Reprinted from the

Advances and Applications in Statistics
Volume 25, Number 1, 2011, pp 31-45

ON ULTIMATE EXTINCTION PROBABILITIES AND MEAN BEHAVIOUR OF SPATIAL PATTERNS

by

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Volume 25, Number 1, 2011, Pages 31-45
Available online at http://pphmj.com/journals/adas.htm
Published by Pushpa Publishing House, Allahabad, INDIA

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Abstract

The three basic spatial patterns of organisms are clustering (overdispersion), randomness and uniformity (underdispersion). In this paper, deterministic and stochastic models are employed to describe the dynamics of the number of individuals in a habitable site called a unit. Stochastic model discriminates spatial patterns whereas deterministic model does not, however, the mean of stochastic model is equivalent to the deterministic model. The probabilities of ultimate extinction and ultimate mean number of individuals in a unit are determined using the stochastic model. The analysis demonstrated that if spatial pattern is uniform (underdispersed), ultimate extinction is certain; if spatial pattern is clustered (overdispersed), ultimate explosion is certain and if spatial pattern is random, ultimately it stabilizes.

2010 Mathematics Subject Classification: 60G99.

Keywords and phrases: dispersion, spatial pattern, deterministic model, stochastic model, ultimate extinction probability, ultimate mean.

Received September 6, 2011

1. Introduction

1.1. Dispersion

Dispersion is the description of the pattern of distribution of organisms in space (Southwood [7]) and is often referred to as *spatial distribution*. Spatial distribution is a visual description and not a probability distribution. Probability distribution models are used to quantify and classify the dispersion of organisms. They have been widely used in entomological research to describe the dispersion of insects.

In order to describe dispersion, it is assumed that organisms are confined to discrete habitable sites called *units* (*sampling units*). We further suppose that a random variable X represents the number of individuals that a unit may contain and let $m = E(X)$ and $v = \text{var}(X)$.

If the individuals are distributed randomly, then the spatial distribution is said to be *random* and the population pattern is also said to be *random*. If the individuals are distributed uniformly, then the spatial distribution is said to be *regular* and the population pattern is said to be *uniform* or *underdispersed*. If the individuals are distributed in clusters, then the spatial distribution is said to be *contagious* and the population pattern is said to be *clustered* or *overdispersed* or *aggregated* or *clumped* or *patchy*. The population pattern is often referred to as *spatial pattern*.

Random spatial pattern is described by Poisson distribution $(v = m)$, uniform spatial pattern is described by the binomial distribution $(v < m)$ and clustered spatial pattern is described by the negative binomial distribution $(v > m)$.

In particular, the negative binomial distribution with parameters k and p is defined as

$$P(X = x) = \binom{k + x - 1}{x}\left(\frac{p}{1+p}\right)^x \left(\frac{1}{1+p}\right)^k, \; x = 0, 1, 2, \ldots; \; k > 0, \; p > 0 \quad (1)$$

having mean $m = kp$ and variance $v = m(1 + p)$.

Anscombe [1] gave statistical analysis of insect counts based on the negative binomial distribution. The negative binomial parameter k is considered as a dispersion parameter. Small values of k $(k \to 0)$ are associated with overdispersion whereas large values of k $(k \to \infty)$ are associated with randomness.

Young and Young [8] reviewed measures of aggregation, namely, variance to mean ratio, index of clumping, index of mean crowding and index of patchiness with respect to Poisson and negative binomial distributions. The four measures of aggregation revealed that decreasing values of k are associated with increasing measures of aggregation (departure from randomness).

Kipchirchir [3] demonstrated analytically that the negative binomial parameter k is a measure of dispersion by analysing equicorrelation matrix in relation to coefficient of determination, partial correlation and principal components with respect to k. The analysis demonstrated that small values of k are associated with overdispersion whereas large values are associated with randomness.

For fixed $m = kp$ and reparameterizing $\beta = \frac{p}{1+p}$, then $k \to \infty$ or $p \to 0$ or $\beta \to 0$ implies a random spatial pattern while $k \to 0$ or $p \to \infty$ or $\beta \to 1$ implies a clustered (an overdispersed) spatial pattern.

1.2. Deterministic model

The deterministic model assumes that each organism reproduces and dies on a completely predictable basis at constant rate. Let n_t be the number of individuals in a unit at time t and suppose that they reproduce at rate λ and die at rate μ. The deterministic equation of a linear birth-death process is

$$\frac{dn_t}{dt} = (\lambda - \mu)n_t \tag{2}$$

with solution

$$n_t = n_0 e^{(\lambda-\mu)t} \tag{3}$$

which is the exponential growth model. If $\lambda = \mu$, $n_t = n_0$ (constant); if $\lambda > \mu$, $n_t \to \infty$ (explosion) and if $\lambda < \mu$, $n_t \to 0$ (extinction). The deterministic model does not discriminate the various spatial patterns.

Once shortage of resources (environmental resistance) preludes exponential growth, we can deduce the logistic growth by introducing the limit imposed by environmental resistance represented by K into (2). Commonly such limit is imposed by exhaustion of either food supplies or space. The deterministic logistic equation is

$$\frac{dn_t}{dt} = (\lambda - \mu)(1 - n_t/K)n_t \tag{4}$$

with solution

$$n_t = \frac{K}{1 + \gamma e^{-(\lambda-\mu)t}}, \quad \gamma = (K - n_0)/n_0. \tag{5}$$

The limit K is often referred to as the carrying capacity and $(K - n_t)/K$ is a proportionate measure of the total resources unutilised (McLeone and Andrews [4]). If environmental resistance is due to exhaustion of resources, then we can interprete $(K - n_t)/K$ as a proportionate measure of the total resources the environment cannot provide.

If $\lambda = \mu$ $(n_t = n_0)$, there is an unstable equilibrium. However, if $n_t = K$, there is a stable equilibrium around which the number of individuals in a unit fluctuates; any perturbations are nullified by opposite forces proportional to $K - n_t$ bringing the number of individuals in a unit back towards the equilibrium level. If $\lambda > \mu$, $n_t \to K$, that is, n_t will stabilize at K (explosion is avoided) whilst if $\lambda < \mu$, $n_t \to 0$ (extinction). Thus, extinction is still inevitable although it is delayed since $(\lambda - \mu)(1 - n_t/K)$ $> (\lambda - \mu)$. In particular, if $\lambda > \mu$ and $n_t < K$, then the growth of the number of individuals in a unit follows a sigmoid curve (logistic curve).

The growth of many species populations of animals, plants and microorganisms follows the sigmoid curve, but it must not be assumed that the growth of these populations is entirely represented by the logistic equation, for numerous mathematical equations can produce a sigmoid curve (McLeone and Andrews [4]).

Introducing immigration into (2) allows us to avoid extinction. Suppose immigrants arrive in a unit randomly at rate ν. The deterministic equation of a linear birth-death process with immigration is

$$\frac{dn_t}{dt} = (\lambda - \mu)n_t + \nu \tag{6}$$

with solution

$$n_t = \begin{cases} n_0 e^{(\lambda-\mu)t} + \frac{\nu}{\lambda - \mu}(e^{(\lambda-\mu)t} - 1), & \lambda \neq \mu, \\ \nu t + n_0, & \lambda = \mu \end{cases} \tag{7}$$

which changes exponentially $(\lambda > \mu)$, linearly $(\lambda = \mu)$ with time towards infinity and exponentially $(\lambda < \mu)$ with time towards $\nu/(\mu - \lambda)$.

In practice, the number of individuals in a unit may fluctuate around n_t or K or $\nu/(\mu - \lambda)$, so there is need to consider a probability distribution of number of individuals in a unit so as to capture the behaviour over all possible realizations, moreover, knowledge of the probability distribution can provide insight into the behaviour of various spatial patterns.

Provided that population numbers never become too small, then a deterministic model may enable sufficient biological understanding to be gained about the system and if at any time population numbers do become small, then a stochastic analysis is vital (Renshaw [6]). So pursuing both approaches simultaneously ensures that we do not become trapped either by deterministic simplicity or detailed stochastic analysis.

1.3. Stochastic model

Let $X(t)$ be the number of individuals in a unit at time t and let $p_n(t)$

$= P(X(t) = n),\ n = 0, 1, 2, \ldots$ be the probability distribution of $X(t)$. Then $p_n(t)$ is a function of t and $\sum_{n=0}^{\infty} p_n(t) = 1$. In particular, $p_0(t)$ is the extinction probability at time t and $\lim_{t\to\infty} p_0(t)$ is the ultimate extinction probability. The probability structure $\{p_n(t)\}_{n=0}^{\infty}$ tells us the likely range of the number of individuals in a unit at time t. It does not explicitly tell us what a particular realization of the process $\{X(t)\}$ looks like, but gives instead the distributional properties of a large ensemble of such realizations.

The mean number of individuals in a unit is $m(t) = E(X(t))$ and the ultimate mean number of individuals in a unit is $\lim_{t\to\infty} m(t)$. It is worth noting that 'mean behaviour' represented by $m(t)$, may be very different from the behaviour of individual realizations.

The differential-difference equations of a stochastic birth-death process are

$$p_0'(t) = -\lambda_0 p_0(t) + \mu_1 p_1(t), \quad n = 0,$$

$$p_n'(t) = \lambda_{n-1} p_{n-1}(t) - (\lambda_n + \mu_n) p_n(t) + \mu_{n+1} p_{n+1}(t), \quad n = 1, 2, 3, \ldots, \quad (8)$$

where λ_n and μ_n are the birth and death rates, respectively (Medhi [5]; Bhat [2]). They are so-called Kolmogorov's forward differential-difference equations for the birth-death process. If $\lambda_0 = 0$, and if the number of individuals reaches zero at any time, then it remains at zero thereafter and hence zero is an absorbing state. In the special case when $\lambda_n = n\lambda,\ n \ge 0$ and $\mu_n = n\mu,\ n \ge 1$, we have a linear birth-death process or linear growth process (Feller-Árley process) and when $\lambda_n = n\lambda,\ n \ge 0$ and $\mu_n = 0$, $n \ge 1$, we have a linear pure birth process (Yule-Furry process).

If a biological process has been developing long enough to ensure that it has stabilized, then steady-state or stable probabilities may be obtained. Their derivation assumes that both population explosion and extinction are unlikely during the observed time span.

Equations (8) represent the transient behaviour of the individuals in a unit. Setting $p'_n(t) = 0$ and letting $p_n = \lim_{t\to\infty} p_n(t)$ (assuming it exists) denote stable or steady-state probability, (8) reduces to the steady-state equations for the birth-death process. The steady-state behaviour provides us with an approximation to that of transient behaviour, for large t, that is, asymptotic behaviour.

If the initial number of individuals in a unit is n_0, that is, $X(0) = n_0$, then the initial conditions are

$$p_n(0) = \begin{cases} 1, & n = n_0, \\ 0, & n \neq n_0. \end{cases} \tag{9}$$

Let

$$g(s, t) = \sum_{n=0}^{\infty} p_n(t) s^n \tag{10}$$

be the probability generating function of the sequence $\{p_n(t)\}_{n=0}^{\infty}$. Then the extinction probability at time t, $p_0(t)$ is $g(0, t)$. The partial derivatives of $g(s, t)$ with respect to s and t are, respectively,

$$\frac{\partial g(s, t)}{\partial s} = \sum_{n=0}^{\infty} n p_n(t) s^{n-1},$$

$$\frac{\partial g(s, t)}{\partial t} = \sum_{n=0}^{\infty} p'_n(t) s^n. \tag{11}$$

2. Linear Birth-death with Immigration (Kendall) Process

This is a linear growth process with immigration (Medhi [5]; Bhat [2]). The rates of this process are $\lambda_n = n\lambda + \nu$, $n \geq 0$ and $\mu_n = n\mu$, $n \geq 1$, where $\nu > 0$ is the immigration rate. Since $\lambda_0 \neq 0$, 0 is not an absorbing state. The differential-difference equations (8) become

$$p_0'(t) = -\nu p_0(t) + \mu p_1(t), \quad n = 0,$$

$$p_n'(t) = ((n-1)\lambda + \nu) p_{n-1}(t) - (n(\lambda + \mu) + \nu) p_n(t)$$
$$+ (n+1)\mu\, p_{n+1}(t), \quad n = 1, 2, 3, \ldots. \tag{12}$$

Now, from (10) and (11), we obtain the partial differential equation

$$\frac{\partial g(s, t)}{\partial t} + (\mu - \lambda s)(s-1)\frac{\partial g(s, t)}{\partial s} = \nu(s-1) g(s, t) \tag{13}$$

having auxiliary equations

$$\frac{dt}{1} = \frac{ds}{(\mu - \lambda s)(s-1)} = \frac{dg(s, t)}{\nu(s-1) g(s, t)}. \tag{14}$$

On solving (14) using initial conditions (9), we obtain

$$g(s, t) = \begin{cases} \left(\frac{1-\beta(t)}{1-s\beta(t)}\right)^{\nu/\lambda}\left(\frac{\alpha(t) - s(\alpha(t)+\beta(t)-1)}{1-s\beta(t)}\right)^{n_0}, & \lambda \neq \mu, \\ \left(\frac{1-\beta(t)}{1-s\beta(t)}\right)^{\nu/\lambda}\left(\frac{\beta(t) + s(1-2\beta(t))}{1-s\beta(t)}\right)^{n_0}, & \lambda = \mu, \end{cases} \tag{15}$$

where

$$\alpha(t) = \frac{\mu(1-e^{(\lambda-\mu)t})}{\mu - \lambda e^{(\lambda-\mu)t}}, \quad \lambda \neq \mu \tag{16}$$

and

$$\beta(t) = \begin{cases} \frac{\lambda(1-e^{(\lambda-\mu)t})}{\mu - \lambda e^{(\lambda-\mu)t}}, & \lambda \neq \mu, \\ \frac{\lambda t}{1+\lambda t}, & \lambda = \mu. \end{cases} \tag{17}$$

Extinction probability at time t is

$$p_0(t) = \begin{cases} (1-\beta(t))^{\nu/\lambda}(\alpha(t))^{n_0}, & \lambda \neq \mu, \\ (1-\beta(t))^{\nu/\lambda}(\beta(t))^{n_0}, & \lambda = \mu \end{cases} \tag{18}$$

and the mean number of individuals at time t is

$$m(t) = \begin{cases} n_0 e^{(\lambda-\mu)t} + \dfrac{\nu}{\lambda - \mu}(e^{(\lambda-\mu)t} - 1), & \lambda \neq \mu, \\ \nu t + n_0, & \lambda = \mu \end{cases} \tag{19}$$

which changes exponentially $(\lambda > \mu)$, linearly $(\lambda = \mu)$ with time towards infinity and exponentially $(\lambda < \mu)$ with time towards $\nu/(\mu - \lambda)$.

From (16), (17) and (18), ultimate extinction probability is

$$\lim_{t\to\infty} p_0(t) = \begin{cases} \left(1 - \dfrac{\lambda}{\mu}\right)^{\nu/\lambda}, & \lambda < \mu, \\ 0, & \lambda \geq \mu \end{cases} \tag{20}$$

and from (19), ultimate mean number of individuals is

$$\lim_{t\to\infty} m(t) = \begin{cases} \dfrac{\nu}{\mu - \lambda}, & \lambda < \mu, \\ \infty, & \lambda \geq \mu \end{cases} \tag{21}$$

which are independent of n_0.

2.1. Dispersion and the Kendall process

In particular, if $n_0 = 0$, then (15) reduces to

$$g(s, t) = \left(\frac{1 - \beta(t)}{1 - s\beta(t)}\right)^{\nu/\lambda}, \tag{22}$$

where $\beta(t)$ is given by (17) and on reparameterizing $\beta(t) = \dfrac{p(t)}{1 + p(t)}$, then

$$p(t) = \begin{cases} \dfrac{\lambda}{\mu - \lambda}(1 - e^{(\lambda-\mu)t}), & \lambda \neq \mu, \\ \lambda t, & \lambda = \mu \end{cases} \tag{23}$$

and (22) becomes

$$g(s, t) = (1 + p(t) - sp(t))^{-\nu/\lambda} \tag{24}$$

which is the probability generating function of the negative binomial distribution with parameters $k = \nu/\lambda$ and $p(t)$. Extinction probability at time t is

$$p_0(t) = (1 - \beta(t))^{\nu/\lambda}, \tag{25}$$

where $\beta(t)$ is given by (17) and the mean number of individuals at time t is

$$m(t) = kp(t) = \begin{cases} \dfrac{\nu}{\lambda - \mu}(e^{(\lambda-\mu)t} - 1), & \lambda \neq \mu, \\ \nu t, & \lambda = \mu \end{cases} \tag{26}$$

which changes exponentially $(\lambda > \mu)$, linearly $(\lambda = \mu)$ with time towards infinity and exponentially $(\lambda < \mu)$ with time towards $\nu/(\mu - \lambda)$.

The ultimate extinction probability and the ultimate mean number of individuals are given by (20) and (21), respectively, since they are independent of n_0.

Since $k = \dfrac{\nu}{\lambda}$, then $\lambda \to 0$ or $\nu \to \infty$, implies a random spatial pattern $(k \to \infty$ or $\beta(t) \to 0)$ and $\lambda \to \infty$ or $\nu \to 0$, implies a clustered (an overdispersed) spatial pattern $(k \to 0$ or $\beta(t) \to 1)$.

From (17),

$$\lim_{t\to\infty} \beta(t) = \begin{cases} \dfrac{\lambda}{\mu}, & \lambda < \mu, \\ 1, & \lambda \geq \mu \end{cases} \tag{27}$$

and hence for $\lambda \geq \mu$, ultimate spatial pattern is overdispersed whereas for $\lambda < \mu$ and $\lambda \to 0$,

$$\lim_{t\to\infty, \lambda\to 0} \beta(t) = 0 \tag{28}$$

and hence ultimate spatial pattern is random. In this case, from (20), the ultimate extinction probability is

$$\lim_{t\to\infty,\lambda\to 0} p_0(t) = \lim_{\lambda\to 0}\left(1-\frac{\lambda}{\mu}\right)^{\nu/\lambda} = \lim_{\lambda\to 0}\left(1-\frac{\nu/\mu}{\nu/\lambda}\right)^{\nu/\lambda} = e^{-\nu/\mu} \tag{29}$$

and from (21), the ultimate mean number of individuals is

$$\lim_{t\to\infty,\lambda\to 0} m(t) = \frac{\nu}{\mu}. \tag{30}$$

We observe that $\lambda \to 0$ is reminiscent of a linear death with immigration process which we discuss in the sequel.

3. Linear Death with Immigration Process

Letting $\lambda = 0$ in linear birth-death with immigration process, we obtain linear death with immigration process and since $\lambda_0 \neq 0$, 0 is not an absorbing state. Letting $\lambda = 0$, (14) reduces to

$$\frac{dt}{1} = \frac{ds}{\mu(s-1)} = \frac{dg(s, t)}{\nu(s-1)g(s, t)} \tag{31}$$

which on solving using initial conditions (9), we obtain

$$g(s, t) = (1-e^{-\mu t} + se^{-\mu t})^{n_0} \exp\left\{\frac{\nu}{\mu}(1-e^{-\mu t})(s-1)\right\} \tag{32}$$

which is the product of probability generating functions of $\text{Bin}(n_0, e^{-\mu t})$ and $\text{Poisson}\left(\frac{\nu}{\mu}(1-e^{-\mu t})\right)$.

Extinction probability at time t is

$$p_0(t) = (1-e^{-\mu t})^{n_0} \exp\left\{-\frac{\nu}{\mu}(1-e^{-\mu t})\right\} \tag{33}$$

and the mean number of individuals is

$$m(t) = n_0 e^{-\mu t} + \frac{\nu}{\mu}(1-e^{-\mu t}) \tag{34}$$

which is the sum of the means of $\text{Bin}(n_0, e^{-\mu t})$ and $\text{Poisson}\left(\frac{\nu}{\mu}(1-e^{-\mu t})\right)$.

The ultimate extinction probability is

$$\lim_{t\to\infty} p_0(t) = e^{-\nu/\mu} \tag{35}$$

and the ultimate mean number of individuals is

$$\lim_{t\to\infty} m(t) = \nu/\mu \tag{36}$$

which are independent of n_0.

3.1. Dispersion and linear death with immigration process

In particular, if $n_0 = 0$, then (32) reduces to

$$g(s, t) = \exp\left\{\frac{\nu}{\mu}(1 - e^{-\mu t})(s - 1)\right\} \tag{37}$$

which is the probability generating function of Poisson$\left(\frac{\nu}{\mu}(1 - e^{-\mu t})\right)$ which describes a random spatial pattern.

Extinction probability at time t is

$$p_0(t) = \exp\left\{-\frac{\nu}{\mu}(1 - e^{-\mu t})\right\} \tag{38}$$

and the mean number of individuals at time t is

$$m(t) = \frac{\nu}{\mu}(1 - e^{-\mu t}) \tag{39}$$

which is a curve with negative curvature and converges to ν/μ, indicative of stability. From (34),

$$\lim_{t\to\infty} g(s, t) = \exp\left\{\frac{\nu}{\mu}(s - 1)\right\} \tag{40}$$

which is the probability generating function of Poisson(ν/μ) and hence the ultimate spatial pattern is random.

The ultimate extinction probability and the ultimate mean number of individuals are given by (35) and (36) since they are independent of n_0, moreover, they confirm (29) and (30), respectively.

Furthermore, from (32),

$$\lim_{\nu \to 0} g(s, t) = (1 - e^{-\mu t} + se^{-\mu t})^{n_0} \tag{41}$$

which is the probability generating function of $\mathrm{Bin}(n_0, e^{-\mu t})$ and hence the spatial pattern is uniform. In this case, from (35), ultimate extinction probability is

$$\lim_{t \to \infty, \nu \to 0} p_0(t) = \lim_{\nu \to 0} e^{-\nu/\mu} = 1 \tag{42}$$

which implies ultimate extinction is certain and from (36), the ultimate mean number of individuals is

$$\lim_{t \to \infty, \nu \to 0} m(t) = \lim_{\nu \to 0} \nu/\mu = 0. \tag{43}$$

We observe that $\nu \to 0$ is reminiscent of a linear death process which we discuss in the sequel.

4. Dispersion and Linear Death Process

Letting $\nu = 0$ in the linear death with immigration process, we obtain a linear death process and since $\lambda_0 = 0$, 0 is an absorbing state. Letting $\nu = 0$, (31) reduces to

$$\frac{dt}{1} = \frac{ds}{\mu(s-1)} = \frac{dg(s, t)}{0} \tag{44}$$

which on solving using initial conditions (9), we obtain

$$g(s, t) = (1 - e^{-\mu t} + se^{-\mu t})^{n_0} \tag{45}$$

which is the probability generating function of $\mathrm{Bin}(n_0, e^{-\mu t})$, $n_0 > 0$ and hence spatial pattern is uniform.

Extinction probability at time t is

$$p_0(t) = (1 - e^{-\mu t})^{n_0} < 1 \tag{46}$$

which implies extinction at time t is not certain and the mean number of individuals is

$$m(t) = n_0 e^{-\mu t} \tag{47}$$

which changes exponentially with time towards zero, moreover, 0 is an absorbing state.

From (46), ultimate extinction probability is

$$\lim_{t \to \infty} p_0(t) = 1 \tag{48}$$

which implies ultimate extinction is certain and from (47), ultimate mean number of individuals is

$$\lim_{t \to \infty} m(t) = 0 \tag{49}$$

which are independent of n_0, moreover, they confirm (42) and (43), respectively.

5. Conclusions

The mean (19) of the stochastic model (12) is equivalent to the deterministic model (7). For clustered and random spatial patterns, 0 is not an absorbing state whereas for a uniform spatial pattern, 0 is an absorbing state.

From stochastic analysis, the ultimate extinction probability is

$$\lim_{t \to \infty} p_0(t) = \begin{cases} 0, & \text{clustered (overdispersed),} \\ e^{-\nu/\mu}, & \text{random,} \\ 1, & \text{uniform (underdispersed)} \end{cases} \tag{50}$$

and the ultimate mean number of individuals is

$$\lim_{t \to \infty} m(t) = \begin{cases} \infty, & \text{clustered (overdispersed),} \\ \dfrac{\nu}{\mu}, & \text{random,} \\ 0, & \text{uniform (underdispersed).} \end{cases} \tag{51}$$

Thus, if spatial pattern is uniform, then ultimate extinction is certain and if spatial pattern is overdispersed, then ultimate explosion is certain. If spatial pattern is random, then ultimate extinction is not certain and ultimate mean stabilizes.

Intuitively, overdispersion overly promotes survival leading to explosion whereas underdispersion overly inhibits survival leading to extinction and randomness is a compromise between these two extreme situations.

Acknowledgement

The author acknowledges EAUMP-ISP for their partial support.

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