth rate of the second population, we put $r = 0.001$ and 0.002 , judging from the analysis of the growth rate of the Jomon people by Koyama (1979).

First, we consider the values of R that guarantee the increase in the frequencies of Yayoi-phenotype $\Delta_t Y_0$ during τ years. Results based on the model I are presented in Table 1. Note that here R does not depend on p (see (25)). Note also that the inequality (26) must be satisfied for the model I. By this inequality, $\beta < 0.2$ and $\beta < 0.1$ are necessary for $Y_t = 0.8$ and $Y_t = 0.9$, respectively. For this reason, we put $\beta = 0, 0.09$ and 0.19 . In Table 1, * means that this condition is not satisfied. We use * as the same meaning in Table 3. Note that the case of $\beta = 0$ is that all of the members of the first population are the

Table 1. The growth rate R of the first population per year for the model I. The cases when the values of τ , r , Y_0 and Y_τ are not consistent with the value of β are denoted by*.

τ	r	Y_0	Y_τ	R		
				$\beta = 0$	$\beta = 0.09$	$\beta = 0.19$
200	0.001	0.001	0.8	0.043	0.046	0.058
200	0.001	0.001	0.9	0.048	0.059	*
200	0.001	0.01	0.8	0.031	0.034	0.046
200	0.001	0.01	0.9	0.036	0.047	*
200	0.001	0.1	0.8	0.019	0.022	0.033
200	0.001	0.1	0.9	0.023	0.035	*
200	0.003	0.001	0.8	0.045	0.048	0.060
200	0.003	0.001	0.9	0.050	0.061	*
200	0.003	0.01	0.8	0.033	0.036	0.048
200	0.003	0.01	0.9	0.038	0.049	*
200	0.003	0.1	0.8	0.021	0.024	0.035
200	0.003	0.1	0.9	0.025	0.037	*
300	0.001	0.001	0.8	0.029	0.031	0.039
300	0.001	0.001	0.9	0.032	0.039	*
300	0.001	0.01	0.8	0.021	0.023	0.031
300	0.001	0.01	0.9	0.024	0.031	*
300	0.001	0.1	0.8	0.013	0.015	0.022
300	0.001	0.1	0.9	0.016	0.023	*
300	0.003	0.001	0.8	0.031	0.033	0.041
300	0.003	0.001	0.9	0.034	0.042	*
300	0.003	0.01	0.8	0.023	0.025	0.033
300	0.003	0.01	0.9	0.026	0.034	*
300	0.003	0.1	0.8	0.015	0.017	0.024
300	0.003	0.1	0.9	0.018	0.025	*
400	0.001	0.01	0.8	0.016	0.017	0.023
400	0.001	0.1	0.8	0.010	0.011	0.017

immigrant-type A_1A_1 . We can see that R is an increasing function of β . The reason of this phenomenon is as follows. The smaller the value of β is, the smaller the frequency of A_2 at time $t = 0$ in the first population is. When the value of the latter quantity is small, a small value of R guarantees the increase ΔY_0 . For example, if $\tau = 300$, $r = 0.001$, $Y_\tau = 0.8$ and $Y_0 = 0.01$, then $R = 0.021$, 0.023 and 0.031 for $\beta = 0$, 0.09 and 0.19 , respectively. Results when $\beta = 0$ are the same as those we obtained for the corresponding continuous time model in our previous study (Nakahashi and Iizuka, 1998). Results of new excavations show that the origin of wet rice cultivation may go back to the late or the middle Jomon Period (Shitara, 2002). Then τ may be larger than 300. As a reference for such a case, we added two extra results for $\tau = 400$ in Table 1.

The corresponding results from the model II are presented in Table 2 and Table 3 for $q = 1$ and 10 . Note that when $q = 1$ the fitness of the Jomon-type in the first pop-

ulation is the same as that of the second population. In other words, the fitness is determined by genetic state and does not depend on the environmental condition. When $q = 10$ the growth rate of the Jomon-type in the first population is ten times greater than that in the second population. We presented the corresponding value of the model I ($q = R/r$) for comparison. Note that here R depends on p (see (35)). Table 2 shows the dependence of p on R . The effect of p on R is small and R is an increasing function of p since the smaller the value of p is, the smaller the frequency of A_2 at time $t = 0$ in the first population is. The dependence of q on R is also small. The dependence of β on R is given in Table 3. Again, as expected the effect of β on R is small and R is an increasing function of β .

The cases with $R \geq 0.03$ in Table 1 – 3 may be unrealistic by judging from the results for the growth rates at various places in the world (Ammerman and Cavalli-Sforza, 1984). For some of the cases, however, we have

Table 2. The growth rate R of the first population per year for the model II as a function of p .

τ	r	Y_0	Y_τ	β	p	R		
						$q = 1$	$q = 10$	model I
200	0.003	0.001	0.9	0.09	1	0.053	0.053	0.061
200	0.003	0.001	0.9	0.09	0.9	0.052	0.052	0.061
200	0.003	0.001	0.9	0.09	0.7	0.051	0.051	0.061
200	0.003	0.001	0.9	0.09	0.5	0.050	0.051	0.061
200	0.001	0.01	0.8	0.09	1	0.034	0.034	0.034
200	0.001	0.01	0.8	0.09	0.9	0.034	0.033	0.034
200	0.001	0.01	0.8	0.09	0.7	0.032	0.033	0.034
200	0.001	0.01	0.8	0.09	0.5	0.032	0.032	0.034
200	0.001	0.1	0.8	0.09	1	0.022	0.021	0.022
200	0.001	0.1	0.8	0.09	0.9	0.021	0.021	0.022
200	0.001	0.1	0.8	0.09	0.7	0.020	0.020	0.022
200	0.001	0.1	0.8	0.09	0.5	0.020	0.020	0.022
300	0.001	0.01	0.8	0.09	1	0.023	0.023	0.023
300	0.001	0.01	0.8	0.09	0.9	0.023	0.023	0.023
300	0.001	0.01	0.8	0.09	0.7	0.022	0.022	0.023
300	0.001	0.01	0.8	0.09	0.5	0.022	0.022	0.023
300	0.001	0.1	0.8	0.09	1	0.015	0.014	0.015
300	0.001	0.1	0.8	0.09	0.9	0.014	0.014	0.015
300	0.001	0.1	0.8	0.09	0.7	0.014	0.014	0.015
300	0.001	0.1	0.8	0.09	0.5	0.013	0.014	0.015

Table 3. The growth rate R of the first population per year for the model II as a function of β . The case when the values of τ , r , Y_0 and Y_τ are not consistent with the value of β is denoted by*.

τ	r	Y_0	Y_τ	β	p	R		
						$q = 1$	$q = 10$	model I
200	0.003	0.001	0.9	0	1	0.050	0.050	0.050
200	0.003	0.001	0.9	0.09	1	0.053	0.053	0.061
200	0.003	0.001	0.9	0.19	1	0.055	0.054	*
200	0.001	0.01	0.8	0	1	0.031	0.031	0.031
200	0.001	0.01	0.8	0.09	1	0.034	0.034	0.034
200	0.001	0.01	0.8	0.19	1	0.036	0.036	0.046
200	0.001	0.1	0.8	0	1	0.019	0.019	0.019
200	0.001	0.1	0.8	0.09	1	0.022	0.021	0.022
200	0.001	0.1	0.8	0.19	1	0.023	0.023	0.033
300	0.001	0.01	0.8	0	1	0.021	0.021	0.021
300	0.001	0.01	0.8	0.09	1	0.023	0.023	0.023
300	0.001	0.01	0.8	0.19	1	0.024	0.024	0.031
300	0.001	0.1	0.8	0	1	0.013	0.013	0.013
300	0.001	0.1	0.8	0.09	1	0.015	0.014	0.015
300	0.001	0.1	0.8	0.19	1	0.016	0.015	0.022

$0.01 < R < 0.03$. This range of R is consistent with paleodemographical studies (Hassan, 1973, 1981; Hamond, 1981; Kirch, 1984; Renfrew, 1984; Nakahashi, 1993b). As a conclusion, the change $\Delta_\tau Y_0$ ($200 \leq \tau \leq 300$) can be

guaranteed by realistic values of R even if we use various values of p with $0.5 \leq p \leq 1$.

Next, we consider the values of α and β when $(\tau, r, R, Y_0, Y_\tau, p, q)$ are given. For the model I, α and β can be

obtained by (23) and (12), respectively. Note that these values do not depend on p . The results are presented in Table 4. Note also that (27) must be satisfied in this case. The cases other than those presented in Table 4 do not satisfy (27). In other words, we can not put arbitrary values of τ , r , R , Y_0 , Y_τ , p and q to obtain α and β . The values of α are not significantly different from the values

of Y_0 . Note that α must not be larger than $Y_0/0.8$ (resp. $Y_0/0.9$) when $Y_\tau = 0.8$ (resp. $Y_\tau = 0.9$). On the other hand, the values of β range from 0.040 to 0.199. The ratio of the Jomon-phenotype at $t = 0$ in the first population, however, is not so large (less than 0.2). This is consistent with our previous study (Nakahashi and Iizuka, 1998).

Table 4. The values of α , β and θ for the model I.

τ	r	R	Y_0	Y_τ	α	β	θ			
							$p = 1$	$p = 0.9$	$p = 0.7$	$p = 0.5$
200	0.001	0.02	0.1	0.8	0.104	0.040	0.399	0.262	0.128	0.080
200	0.001	0.03	0.1	0.8	0.122	0.181	0.851	0.734	0.515	0.362
200	0.001	0.03	0.1	0.9	0.108	0.075	0.549	0.413	0.233	0.151
200	0.003	0.03	0.1	0.8	0.121	0.171	0.828	0.709	0.491	0.343
200	0.003	0.03	0.1	0.9	0.107	0.063	0.501	0.364	0.197	0.126
300	0.001	0.02	0.1	0.8	0.122	0.180	0.847	0.730	0.511	0.359
300	0.001	0.02	0.1	0.9	0.108	0.074	0.543	0.406	0.228	0.147
300	0.001	0.03	0.001	0.8	0.001	0.057	0.476	0.338	0.178	0.113
300	0.001	0.03	0.01	0.8	0.012	0.188	0.867	0.751	0.532	0.376
300	0.001	0.03	0.01	0.9	0.011	0.085	0.581	0.446	0.259	0.169
300	0.001	0.03	0.1	0.8	0.125	0.199	0.892	0.778	0.559	0.398
300	0.001	0.03	0.1	0.9	0.111	0.099	0.628	0.495	0.299	0.197
300	0.003	0.02	0.1	0.8	0.119	0.162	0.805	0.684	0.467	0.324
300	0.003	0.02	0.1	0.9	0.105	0.051	0.450	0.312	0.160	0.101
300	0.003	0.03	0.01	0.8	0.012	0.178	0.843	0.725	0.506	0.355
300	0.003	0.03	0.01	0.9	0.011	0.071	0.534	0.398	0.222	0.143
300	0.003	0.03	0.1	0.8	0.125	0.198	0.890	0.776	0.557	0.396
300	0.003	0.03	0.1	0.9	0.111	0.098	0.625	0.492	0.296	0.195
400	0.001	0.02	0.01	0.8	0.012	0.164	0.811	0.690	0.473	0.328
400	0.001	0.02	0.1	0.8	0.125	0.197	0.888	0.773	0.554	0.394

Table 5. The values of α , β and θ as functions of q for the model II.

τ	r	R	Y_0	Y_τ	p	q	α	β	θ
200	0.001	0.02	0.1	0.8	1	1	0.101	0.011	0.245
200	0.001	0.02	0.1	0.8	1	5	0.101	0.013	0.260
200	0.001	0.02	0.1	0.8	1	10	0.102	0.019	0.299
200	0.001	0.02	0.1	0.8	1	20	0.104	0.040	0.399
200	0.003	0.03	0.1	0.9	1	1	0.129	0.228	0.965
200	0.003	0.03	0.1	0.9	1	5	0.127	0.211	0.929
200	0.003	0.03	0.1	0.9	1	10	0.107	0.063	0.501
300	0.001	0.03	0.001	0.8	1	1	0.001	0.019	0.338
300	0.001	0.03	0.001	0.8	1	5	0.001	0.020	0.333
300	0.001	0.03	0.001	0.8	1	10	0.001	0.021	0.332
300	0.001	0.03	0.001	0.8	1	30	0.001	0.057	0.476
300	0.003	0.02	0.1	0.9	1	1	0.114	0.122	0.734
300	0.003	0.02	0.1	0.9	1	5	0.111	0.101	0.647
300	0.003	0.02	0.1	0.9	1	6.67	0.105	0.051	0.450

For the model II, β can be obtained by (13) and (32). The value of α can be obtained by (12). Note that α and β depend on p for the model II. Table 5 represents α and β as functions of q with $p = 1$ for the model II. The dependence of q on α is very small compared with that on β . Table 6 shows α and β as functions of p for the model II. The dependence of p on α is very small compared with that on β . As we can see in Table 6, the dependence of r, R, p and q on β is very complicated and it is difficult to find which parameters are deeply related to β . The value of β for the model II is larger than that for the model I if we fix the values of τ, r, R, Y_0 and Y_τ (see Tables 4, 5 and 6). In other words, the value of β that attains a fixed value of $\Delta_\tau Y_0$ is larger for the model II than that

for the model I. The reason of this is that A_2 is selected against in the first population for the model II.

So far, we have assumed implicitly that the frequencies of A_1A_1, A_1A_2 and A_2A_2 are the same for male and female in the first population. The sex ratio of the immigrant people, however, might be biased to male as we can see in the history of immigration in the world and they might have incorporated some Jomon-type women to form the first population. In such a case, the corresponding frequencies become the same for male and female after one generation and the random mating ratios (3) are attained after two generations by the assumption of random mating (Crow and Kimura, 1970). We are interested in the extent of Jomon-type women that were incorporated into

Table 6. The values of α, β and θ as functions of p for the model II.

τ	r	R	Y_0	Y_τ	p	q	α	β	θ
200	0.001	0.02	0.1	0.8	1	1	0.101	0.011	0.245
200	0.001	0.02	0.1	0.8	0.9	1	0.103	0.031	0.250
200	0.001	0.02	0.1	0.8	0.7	1	0.108	0.073	0.261
200	0.001	0.02	0.1	0.8	0.5	1	0.114	0.119	0.274
200	0.001	0.02	0.1	0.8	1	10	0.102	0.019	0.299
200	0.001	0.02	0.1	0.8	0.9	10	0.104	0.036	0.260
200	0.001	0.02	0.1	0.8	0.7	10	0.106	0.061	0.206
200	0.001	0.02	0.1	0.8	0.5	10	0.109	0.079	0.171
200	0.003	0.03	0.1	0.9	1	1	0.129	0.228	0.965
200	0.003	0.03	0.1	0.9	0.9	1	0.135	0.260	0.935
200	0.003	0.03	0.1	0.9	0.7	1	0.149	0.327	0.881
200	0.003	0.03	0.1	0.9	0.5	1	0.166	0.396	0.832
200	0.003	0.03	0.1	0.9	1	5	0.127	0.211	0.929
200	0.003	0.03	0.1	0.9	0.9	5	0.124	0.192	0.787
200	0.003	0.03	0.1	0.9	0.7	5	0.124	0.192	0.578
200	0.003	0.03	0.1	0.9	0.5	5	0.126	0.206	0.448
300	0.001	0.03	0.001	0.8	1	1	0.001	0.019	0.338
300	0.001	0.03	0.001	0.8	0.9	1	0.001	0.048	0.365
300	0.001	0.03	0.001	0.8	0.7	1	0.001	0.123	0.433
300	0.001	0.03	0.001	0.8	0.5	1	0.001	0.231	0.533
300	0.001	0.03	0.001	0.8	1	10	0.001	0.021	0.332
300	0.001	0.03	0.001	0.8	0.9	10	0.001	0.050	0.352
300	0.001	0.03	0.001	0.8	0.7	10	0.001	0.119	0.400
300	0.001	0.03	0.001	0.8	0.5	10	0.001	0.207	0.462
300	0.003	0.02	0.1	0.9	1	1	0.114	0.122	0.734
300	0.003	0.02	0.1	0.9	0.9	1	0.119	0.160	0.713
300	0.003	0.02	0.1	0.9	0.7	1	0.130	0.232	0.675
300	0.003	0.02	0.1	0.9	0.5	1	0.143	0.301	0.641
300	0.003	0.02	0.1	0.9	1	5	0.111	0.101	0.647
300	0.003	0.02	0.1	0.9	0.9	5	0.110	0.091	0.483
300	0.003	0.02	0.1	0.9	0.7	5	0.110	0.092	0.289
300	0.003	0.02	0.1	0.9	0.5	5	0.111	0.096	0.199

the first population at the time of its formation since this problem is related to the following. It is reported that most of potteries in early Yayoi populations are the Jomon-type (Mori, 1966; Hashiguchi, 1985; Tanaka, 1986; Yane, 1993) and potteries are considered to be made mainly by women. Then it is important to see whether the ratio of the Jomon-type women in the first population is consistent with results of archeological survey such as the ratio of the types of pottery. Let $y_{ij}^{(+)}$ and $y_{ij}^{(-)}$ be the relative frequency of A_iA_j at two generations before 0 ($n = -2$) in male and female of the first population, respectively. Note that

$$y_{11}^{(+)} + y_{12}^{(+)} + y_{22}^{(+)} = 1 \quad (38)$$

holds. Assuming random mating, we have

$$\begin{cases} y_{11}(-1) = y_{11}^{(+)}y_{11}^{(-)} + \frac{1}{2}y_{11}^{(+)}y_{12}^{(-)} + \frac{1}{2}y_{12}^{(+)}y_{11}^{(-)} + \frac{1}{4}y_{12}^{(+)}y_{12}^{(-)} \\ y_{22}(-1) = y_{22}^{(+)}y_{22}^{(-)} + \frac{1}{2}y_{22}^{(+)}y_{12}^{(-)} + \frac{1}{2}y_{12}^{(+)}y_{22}^{(-)} + \frac{1}{4}y_{12}^{(+)}y_{12}^{(-)} \\ y_{12}(-1) = 1 - y_{11}(-1) - y_{22}(-1) \end{cases} \quad (39)$$

and

$$X_0 = \frac{W_{11}y_{11}(-1) + \frac{1}{2}W_{12}y_{12}(-1)}{W_{11}y_{11}(-1) + W_{12}y_{12}(-1) + W_{22}y_{22}(-1)}. \quad (40)$$

In the following, we assume that

$$y_{11}^{(+)} = 1, y_{12}^{(+)} = y_{22}^{(+)} = 0 \quad (41)$$

and

$$y_{11}^{(-)} = 1 - \theta, y_{12}^{(-)} = 0, y_{22}^{(-)} = \theta. \quad (42)$$

In other words, all males are the immigrant-type, whereas females are either Jomon-type (θ) or the immigrant-type ($1 - \theta$) when the first population was formed. Then we have

$$X_0 = 1 - \frac{W_{12}\theta}{2\{W_{11}(1 - \theta) + W_{12}\theta\}} \quad (43)$$

and by solving this equation for θ , we have

$$\theta = \frac{2W_{11}(1 - X_0)}{W_{12} + 2(W_{11} - W_{12})(1 - X_0)}. \quad (44)$$

Note that for $0 \leq \theta \leq 1$, X_0 must satisfy that $\frac{1}{2} \leq X_0 \leq 1$ by this formula. In other words, we are not able to assume the initial conditions of (41) and (42) if $X_0 < \frac{1}{2}$.

For the model I, we have

$$\theta = 2 \left\{ 1 - \frac{1 - \beta}{p + \sqrt{p^2 - (2p - 1)(1 - \beta)}} \right\} \quad (45)$$

by (14), (19) and (44). The values of θ for the model I are given in Table 4. These values depend largely on p and the parameter set $(\tau, r, R, Y_0, Y_\tau)$. Note that θ depends

on p , though α and β do not. By (45), we have

$$\beta = (1 - p)\theta + \frac{2p - 1}{4}\theta^2. \quad (46)$$

The value of θ can be very large ($\theta > 0.8$ for some parameter sets), though the value of β is not so large ($\beta < 0.2$). This means that it is possible that there were many female individuals of the Jomon-type at the formation of the first population if all of male are the immigrant-type at that time. This result is consistent with archeological results.

On the other hand, we have

$$\theta = \frac{2 \left\{ 1 - \frac{1 - \beta}{p + \sqrt{p^2 - (2p - 1)(1 - \beta)}} \right\}}{C^g + 2(1 - C^g) \left\{ 1 - \frac{1 - \beta}{p + \sqrt{p^2 - (2p - 1)(1 - \beta)}} \right\}} \quad (47)$$

for the model II by substituting (14) and (29) to (44). Note that (47) reduces to (45) if $C = 1$ ($q = R/r$). The values of θ for the model II are given in Table 5 and Table 6. The value of θ can be very large ($\theta > 0.8$ for some parameter sets) as in the model I.

Finally, we consider the stationarity of Y_τ . As stated in our previous study (Nakahashi and Iizuka, 1998), the frequency of the immigrant-type is almost the same when we classify skeletons of the middle Yayoi Period into two groups by the time of its duration (the early stage and the late stage). This suggests that the frequency Y_τ may be in a stationary state approximately, though more data are necessary to conclude the stationarity of Y_τ . Here we assume, however, the stationarity of Y_τ in the sense that $\Delta_{100}Y_\tau$ is small and see the consequences of this assumption. Let

$$Y_\infty = \lim_{t \rightarrow \infty} Y_t \quad (48)$$

be the equilibrium value of Y_t . It is easy to see that $Y_\infty = 1 - \beta$ for the model I and $Y_\infty = 1$ for the model II. To obtain $Y_{\tau+100}$ and Y_∞ for the model I, we first determine the values of α and β by (23) for given $(\tau, r, R, Y_0, Y_\tau)$. Then Y_∞ is equal to $1 - \beta$ and $Y_{\tau+100}$ can be obtained using (21) by substituting $t = \tau + 100$. On the other hand, $Y_\infty = 1$ for the model II. For $Y_{\tau+100}$, we first determine the value of X_0 by using (32) for given $(\tau, r, R, Y_0, Y_\tau)$. Then $Y_{\tau+100}$ can be obtained using (59) by substituting $t = \tau + 100$.

First, we consider the model I. If Y_τ is approximately in the stationary state, the values of $\Delta_{100}Y_\tau$ and $Y_\infty - Y_\tau$ must be small and β can be approximated by

$$\beta_\tau = 1 - Y_\tau \quad (49)$$

since $\beta_\tau - \beta = Y_\infty - Y_\tau$. The values of $Y_{\tau+100}$, Y_∞ , $\Delta_{100}Y_\tau$ and $\beta_\tau - \beta$ are given in Table 7. For most of the cases in Table 7, the values of $\Delta_{100}Y_\tau$ are less than 0.04 and the values of $\beta_\tau - \beta$ are less than 0.05. This means that most of the

Table 7. The frequencies of the Yayoi-phenotype at time $\tau + 100$ and in equilibrium ($t = \infty$) for the model I when τ , r , R , Y_0 and Y_τ are given.

τ	r	R	Y_0	Y_τ	$Y_{\tau+100}$	Y_∞	$\Delta_{100}Y_\tau$	$\beta_\tau - \beta$
200	0.001	0.02	0.1	0.8	0.932	0.960	0.132	0.160
200	0.001	0.03	0.1	0.8	0.818	0.819	0.018	0.019
200	0.001	0.03	0.1	0.9	0.923	0.925	0.023	0.025
200	0.003	0.03	0.1	0.8	0.827	0.829	0.027	0.029
200	0.003	0.03	0.1	0.9	0.934	0.937	0.034	0.037
300	0.001	0.02	0.1	0.8	0.817	0.820	0.017	0.020
300	0.001	0.02	0.1	0.9	0.922	0.926	0.022	0.026
300	0.001	0.03	0.001	0.8	0.934	0.943	0.134	0.143
300	0.001	0.03	0.01	0.8	0.811	0.812	0.011	0.012
300	0.001	0.03	0.01	0.9	0.915	0.915	0.015	0.015
300	0.001	0.03	0.1	0.8	0.801	0.801	0.001	0.001
300	0.001	0.03	0.1	0.9	0.901	0.901	0.001	0.001
300	0.003	0.02	0.1	0.8	0.831	0.838	0.031	0.038
300	0.003	0.02	0.1	0.9	0.940	0.949	0.040	0.049
300	0.003	0.03	0.001	0.8	0.821	0.822	0.021	0.022
300	0.003	0.03	0.01	0.9	0.927	0.929	0.027	0.029
300	0.003	0.03	0.1	0.8	0.802	0.802	0.002	0.002
300	0.003	0.03	0.1	0.9	0.902	0.902	0.002	0.002
400	0.001	0.02	0.01	0.8	0.830	0.836	0.030	0.036
400	0.001	0.02	0.1	0.8	0.803	0.803	0.003	0.003

Table 8. The frequencies of the Yayoi-phenotype at time $\tau + 100$ and in equilibrium ($t = \infty$) for the model II as functions of q when τ , r , R , p , Y_0 and Y_τ are given.

τ	r	R	Y_0	Y_τ	p	q	$Y_{\tau+100}$	$\Delta_{100}Y_\tau$	$\Delta_\infty Y_{\tau+100}$
200	0.001	0.02	0.1	0.8	1	1	0.962	0.162	0.038
200	0.001	0.02	0.1	0.8	1	5	0.962	0.162	0.038
200	0.001	0.02	0.1	0.8	1	10	0.961	0.161	0.039
200	0.003	0.03	0.1	0.9	1	1	0.992	0.092	0.008
200	0.003	0.03	0.1	0.9	1	5	0.986	0.086	0.014
300	0.001	0.03	0.001	0.8	1	1	0.986	0.186	0.014
300	0.001	0.03	0.001	0.8	1	5	0.986	0.186	0.014
300	0.001	0.03	0.001	0.8	1	10	0.986	0.186	0.014
300	0.003	0.02	0.1	0.9	1	1	0.979	0.079	0.021
300	0.003	0.02	0.1	0.9	1	5	0.964	0.064	0.036

cases in the model I are consistent with the assumption of stationarity of Y_τ and β can be approximated by $1 - Y_\tau$.

Next, we consider the model II. If Y_τ is approximately in the stationary state, $\Delta_{100}Y_\tau$ must be small and β is close to 0 since $Y_\infty = 1$. The values of $Y_{\tau+100}$, $\Delta_{100}Y_\tau$ and $\Delta_\infty Y_{\tau+100} = Y_\infty - Y_{\tau+100}$ are given in Table 8 and Table 9. For all cases presented in these tables, the values of $\Delta_{100}Y_\tau$ are larger than 0.05 and the stationarity of Y_τ does not hold, though $Y_{\tau+100}$ is close to Y_∞ (the values of $\Delta_\infty Y_{\tau+100}$ are less

than 0.05 for all the cases in Table 8 and Table 9). In other words, $Y_{\tau+100}$ must be close to 1. Then the model II is not consistent with the stationarity of Y_τ . These results show that the model I is consistent with the assumption of stationarity but the model II is not consistent with the assumption. In other words, fitness of the Jomon-type people in the first population must be almost the same as that of the immigrant-type people in the population if the stationarity holds.

Table 9. The frequencies of the Yayoi-phenotype at time $\tau + 100$ and in equilibrium ($t = \infty$) for the model II as functions of p when τ , r , R , q , Y_0 and Y_τ are given.

τ	r	R	Y_0	Y_τ	p	q	$Y_{\tau+100}$	$\Delta_{100}Y_\tau$	$\Delta_\infty Y_{\tau+100}$
200	0.001	0.02	0.1	0.8	1	1	0.962	0.162	0.038
200	0.001	0.02	0.1	0.8	0.9	1	0.962	0.162	0.038
200	0.001	0.02	0.1	0.8	0.7	1	0.960	0.160	0.040
200	0.001	0.02	0.1	0.8	0.5	1	0.958	0.158	0.042
200	0.001	0.02	0.1	0.8	1	10	0.961	0.161	0.039
200	0.001	0.02	0.1	0.8	0.9	10	0.957	0.157	0.043
200	0.001	0.02	0.1	0.8	0.7	10	0.953	0.153	0.047
200	0.001	0.02	0.1	0.8	0.5	10	0.950	0.150	0.050
200	0.003	0.03	0.1	0.9	1	1	0.992	0.092	0.008
200	0.003	0.03	0.1	0.9	0.9	1	0.989	0.089	0.011
200	0.003	0.03	0.1	0.9	0.7	1	0.986	0.086	0.014
200	0.003	0.03	0.1	0.9	0.5	1	0.983	0.083	0.017
200	0.003	0.03	0.1	0.9	1	5	0.986	0.086	0.014
200	0.003	0.03	0.1	0.9	0.9	5	0.979	0.079	0.021
200	0.003	0.03	0.1	0.9	0.7	5	0.972	0.072	0.028
200	0.003	0.03	0.1	0.9	0.5	5	0.969	0.069	0.031
300	0.001	0.03	0.001	0.8	1	1	0.986	0.186	0.014
300	0.001	0.03	0.001	0.8	0.9	1	0.986	0.186	0.014
300	0.001	0.03	0.001	0.8	0.7	1	0.985	0.185	0.015
300	0.001	0.03	0.001	0.8	0.5	1	0.985	0.185	0.015
300	0.001	0.03	0.001	0.8	1	10	0.986	0.186	0.014
300	0.001	0.03	0.001	0.8	0.9	10	0.985	0.185	0.015
300	0.001	0.03	0.001	0.8	0.7	10	0.984	0.184	0.016
300	0.001	0.03	0.001	0.8	0.5	10	0.981	0.181	0.019
300	0.003	0.02	0.1	0.9	1	1	0.979	0.079	0.021
300	0.003	0.02	0.1	0.9	0.9	1	0.977	0.077	0.023
300	0.003	0.02	0.1	0.9	0.7	1	0.974	0.074	0.026
300	0.003	0.02	0.1	0.9	0.5	1	0.971	0.071	0.029
300	0.003	0.02	0.1	0.9	1	5	0.964	0.064	0.036
300	0.003	0.02	0.1	0.9	0.9	5	0.958	0.058	0.042
300	0.003	0.02	0.1	0.9	0.7	5	0.953	0.053	0.047
300	0.003	0.02	0.1	0.9	0.5	5	0.951	0.051	0.049

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APPENDIX

In the following, we use the original time unit of generation.

Appendix 1: The derivation of (13) and (14)

Note that

$$Y(0) = \alpha \{y_{11}(0) + py_{12}(0)\} \quad (50)$$

holds. By (3), (12) and (50), we have (13). By solving (13) for $X(0)$, we have (14), since $X(0)$ is a solution of the quadratic equation

$$G(x) = (2p - 1)x^2 - 2px + 1 - \beta = 0 \quad (51)$$

with $0 < X(0) < 1$. Note that $G(0) > 0$ and $G(1) < 0$.

Appendix 2: The derivation of (30) and (32)

By noting that

$$\bar{W}(n) = \{\sqrt{W_{11}}X(n) + \sqrt{W_{22}}[1 - X(n)]\}^2 \quad (52)$$

and

$$W_{11}y_{11}(n) + \frac{1}{2}W_{12}y_{12}(n) = \sqrt{W_{11}}X(n)\{\sqrt{W_{11}}X(n) + \sqrt{W_{22}}[1 - X(n)]\}, \quad (53)$$

we have

$$X(n+1) = \frac{\sqrt{W_{11}}X(n)}{\sqrt{W_{11}}X(n) + \sqrt{W_{22}}\{1 - X(n)\}} \quad (54)$$

by (4). By solving this difference equation, we have

$$X(n) = \frac{X(0)}{X(0) + \left(\frac{W_{22}}{W_{11}}\right)^{n/2} \{1 - X(0)\}}. \quad (55)$$

We have (30) by (15), (17), (28) and (55).

Note that

$$\bar{W}(n) = W_{11} \left\{ \frac{X(n)}{X(n+1)} \right\}^2 \quad (56)$$

by (51) and (53). Note also that

$$Y(n) = \frac{\alpha \{y_{11}(n) + py_{12}(n)\}}{\alpha + (1 - \alpha) \frac{w^n}{\prod_{k=0}^{n-1} \bar{W}(k)}} \quad (57)$$

holds for $n \geq 1$. Then we have

$$Y(n) = \frac{X(0)^2 + 2p \left\{ \sqrt{\frac{W_{22}}{W_{11}}} \right\}^n X(0) \{1 - X(0)\}}{\left\{ X(0) + \left(\sqrt{\frac{W_{22}}{W_{11}}} \right)^n [1 - X(0)] \right\}^2 + \left\{ \frac{X(0)[(1 - 2p)X(0) + 2p]}{Y(0)} - 1 \right\} \left(\frac{w}{W_{11}} \right)^n} \quad (58)$$

by (3), (12), (13), (30), (55), (56) and (57). By changing time unit from n to t , we have

$$Y_t = \frac{X_0^2 + 2pC^tX_0(1-X_0)}{\{X_0 + (1-X_0)C^t\}^2 + \left\{\frac{X_0[(1-2p)X_0 + 2p]}{Y_0} - 1\right\}D^t} \quad (59)$$