Stochastic Model for Colony Dispersal

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Abstract A mathematical model of the dispersal of colonies produced by the stochastic migration process depending on the total population of the group is considered. The expected velocity of the spatial expanding of the settlement range of colonies is analyzed, utilizing the fractal concept applied to the pattern of spatial distribution of colonies. The model is used to consider the spreading phenomenon of early farming in Europe, with the data of neolithic sites with C-14 dates.

Key Words: colony settlement, mathematical model, dispersal velocity

INTRODUCTION

The expanding of the distribution area of some animals has been theoretically studied by mathematical models. As for patterns of spatial distribution and the expanding velocity, some diffusion models have been applied to understand such phenomena (Ammerman and Cavalli-Sforza, 1984; Martin, 1973; Mosimann and Martin, 1975; Okubo, 1980; Skellam, 1951). those phenomena considered by diffusion models should have such a characteristic that the spatial distribution can be regarded as continuous in space. However, for such phenomena that the spatial distribution essentially consists of a number of spatially disconnected islands, that is colonies, the analysis by the diffusion model has to require some additional assumptions, and should be regarded as an approximate approach.

In this paper, for the expanding of settlement area consisting of a number of colonies is presented, a mathematical model of stochastic migration processes is proposed (Bartlett, 1978). In order to give the relation between the number of colonies and the settlement area occupied by them, the fractal concept is introduced. Analyzing the model, we derive the expected velocity of the expanding of settlement area. The model is applied to the data of neolithic sites with C-14 dates. which was used by Ammerman and Cavalli-Sforza (1984) in order to discuss the spreading phenomenon of early farming in Europe. The expanding velocity of the settlement area of farming colonies is estimated by our model.

COLONY PRODUCTION

Free Migration Process: A new colony is produced by a random migration process in the existing group of colonies, with a constant migration probability

independent of any other parameter (Bartlett, 1978). That is, the probability of the production of a new colony is constant, independent of any other parameters. Now, it is assumed that the colony does not become extinct once it is produced. Under these assumptions the following model can be defined:

$$\frac{d}{dt} P(k, t) = -\lambda P(k, t) + \lambda P(k - 1, t) \tag{1}$$

$$P(k, 0) = \delta_{k0},$$

where

λdt: the probability of production of new colony during $(t, t + dt)$
$P(k, t)$: the probability of k colony productions during time-period $(0, t)$.

δ_{k0} is the kronecker's delta so that the initial condition means that there is no colony production at $t = 0$. This colony production system results in the Poisson probability distribution $P(k, t)$:

$$P(k, t) = e^{-\lambda t} \frac{(\lambda t)^k}{k!}. \tag{2}$$

The expected number of colonies produced during $(0, t)$ is

$$<k>_t = \sum_{k=0}^{\infty} kP(k, t) = \lambda t, \tag{3}$$

and the expected time of the k-th colony production is

$$<t>_k = \int_0^{\infty} \tau P(k - 1, \tau)\lambda d\tau = \frac{k}{\lambda}. \tag{4}$$

Size-dependent Migration Process: The migration probability is assumed to depend on the total population of the group (Fig. 1). This means that the colony production is enhanced more and more as the total population becomes larger. Under this assumption, we consider the following model:

$$\frac{d}{dt} P(k, t) = -\mu N(t)P(k, t) + \mu N(t)P(k - 1, t) \tag{5}$$

$$P(k, 0) = \delta_{k0},$$

where

$N(t)$: the total population size of the group of colonies at time t

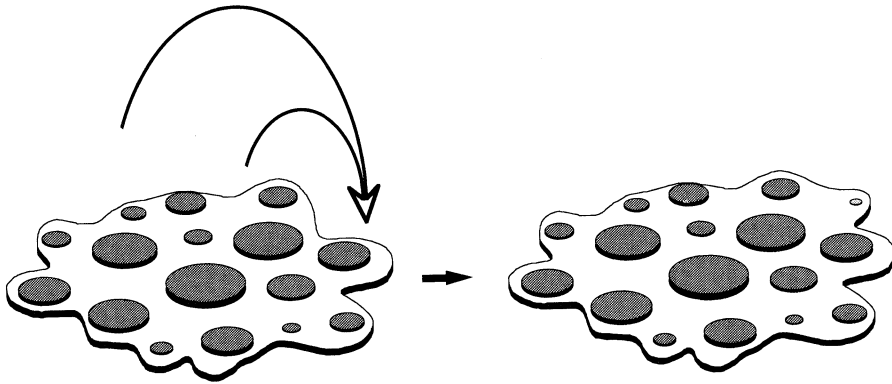$\mu N(t)dt$: the probability of production of new colony during time-period $(t, t + dt)$.

Fig. 1. Schematic description of the expanding of settlement range by the size-dependent migration process. For detail explanation, see text.

This colony production system in time t results in the Poisson probability distribution $P(k, T)$ in time T:

$$P(k, T) = e^{-\mu T} \frac{(\mu T)^k}{k!} , \tag{6}$$

where the time T is now transformed from time t as follows:

$$T = T(t) = \int_0^t N(\tau)d\tau. \tag{7}$$

Since a colony does not become extinct after its production, we find that $T \to \infty$ as $t \to \infty$. The above result in time T coincides with that for the previous case, that is, for the case of free migration process. Therefore, the expected number of colonies produced during $(0, t)$ is

$$\langle k \rangle_t = \sum_{k=0}^{\infty} kP(k, T) = \mu T = \mu \int_0^t N(\tau)d\tau, \tag{8}$$

and the expected time of the k-th colony production is

$$\langle T \rangle_k = \int_0^{\infty} \tau P(k - 1, \tau)\mu d\tau = \frac{k}{\mu}. \tag{9}$$

Then, the expected time in t can be obtained through the following relation:

$$\langle t \rangle_k = T^{-1}(\langle T \rangle_k) = T^{-1}\left(\frac{k}{\mu}\right), \tag{10}$$

where T^{-1} denotes the inverse function of $T = T(t)$.

EXPANSION OF SETTLEMENT AREA

Next, we consider the settlement area of the group of colonies. The settlement area at time t corresponds to the area that has been occupied by those existing colonies at the time. We characterize the settlement range by the minimal diameter, say R, which can include all existing colonies.

In the case when the settlement area expands in every direction with the same probability, the shape of the settlement area can be approximated by the disc, and therefore, when the spheric nature of the earth can be negligible and be approximated well by the plane, the range R approximately has the following relation with the total number of colonies M: $M \propto R^2$. However, since the expanding of the settlement area is constrained by geography, climate, cultural factors, etc., the shape is in general possibly inhomogeneous in direction. It is likely that the shape has a *fractal* nature (for the concept of 'fractal', see, for instance, Mandelbrot, 1982). To deal with such cases, we assume the generalized relation between the settlement range and the total number of colonies as follows:

$$M \propto R^d \qquad (1 \leq d \leq 2), \tag{11}$$

where the power d characterizes the spatial pattern of the settlement area occupied by colonies (Fig. 2). It is called *cluster dimension* or *mass dimension*, which is one of *fractal dimensions*. When $d \sim 2$, the spatial distribution of colonies can be approximated by a disc. When $d \sim 1$, the distribution is one dimensional, that is,

the colonies are arrayed on a curve. For example, the latter case may correspond to the case when the colonies are located along a river.

Through the relation (11), we can consider the velocity of the expanding of the settlement range. That is, the velocity V is given by

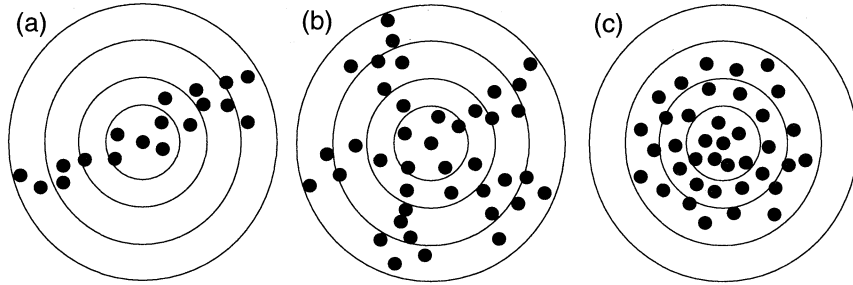$$V = \frac{dR}{dt} \propto \frac{d}{dt}(M^{1/d}) = \frac{1}{d} \cdot M^{(1-d)/d} \cdot \frac{dM}{dt}. \tag{12}$$

Fig. 2. Illustrative explanation of the relation of the fractal dimension d to the spatial pattern of colony distribution. Each black disc shows each colony. (a) $d \sim 1$; (b) $1 < d < 2$; (c) $d \sim 2$.

Since the expected total number of colonies at time t is given by $<k>_t$, the expected range of the settlement area is proportional to $<k>_t^{1/d}$. Therefore, we consider the expected velocity $\overline{V}_t$ at time t as follows:

$$\overline{V}_t \propto \frac{1}{d} \cdot <k>_t^{(1-d)/d} \cdot \frac{d<k>_t}{dt}. \tag{13}$$

For the case of the free migration process, the expected velocity is

$$\overline{V}_t \propto \frac{\lambda^{1/d}}{d} \cdot t^{(1-d)/d}, \tag{14}$$

and, for the case of the size-dependent migration process, it is

$$\overline{V}_t \propto \frac{\mu^{1/d}}{d} \cdot N(t) \cdot \left[\int_0^t N(\tau)d\tau \right]^{(1-d)/d}. \tag{15}$$

LOGISTIC GROWTH OF POPULATION

As an example of the size-dependent migration process, we deal with the case when the total population size of the group of colonies grows in the logistic manner (Fig. 3(a)):

$$
N(t) = N(0) \cdot \left[\left(1 - \frac{N(0)}{K} \right) e^{-\varepsilon t} + \frac{N(0)}{K} \right]^{-1},
\tag{16}
$$

where ε is the intrinsic growth rate of the population and K is the carrying capacity for the total population of the group. In this case, some fundamental calculations show

$$
<k>_t = \frac{\mu}{\varepsilon} \cdot K \cdot \ln \left| \frac{N(0)}{K} \cdot (e^{\varepsilon t} - 1) + 1 \right|
\tag{17}
$$

$$
<t>_k = \frac{1}{\varepsilon} \ln \left| \frac{K}{N(0)} \cdot (e^{(\varepsilon/\mu)k/K} - 1) + 1 \right|.
\tag{18}
$$

Generic feature of these expected values is shown in Fig. 3(b) and Fig. 3(c). The time interval between the nearest two colony productions is given by

$$
<t>_{k+1} - <t>_k = \frac{1}{\varepsilon} \ln \left\{ \frac{e^{\varepsilon/(\mu K)} + \dfrac{N(0)}{K} \left(1 - \dfrac{N(0)}{K} \right) \cdot e^{-(\varepsilon/\mu)k/K}}{1 + \dfrac{N(0)}{K} \left(1 - \dfrac{N(0)}{K} \right) \cdot e^{-(\varepsilon/\mu)k/K}} \right\}
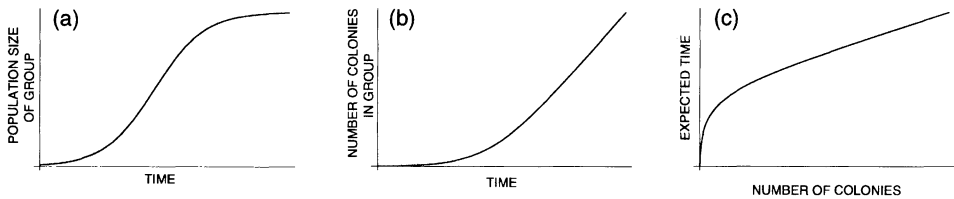\tag{19}
$$

Fig. 3. The size-dependent immigration model for the logistic growing population. (a) Typical time-development of logistic population growth; (b) Typical $<k>_t$; (c) Typical $<t>_k$.

This value tends to a constant $1/\mu K$ as $k \to \infty$, which means that the colony production is expected to occur periodically. In addition, from (17) and (18), for sufficiently large t and sufficiently large k,

$$<k>_t \sim t \tag{20}$$

$$<t>_k \sim k. \tag{21}$$

That is, these expected values increase linearly in a sufficiently grown group, which is the same as for the case of the free migration process.

In this case, the expanding way of settlement range essentially depends on the fractal dimension d (Fig. 4(a, b)). The expected velocity of expanding of settlement range is expressed as follows:

$$\overline{V}_t \propto \frac{\varepsilon}{d} \cdot \left(\frac{\mu K}{\varepsilon}\right)^{1/d} \cdot \frac{N(0)}{K} \cdot \frac{e^{\varepsilon t}}{\left\{\frac{N(0)}{K} \cdot (e^{\varepsilon t} - 1) + 1\right\}\left[\ln\left\{\frac{N(0)}{K} \cdot (e^{\varepsilon t} - 1) + 1\right\}\right]^{1-1/d}}. \tag{22}$$

For $1 < d \leq 2$, this expected velocity decreases to zero at a sufficiently large time (Fig. 4(c, d)). This means that, for a sufficiently grown group, the velocity of the expanding of settlement range is very small, while the number of colonies continuously increases; that is, the new colonies tend to be produced within the vacant areas among the pre-settled colonies. On the other hand, the time-development of the expected velocity in the earlier period depends on the initial population size of the group (Fig. 4(d)). In the case when the initial population is sufficiently large, the expected velocity monotonically decreases in time, while in the case when it is small, the expected velocity increases in the earlier period and decreases after peaking. Analytically, if the following condition is satisfied, the former case occurs, and otherwise the latter (Fig. 4(d)):

$$1 - \left(1 - \frac{1}{d}\right) \cdot e^{1/d} \leq \frac{N(0)}{K} . \tag{23}$$

This condition can be easily derived by examining the sign of the t-derivative of (22).

In the period when the population size $N(t)$ is sufficientry small, the population growth can be well-approximated by exponential growth. In this period, the same argument as above gives the approximate results on the behavior of colony dispersal as follows:

$$N(t) \approx N(0)e^{\varepsilon t} \tag{24}$$

$$<k>_t \approx \frac{\mu}{\varepsilon} \, N(0)\left(e^{\varepsilon t} - 1\right) \tag{25}$$

$$<t>_k \approx \frac{1}{\varepsilon} \, \ln\left(\frac{\varepsilon/\mu}{N(0)} \, k + 1\right) \tag{26}$$

$$<t>_{k+1} - <t>_k \approx \frac{1}{\varepsilon} \, \ln\left(\frac{N(0) + \varepsilon(k+1)/\mu}{N(0) + \varepsilon k/\mu}\right) \tag{27}$$

$$\overline{V}_t \propto \frac{\varepsilon}{d} \cdot \left(\frac{\mu N(0)}{\varepsilon}\right)^{1/d} \cdot \frac{e^{\varepsilon t}}{\left(e^{\varepsilon t} - 1\right)^{1-1/d}} . \tag{28}$$

In this case, the expected velocity increases exponentially while the number of colonies grows exponentially.
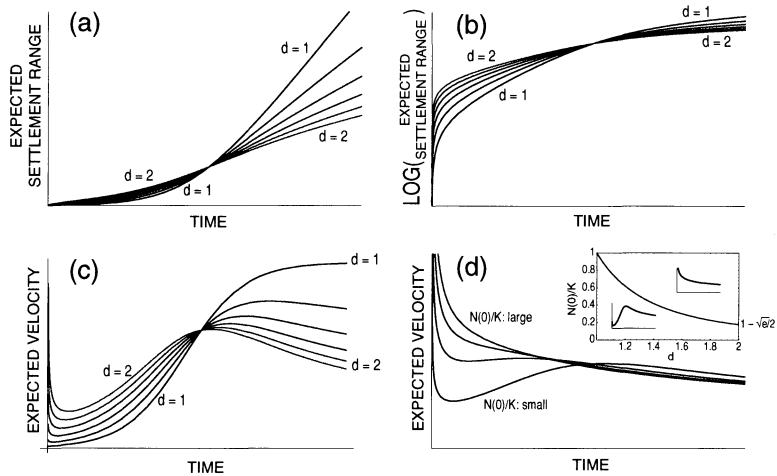

Fig. 4. In the size-dependent immigration process model for the logistic population growth, the contribution of the fractal dimension d and the initial population size $N(0)/K$ to; (a, b) the time-development of the expected settlement range R, that is, $<k>_t^{1/d}$; (c, d) the time-development of the expected velocity $\overline{V}_t$. For (c), $N(0)/K = 0.1$, and for (d), $d = 1.5$. The graph shape of the expected velocity $\overline{V}_t$ depends on d and $N(0)/K$ as shown totally in the figure attached to (d).

SPREAD OF EARLY FARMING IN EUROPE

Ammerman and Cavalli-Sforza (1984) calculated the isochron map of the spread of early farming in Europe from the data of 106 neolithic European sites with C-14 dates (9690 B.C. – 4160 B.C.). The computer-generated isochron map gives the impression that early farming might have spread in a spatially continuous manner in Europe. This is an approximation to the spatial spread through the analogy of diffusion process. However, in contrast to the spatial spread of various species of animals, insects, and plants, the spatial spread of a group of humans frequently involves the production spatially disconnected units, that is, colonies. The spatial distribution expands essentially by a series of productions of new colonies. The spread of early farming in Europe, dealt with by Ammerman and Cavalli-Sforza (1984), can be regarded as such a case.

In this section, we apply our mathematical model described above to the data and estimate the parameters of the model to try to discuss some features of the spread of early farming in Europe.

As for the way of population growth, we assume the exponential one given by (24). This is appropriate in the case when the population growth does not cause the depletion of environmental factors necessary for survival.
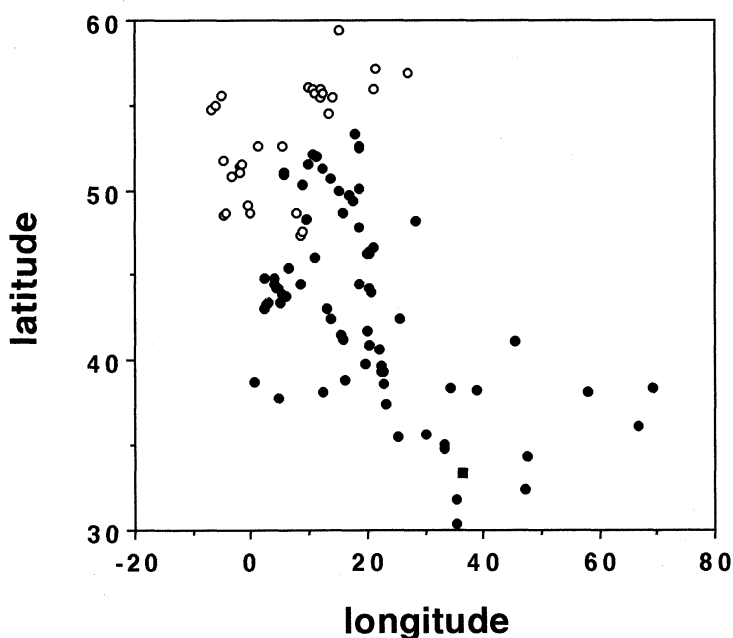

Fig. 5. 106 neolithic European sites in the geographic coordinates, used by Ammerman and Cavalli-Sforza (1984). The black square indicates the oldest site, Aswad (9690 B.C., C-14 date). Black discs are for those sites before 5800 B.C. (C-14 date), and white ones for those after 5800 B.C.

Fig. 5 shows the 106 neolithic European sites in the geographic coordinates used by Ammerman and Cavalli-Sforza (1984). Their spatial distribution seems to show inhomogeneity in direction. Beginning with the oldest site, Aswad (9690 B.C.; 33.36N, 36.30E), we count the cumulative number of colonies in order of descending C-14 date as shown in Fig. 6. Plots in the figure indicate that the continuity of the time-development of the number of colonies seems to break at around 3800 years after Aswad (i.e., around 5800 B.C.). Thus, we use only the 76 data before 5800 B.C., up to the site Reichtett (5940 B.C.; 48.6N, 7.75E).

Since Fig. 6 can be regarded as corresponding to the time-development of $<k>_t$, we try to fit $<k>_t$ given by (25) to the data. The result is overlaid in Fig. 6. The estimated parameters result in $\mu N(0)/\varepsilon = 3.572$; $\varepsilon = 8.233 \times 10^{-4}$.
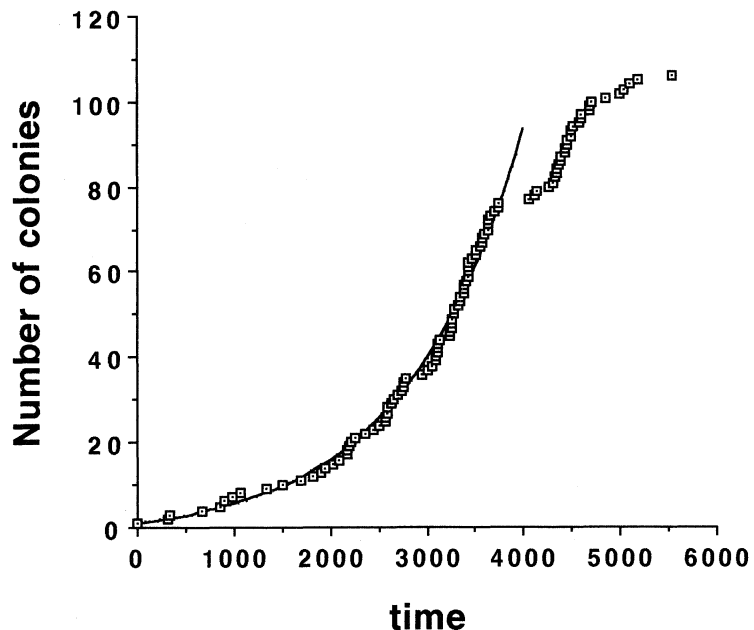

Fig. 6. Time-development of the number of neolithic sites, which is cumulated after the oldest site, Aswad (9690 B.C., C-14 date). Time axis shows the C-14 date passed after 9690 B.C. All 106 neolithic sites are plotted for the data of Ammerman and Cavalli-Sforza (1984). $<k>_t$ curve for the exponential growth in the size-dependent migration process model is overlaid, fit to 76 data of neolithic sites (•) before 5800 B.C. (C-14 date). $\mu N(0)/\varepsilon = 3.352$ and $\varepsilon = 8.233 \times 10^{-4}$ in (25).

Next, we try to estimate the fractal dimension d that characterizes the pattern of spatial distribution. From (11), the range R of the settlement area and the number M of colonies within it have the relation: $\log M = d \cdot \log R + \text{const}$. Therefore, we can estimate d from the slope of the line fit to the plots of $\log M$ against $\log R$. The diameter can be calculated from the data of the locations of neolithic sites (Fig. 7). We use the gyration-radius method to estimate the parameter d (as for the method, see, for instance, Mandelbrot, 1982). All 76 sites before 5800 B.C. are considered. The number of sites distributed within the disc centered at the oldest site, Aswad, is counted. For disc radius large enough to contain more than 10 colonies, the plot of the number of sites against the disc radius can be fitted well by a straight line with slope 1.671, as estimated by the least-square method (Fig. 8(a)). Hence, the spatial distribution of neolithic sites is estimated to have the characteristic fractal dimension $d = 1.671$. Since the diameter and the number of neolithic sites are time-dependent, it is likely that the parameter d might change in time in the period considered now. However, as Fig. 8(b) shows, the time-dependent relation between the expanded diameter and the number of colonies in log-log coordinates, the estimated $d = 1.671$ even holds well. Therefore, we deal with d as time-independent constant: $d = 1.671$.
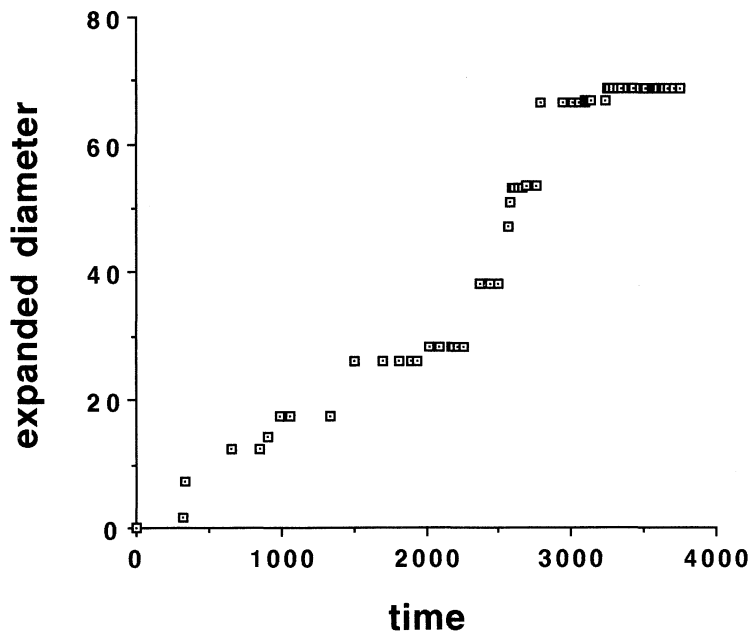

Fig. 7. Expanded diameter of the settlement range. Time axis shows the C-14 date passed after 9690 B.C.
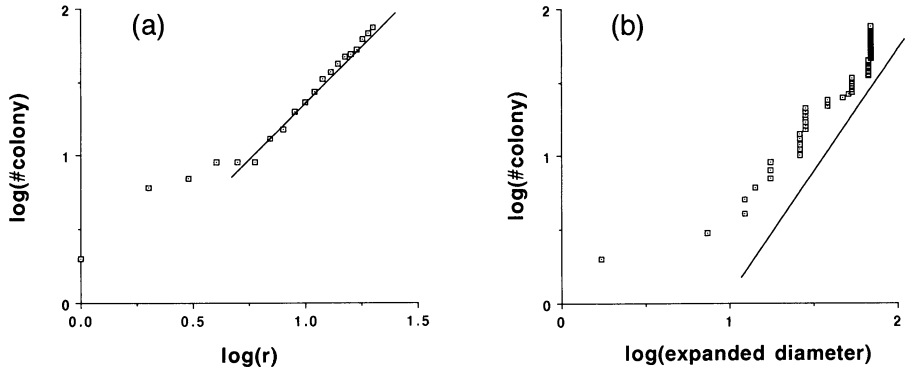
Fig. 8. (a) Number of sites within the distance r from the oldest site, Aswad, in log-log coordinates. For the distance r that contains more than 10 sites, plots fit well to the line with the slope 1.671.

(b) Relation between the expanded diameter of settlement area and the number of colonies in log-log coordinates. The overlaid line indicates the slope 1.671. The unit of measured distance is conventionally selected.

From (28) with these estimated parameters, the time-development of the expected velocity of the expanding of settlement range can be drawn, resulting in Fig. 9(a). It can be seen that the velocity is relatively small in the first century after Aswad and then increases exponentially. In Fig. 9(b), the same expected velocity is plotted against the time-development of the expected number of colonies, which follows (25). As the number of colonies becomes sufficiently large, the velocity of the expanding of the settlement area increases.
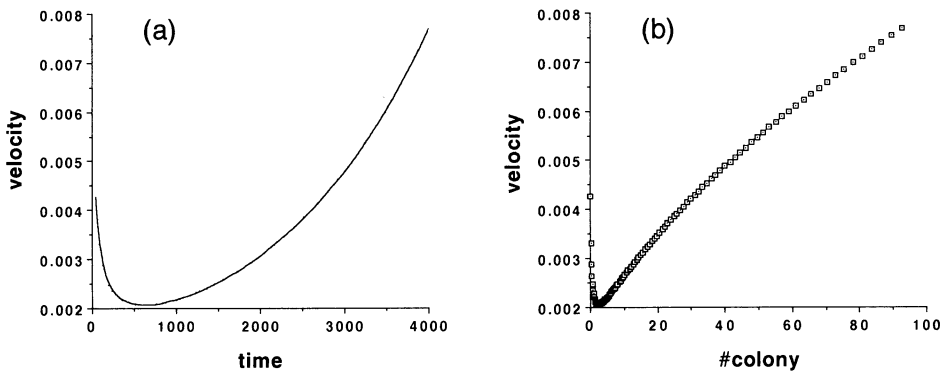

Fig. 9. Time-development of the expected velocity (28) of the expanding of the settlement area, for $\mu N(0)/\varepsilon = 3.352$; $\varepsilon = 8.233 \times 10^{-4}$; $d = 1.671$. (a) time-development of the expected velocity (28); (b) the expected velocity (28) against the expected number of colonies (25).

CONCLUSION

The mathematical model discussed in this paper is a new approach to consider the expanding of the settlement range of a number of colonies. The velocity of the range expanding is shown to increase exponentially as the number of colonies becomes large enough. This nature of the expanding velocity differs markedly from that obtaining under diffusion with a constant diffusion coefficient, which was discussed in Ammerman and Cavalli-Sforza (1984). For some diffusion systems with a constant diffusion coefficient, it has been shown that the travelling wave has a constant velocity of propagation (Britton, 1986; Murray, 1989).

Moreover, our stochastic model for the colony dispersal shows that the velocity in general decreases to zero. This result follows from the fractal nature of the spatial distribution of settled colonies. As the number of colonies grows larger and the range expanded by those colonies gets wider, the gap space among colonies becomes the more available for the settlement of a new colony. Thus, the velocity of the expanding of settlement range decreases, while the number of colonies increases. This nature of colony dispersal has not ever been pointed out with the mathematical model by the diffusion equation.

As shown by the analysis on the data of neolithic sites for the spread of early farming in Europe, our stochastic model seems useful to consider the spatial expanding of colony distribution.

In the various other cases when dispersal occurs by the production of colonies our model may be applicable, and it is expected that the analysis will give some information valuable for the discussion on the phenomena.

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