Mathematical Equivalence of Geometric Mean Fitness with Probabilistic Optimization under Environmental Uncertainty: Natural Selection under Environmental Uncertainty: a Canonical Form of Probabilistic Optimization

The evolution of prime number intervals in periodical cicadas

Jin Yoshimura1,2,3*, Yumi Tanaka4, Tatsuya Togashi22, Shigehide Iwata1 and Kei-ichi Tainaka1

Jin Yoshimura1,2,3*, Yumi Tanaka4, Tatsuya Togashi22, Shigehide Iwata1 and Kei-ichi Tainaka1

* Equally contributed.

1Department of Systems Engineering, Shizuoka University, Hamamatsu 432-8561, Japan.
2Marine Biosystems Research Center, Chiba University, Uchiura, Amatsu-Kominato, Chiba, 299-5502, Japan
3Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York 13210 USA
4Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT.

* Equally contributed.
# To whom correspondences should be addressed at Dept. Systems Engineering, Shizuoka University, 3-5-1 Johoku, Hamamatsu 432-8561, Japan. E-mail: jin@sys.eng.shizuoka.ac.jp

1Department of Systems Engineering, Shizuoka University, 3-5-1 Johoku, Naka-ku, Hamamatsu 432-8561, Japan

2Marine Biosystems Research Center, Chiba University, 1 Uchiura, Kamogawa, Chiba 299-5502, Japan

3Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York 13210, USA

4School of Human Science and Environment, University of Hyogo, 1-1-12 Shinzaike-honcho, Himeji 670-0092, Japan

*Corresponding author: Jin Yoshimura (jin@sys.eng.shizuoka.ac.jp)

Other authors: Yumi Tanaka (nd08x012@stshse.u-hyogo.ac.jp)
Tatsuya Togashi (togashi@faculty.chiba-u.jp)
Shigehide Iwata (f5645023@ipc.shizuoka.ac.jp)
Kei-ichi Tainaka (tainaka@sys.eng.shizuoka.ac.jp)
To whom correspondence should be addressed—jin@sys.eng.shizuoka.ac.jp
Abstract

Natural selection can be considered as optimising fitness. Because 'mean' fitness is maximized with respect to the genotypes of carriers, traditional theory can be viewed as a statistical theory of natural selection. Probabilistic optimisation is a way to incorporate such uncertainty into optimality analyses of natural selection, where environmental uncertainty is expressed as a probability distribution. Its canonical form is a weighted average of fitness with respect to a given probabilistic distribution. This concept should be applicable to three different levels of uncertainty: (1) behavioural variations of an individual, (2) individual variations within a generation, and (3) temporal change over generations (geometric mean fitness). The former two levels are straightforward with many empirical evidences, but the last category, the geometric mean fitness, has not well understood. Here we studied the geometric mean fitness by taking its logarithm, where the log growth rates become the fitness value. By further transforming the log growth rates, the fitness of log growth rates becomes its linear function. Therefore, a simple average of these distributions becomes the fitness measure across generations and consideration of variance discount or the entire probability distributions becomes unnecessary. We discuss some characteristic features of probabilistic optimization in general. Our view is considered a probabilistic view of natural selection, in contrast with the We try to understand what can be viewed as fitness under environmental uncertainty, and how and when does the solution change from those expected from the traditional statistical view of...
natural selection. Environmental uncertainty can be expressed as a probability distribution.

Probabilistic optimization is a way to incorporate such uncertainty into optimality analyses of natural selection. A canonical form of probabilistic optimization is a weighted average of fitness with respect to a given probabilistic distribution. This concept can be applicable to three different levels of uncertainty: (1) behavioural variations of an individual, (2) individual variations within a generation, and (3) temporal change over generations (geometric mean fitness). Discrepancy between genetic and phenotypic optima often tends to increase with the variance of a probability distribution that is a measure of the degree of uncertainty. For geometric mean fitness, if the probabilistic distribution of generational fitness follows lognormal distribution, its average becomes a measure of fitness, irrespective of its variance.

**Keywords:** fitness criteria, weighted average, variable unpredictable environments, geometric mean fitness, probabilistic optimization by distribution.

**Background:** Two hypotheses compete to explain the evolution of prime number reproductive intervals (life cycles) among periodical cicadas: the 1) anti-predatory hypothesis and 2) hybridization one. The anti-predatory hypothesis claims that prime number intervals help to protect cicadas from being overwhelmed by their predators. The hybridization hypothesis claims that prime numbers greatly reduce the chance of hybridization among cicada broods.

**Goal:** To test the hybridization hypothesis using a simulation model.

**Models:** A deterministic, discrete population model with three parameters: larval
survival per year; clutch size; emergence success. Reproductive intervals from ten-
years to twenty years compete for survival in the simulations. The model makes-
three key assumptions: a Mendelian genetic system, and random mating among
sympatric or parapatric broods of different life cycle lengths, and integer-
population sizes. In addition, longer-interval phenotypes have larger broods but
suffer higher total mortality than shorter-interval broods. We keep track of all
population sizes of all pure intervals and hybrids with birth year. The life cycle-
length of hybrids is assumed to be Mendelian inheritance with shorter-cycle
dominance.

Results: Non-prime number reproductive intervals rapidly disappear. Then the
19-year phenotype is gradually eliminated by the 13- and 17-year phenotypes. The
13- and 17-year phenotypes may coexist. The selection of 13- or 17-year intervals-
 happens only when populations are at the verge of extinction.

Keywords: Periodical cicadas, prime number intervals, 13/17-year, co-emergence,
hybridization, extinction threshold, frequency dependence, discrete population model
1. INTRODUCTION

Periodical cicadas are among the most remarkable of insects, known for their long, perfectly synchronized life cycles and the explosive emergence of the adults (Marshall, 2001; Alexander and Moore, 1962; Dybas and Davis, 1962; Lloyd and Dybas, 1966; Simon 1988; Williams and Simon, 1995). Two types of life cycle are known, 17- and 13-year, both prime numbers. The emergence of periodical cicadas is perfectly synchronized in each locality; no little emergence is seen except emergence years (occasional stragglers are seen one or four years early or late Marshall 2001). The periodical cicadas also show very strong site tenacity (Williams and Simon 1995) and a strong tendency for aggregation (Simon et al., 1981).

INTRODUCTION

Natural selection is often viewed as a statistical process, maximizing the expected or mean reproductive success of individuals carrying a certain gene or genotype (Darwin, 1859; Fisher, 1930). The expected reproductive success is then called 'mean' fitness. In this sense, we can refer to standard theory as a 'statistical' theory of natural selection. In order to analyze the optimality of a phenotypic trait based on mean fitness, most traditional theories of natural selection almost invariably assume constant and predictable environments.

However, for almost all organisms in the wild, environments are variable and unpredictable (Yoshimura and Clark, 1993). Both abiotic components of environments, such as weather, and biotic components, such as the locations of competitors and predators are always unpredictable to the organisms to some extent. In this sense, environmental uncertainty is an unavoidable factor for all...
living systems if they are to persist and evolve through time. Accordingly the statistical theory of
natural selection needs to incorporate factors and constraints associated with optimization processes
(Parker and Maynard Smith, 1990; Williams, 1992). Here environmental uncertainty is one of the
most influential and common factors affecting natural selection, as it changes the statistical
(mean-fitness) concepts of optimisation (Yoshimura and Shields, 1987; Frank and Slatkin, 1989;
Cohen, 1993). However, probabilistic/stochastic models are widely scattered in various
fields of ecology and evolution without any generalisation. Many of them are not accessible to
empirical researchers because of mathematical difficulty and complexity that is and technical details
inherent in each specific model. We should also note that the problem of uncertainty is extremely
well documented in foraging behaviour both from the theoretical and empirical standpoints (for
example, see Stephens and Krebs, 1986; Real and Caraco, 1986). However, the generalization and
conceptual developments of the effects of uncertainty in all levels are still lacking.

In order to understand the basic properties of uncertainty, we need a probabilistic perspective for
natural selection, a synthetic or integrated view of the effects of uncertainty on natural selection. We
can classify environmental uncertainty into three categories based on the level of integration: (1)
short-term temporal change experienced by an individual (individual level within a generation), (2)
phenotypic variation among individuals (population level within a generation) and (3) population
fluctuation across generations due to long-term environmental changes (cross-generation level).

First, we describe three major categories of uncertainty: (1) the variable daily experience of an individual,
(2) variation among individuals and (3) long-term fluctuations across generations (Yoshimura and
Shields, 1992; Yoshimura, 1995). It is important to know how these uncertainties can be
incorporated into optimality analyses of natural selection. The mathematical principles of probabilistic optimization in these categories are crucial in how uncertainty can be
incorporated into optimality analyses. A canonical form of probabilistic optimization is a simple weighted average with respect to a given probabilistic distribution. It can be considered a
canonical form of probabilistic optimization under uncertainty (Yoshimura 1995). The fitness
measure across generations (the third category) is the geometric mean fitness (or the expected
multiplicative growth rate) (Lewontin and Cohen, 1969). Certainly, by taking the logarithm, the
geometric mean fitness becomes a weighted average of the population growth rates (Yoshimura and
Clark, 1991). However, the exact mathematical equivalence of geometric mean fitness is not yet well
understood.

This short paper deals with the mathematical nature of geometric mean fitness and its mathematical
equivalence with other forms of probabilistic optimization. Here, we first explain in the section of
theoretical rationale, the weighted average used for the first two categories of uncertainty at the level
of an individual and a population in a single generation. We then show that the geometric mean fitness can be transformed a simple weighted average of the logarithm of multiplicative growth rates. We further shows that the logarithm of the growth rates becomes an exact value of fitness. The variance discount is not necessary in this logarithmic form of geometric mean fitness. This formula is conceptually true for any type of optimization under uncertainty. Next I describe three major categories of uncertainty: (1) the variable daily experience of an individual; (2) variation among individuals; and (3) long-term fluctuations across generations. Lastly I discuss briefly the characteristics of the effects of uncertainty on natural selection.

2. THE THEORETICAL RATIONALE

2.1 UNCERTAINTY AT INDIVIDUAL LEVEL

An individual experiences temporal changes in environments. An individual lives in daily changing environments, unstable and unpredictable in many aspects. How an individual behaves, grows and reproduces in such changing environments has often been dealt as a problem of optimisation in behavioral and physiological ecology (Krebs and Davies, 1993; Sibly and Calow, 1986; Mangel and Clark, 1988; Stephens and Krebs, 1986; Real and Caraco, 1986). Here the underlying principle can be illustrated as follows: individual animal forages for varying, and thus unpredictable amounts of
food daily. Daily food amounts are then expressed as a probability distribution. The overall fitness of
an individual associated with a given phenotype is a weighted sum of all the fitnesses of daily food
intake during its life time (Yoshimura and Shields, 1992; Yoshimura, 1995). The optimum based on
the overall fitness is a probabilistic optimum that is different from the fitness at the average food
intake, a deterministic optimum.

We first consider the fitness of an individual associated with a phenotype \( y \). Here the notation is
listed in Table 1. The fitness \( w_i(y) \) of an individual associated with a phenotype \( y \) is a weighted sum
of all possible environmental fitnesses \( f_i(x,y) \) with the distribution of the environments \( h_i(x) \), shown
in the equation (1) of Table 1.

For an illustrative example, we consider daily uncertainty in foraging animals (Fig. 1) (Yoshimura,
1995). Let \( x \) be daily food amounts as an environmental factor, where \( x = 0 \) in the worst environment
and \( x = 100 \) in the best environment, and \( f_i(x,y) \) be the fitness of an individual with a phenotype \( y \) in
environment \( x \). Naturally \( f_i(x,y) \) is an increasing function of \( x \) (Fig. 1a). The difference in phenotype
\( y \) indicates what kind of food environments an individual is adapted for: if \( y = 10 \), an individual is
adapted for bad environments, i.e., fitness is fairly similar for bad and good environments (10 < \( x \) < 50,
and \( x > 50 \)). However, if \( y = 50 \), an individual is adapted for good environments, i.e., fitness is low.
(zero) for bad environments ($x<50$) and extremely high for good environments ($x>>50$). The fitness function $f(x, y)$ for phenotypes $y$ in a given environment $x$ is a function with a peak (Fig. 1b).

Suppose that the probability distribution of daily food abundance $h(x)$ is approximated by a distribution with mean $E(x) = 50$ (Fig. 1c). Then the fitness $w_i(y)$ of an individual associated with a phenotype $y$ is an weighted sum of all possible environmental fitnesses $f(x, y)$ by their distribution $h(x)$ (equation (1) of Table 1). The probabilistic optimum $Y_p$ is then defined on the phenotypic fitness $w_i(y)$ as: $w_i(Y_p) = \max w_i(y)$ (Fig. 1d). In contrast, the deterministic optimum $Y_d$ is the optimal phenotype in the average environment, that is $f(M, Y_d) = \max f(M, y)$, where $M = 50$ is the expectation of $x$, i.e., $M = \int h(x) \, dx$ (Fig. 1d). In this case, the probabilistic optimum $Y_p (=30.89)$ is always smaller than the optimum in the average environment $Y_d (=33)$.

In foraging theories, the concept of risk-sensitivity has been specifically developed to deal with daily uncertainty in food acquisition by animals (Caraco, 1980; Stephens and Krebs, 1986; Real and Caraco, 1986). This body of theory and empirical studies reveal that animals often show sensitivity to the variance and skewness of a temporal distribution of foods (Caraco et al., 1980; Caraco and Chasin, 1984). This demonstrates that not only the mean, but also the entire distribution of food availability is important for the evolution of animal behaviour. The expected utility theory used in
risk-sensitive foraging (Caraco, 1980; Real and Caraco, 1986) is a specific form of weighted average, in which the fitness function is an increasing function of the amount of food. In dynamic programming, in every time step of decision-making, the overall fitness of an individual is calculated from the weighted average of individual fitnesses of all possible states (Mangel and Clark, 1988).

We should note that the risk-sensitive foraging has been empirically (in fields and laboratories) demonstrated well in many animals, such as the seminal work of yellow-eyed juncos by Caraco and others (Caraco et al., 1980).

2.2 UNCERTAINTY AT POPULATION LEVEL

Phenotypic variation among individuals of a population is common in many traits, such as body size. Such individual variation arises because environments differ among individuals. Therefore, environmental uncertainty may also appear as phenotypic variation in a population. Most important cases are when phenotypic variation occurs as a result of cumulative effects of past environmental differences.

Here probabilistic optimization can be stated as follows (Yoshimura and Shields, 1987, 1995). Actual (observed) survivorship and reproduction is determined by the phenotype of an individual for a given environment. Therefore, phenotype is the criterion for realised (observed) fitness. Because of
this, we often compare observed mean phenotypes with optimal phenotypes as a measure of
achievement of optimality (adaptation) by natural selection (Price and Waser, 1979; Roff, 1981).
However, the comparison based on this (deterministic) phenotypic optimum is not valid if there is
variation in phenotypes. The evolutionary criterion of fitness is the genotypes that are selected
through natural selection. For a given genotype, phenotypic variation is expressed as a probability
distribution. The fitness of a genotype is the weighted sum of the fitnesses of all the phenotypes
associated with the genotype, the probabilistic genetic optimum. We can then compare the observed
mean phenotype with this genetic optimum.

The mathematical expression of the fitness \( w_p(z) \) of an individual associated with a genotype is
shown in the equation (2) of Table 1. It is the weighted sum of all the phenotypic fitnesses \( f_p(y) \)
multiplied by the distribution of phenotypes \( h_p(y, z) \) (equation (2) of Table 1). If the phenotype \( x \) is
discrete, e.g., clutch size, then \( w_p(z) \) becomes the summation (equation (3) of Table 1). This is the
weighted average of discrete phenotypes at the population level within a generation.

An illustrative example is the phenotypic variation in body size (Fig. 2) (Yoshimura, 1995). Let
phenotypic fitness \( f_p \) be a function of body size \( y \), i.e., \( f_p = f_p(y) = w_i(y) \), with a single peak (Fig. 2a;
dotted line), and \( h_p(y, z) \) be a probability distribution of body size \( y \) for a given genotype \( z \) (Fig. 2b).
Suppose that genotype \( z \) controls the mean body size of a normal distribution with a constant variance (Fig. 2b: three genotypes are shown). We assume here that the mean body size can shift continuously by changing genotypes. Then the fitness of the genotype \( w_p(z) \) is the weighted sum of all the phenotypic fitnesses \( f_p(y) \) with their distribution \( h_p(y, z) \) (Fig. 2a: solid line; equation (2) of Table 1). Here the phenotypic optimum \( Y_{\text{max}} \) represents the trait that achieves the highest reproductive success in the environment, i.e., \( f(Y_{\text{max}}) = \max f(y) \). In contrast, the genotypic optimum \( Z_{\text{max}} \) is the trait selected by natural selection, i.e., \( w_p(Z_{\text{max}}) = \max w_p(z) \). In general, the two optima differ in their values. In this example, the genetic optimum \( Z_{\text{max}} \) is always smaller than the phenotypic optimum \( Y_{\text{max}} \) (Fig. 1a).

The discrepancy between genetic and phenotypic optima can be illustrated as follows: Suppose that 2 meters is the optimum height for a man, but that if he is more than 2 meters tall (even slightly) he tends to kill himself by bumping into the tops of door frames. A critical point is that genotypes determine the height only on average, because their environments vary. We have to consider all the individuals for a given genotype. For people associated with an average 2-meter genotype, nearly half of them become more than 2 meters tall and are knocked out by the door frame. Therefore, the optimal average height (genotype) is actually smaller than 2 meters. For this optimal genotype, most people are suboptimal, but their loss of fitness is much less than killing themselves; and a very few...
will be lost due to their being >2 meters in height. In other words, the deterministic optimum height lies above the probabilistic genetic optimum.

More generally, it is well known that there is a discrepancy between phenotypic and genetic optima in most genetic systems because of various genetic constraints, such as segregation, recombination and mutation (Crow and Kimura, 1970), and because of environmental variation (Mountford, 1968; Lalonde, 1991). For example, in quantitative traits like body size, the phenotypes of offspring vary from parental phenotypes. The discrepancies between phenotypic and genetic optima have been observed in the pollen dispersal of a plant (Price and Waser, 1979) and the body size of a fruit fly, *Drosophila melanogaster* (Roff, 1981; Yoshimura and Shields, 1995).

The current analyses focus on the uncontrolled phenotypic variation. However, individual variation may be induced as an adaptive response (Pigliucci, 2001; Dewitt and Scheiner, 2004). Phenotypic plasticity may thus increase the fitness of a population (Via and Lande, 1985). In this case, we have diversification of phenotypes with respect to environmental factors. Many individual variations are indeed adaptive variations (Dewitt and Scheiner, 2004). Clutch size variation may be an adaptive plasticity. In the great tit, the variation in clutch size is partly reflecting the parental ability of rearing young (Pettifor et al., 1988). Inducible defence is very common in many organisms (e.g., DeWitt,
Probabilistic optimization scheme is also useful in conceptualizing the fitness maximization of such adaptive responses (DeWitt and Yoshimura 1998).

The body-size example is a case when phenotypic variation appears on the target trait for which we evaluate the optimality. However, it may also appear in correlated traits, which in turn affect the optimality of the target trait. Here phenotypic correlation can be either positive or negative.

Allometry (e.g., in body size) is an example of a positive correlation (Schmidt-Nielson, 1984).

Negative correlation is often known as a trade-off (Roff, 1992; Stearns, 1992). It is important that phenotypic variation in such correlated traits can affect the optimality of the target traits. For example, if there is a trade-off between current clutch size and future reproduction (via parental survivorship), anticipated variation in future reproduction should be accounted for through the current clutch size (Yoshimura and Shields, 1992; Lalonde, 1991).

2. THE PRINCIPLE OF OPTIMIZATION

The principle of probabilistic optimization is a weighted average of fitnesses (or fitness potentials) according to their probability distributions (Yoshimura and Shields, 1992; Cohen, 1993). Suppose that we measure the fitnesses of an individual over some range of temperatures, where temperature...
changes over time. Obviously we may just consider the fitness of an individual at the mean

temperature. This represents a deterministic optimum, as in the mean fitness concept. However, it
does not account for temperatures other than at one point, the mean temperature. Hence the best way
to evaluate the fitness of an individual is the weighted average of fitnesses according to the
distribution of temperature. This expectation accounts for the entire temperature distribution and
gives a correct estimate of the fitness without any error.

A canonical form of probabilistic optimization is given as follows. Let $x_{\alpha}$ and $y_{\beta}$ be individual
and collective trait values, respectively. For example, if $x_{\alpha}$ is a phenotype value, then $y_{\beta}$ is a

genotype value associated with a distribution of phenotype value $x_{\alpha}$. Suppose $f(x_{\alpha}, y_{\beta})$ is the
fitness potential function of $x_{\alpha}$ given $y_{\beta}$. Then the canonical form of fitness $w(y_{\beta})$ is given as:

$$w(y_{\beta}) = \int f(x_{\alpha}, y_{\beta}) h(x_{\alpha}, y_{\beta}) dx_{\alpha}$$

where $f(x_{\alpha}, y_{\beta})$ and $h(x_{\alpha}, y_{\beta})$ are the fitness potential and the probability distribution of
trait values $x_{\alpha}$ and $y_{\beta}$, respectively. Depending on the situation given these two functions may be.

those of a single variable $x_{\alpha}$ such that $f = f(x_{\alpha})$ and $h = h(x_{\alpha})$.

In other words, the overall fitness is the expectation (weighted average) of all individual fitnesses (or
fitness potentials) associated with each value (probabilistic optimum); this expectation is different.
from the fitness for the mean value (deterministic optimum). Weighted averages appear as an
underlying concept in any stochastic and probabilistic modelling for uncertainty, not only at the
individual level, but also at the population and generation levels. I will discuss how weighted
average fitnesses and mean value fitnesses differ in three different levels later.

3. THE LOGARITHMIC FORM OF GEOMETRIC MEAN FITNESS

Fitness varies over generation times. Natural populations often fluctuate widely due to long-term
environmental changes in weather and other environmental factors (Andrewartha and Birch, 1954).
Similarly, the multiplicative growth rates of a genotype in a population should also vary according to
environmental conditions. Here, variation in growth rates might play an important role in the
evolution of many phenotypic traits (Philippi and Seger, 1989; Bulmer, 1994; Yoshimura and Clark,
1991). In order to assess the effect of the variation in growth rates on natural selection, we have to
evaluate the long-term growth rate of a genotype. Here the appropriate concept of fitness is the
average (expected) growth rate per generation. This average is called geometric mean fitness,
because it is the geometric mean of multiplicative growth rates (Lewontin and Cohen, 1969;,

Mathematically geometric mean fitness can be derived from the population growth as follows.
Geometric mean fitness is a specific form of probabilistic optimization, where the fitness function is a logarithm of population growth rates. Consider the population dynamics of a given genotype \( z \) for an organism with discrete generations: 

\[ N_z(t+1) = r_z(t) \cdot N_z(t), \quad \text{for } t = 0, 1, 2, ... \]

where \( N_z(t) \) is the population size and the fitness of a genotype \( z \), \( r_z(t) \), is expressed as the population growth rate at generation \( t \). Then the population size at generation \( t \) is given by:

\[ N_z(t) = r_z(0)r_z(1) \cdots r_z(t-1)N_z(0) = \left( \prod_{i=0}^{t-1} r_z(i) \right) N_z(0) \quad (7) \]

The geometric mean fitness is then defined as an average population growth rate per generation:

\[ G(z) = \prod_{i=0}^{t-1} r_z(i)^{(1/i)} \]

Suppose that the population growth rate \( r_z(i) \) is randomly drawn from a probability distribution \( h_r(r_z) \) for a given genotype \( z \). Then the geometric mean fitness is expressed by the probability distribution \( h_r(r_z) \) as:

\[ G(z) = \prod_r w_r h_r(r_z) \quad (8) \]

Here genotypes with the highest geometric mean fitness (max \( G(z) \)) should be selected through natural selection. Taking logarithm of equation (8), we get the arithmetic form (weighted average) of the fitness under generational uncertainty (equation (1) of Table 2, Fig. 3), where the notations are shown in Table 2. Here the probabilistic optimization is a weighted average with the weight \( f_r(r) = \log(r) \) (Fig 3a, 3b). This formula is fully equivalent with fitness at the level of an individual and a population (equations (1) and (2) of Table 1).
This example indicates that variation in growth rates decreases geometric mean fitness. Because of this, the geometric mean fitness is often approximated with mean and variance using a variance-discount method (Fig. 4) (Frank and Slatkin, 1989; Gillespie, 1977; Yoshimura and Clark, 1991). Such approximation clearly depicts the effect of variance. As in the previous calculus example, variance in population growth rate $r$ reduces the geometric mean fitness. Even if the mean $r$ is smaller, if the variance of $r$ is smaller, the geometric mean fitness can be higher (Fig. 4).

However, ironically such approximation concentrates only on the effects of mean and variance and ignores the entire distribution of growth rates. In addition, the approximation also assumes the normal distribution of growth rate with small variance (Yoshimura and Jansen, 1996). Therefore, it is not applicable to a case when variance is large or when extinction is a prominent possibility. This is evident from the logarithmic function in geometric mean fitness: the weight of negative growth is much higher than the weight of positive growth, because the logarithm drops faster on the negative side, than increases in the positive side. In the limit, if fitness falls to zero in any generation, arithmetic mean fitness will still be positive, but geometric mean fitness will be zero.

What is the probability distribution best fit to the distribution of population growth rates?

Multiplicative population growth rate $r$ is a nonnegative variable. Therefore, normal distribution that
can take negative values is not appropriate. In this sense, lognormal distribution is more appropriate
or at least applicable. Here we show the geometric mean fitness becomes extremely simple when the
lognormal distribution is assumed in population growth rates. Let population growth rate $r$ follows a
lognormal distribution such that

$$P(r; m_z, \sigma_z) = \frac{1}{\sqrt{2\pi \sigma_z^2}} \exp\left(-\frac{(\log(r) - m_z)^2}{2\sigma_z^2}\right)$$

(9)

Where $P(r) = P(r; m_z, \sigma_z)$ is the probability distribution of $r$ with mean $m_z$ and variance $\sigma_z$ for
genotype $z$. Then the logarithmic form of geometric mean fitness (equation (1) of Table 2) can be
solved analytically and reduces to the mean of the lognormal distribution $m_z$, such that (see
Appendix for derivation):

$$w_g(z) = \log G(z) = \log G(m_z, \sigma_z) = m_z = E_z[\log(r)]$$

(10)

It has been believed that variance is important in adaptation in stochastic environments. However, it
may be an artefact of our use of multiplicative population growth rates.

We should note that the current derivation is not necessary for any distribution of log growth rates.
The correct measure of the fitness at the generation level is the simple ‘arithmetic’ mean of
logarithmic population growth rates, such that $w_g(z) = E_z[\log(r)]$. In this measure, variance and the
shape of the probability distribution does not affect the overall fitness over generation time.
The current analysis of the geometric mean fitness for a lognormal distribution further implies an important feature of the logarithmic growth rates. Let \( R = \log(r) \). Then, the fitness over generation \( w_G(z) \) is given by the simple (un-weighted) average of the value \( R \) (equation (2) of Table 2), such that 
\[
w_G(z) = E\{R\} \quad \text{(Fig. 3c and 3d)}.
\]
Thus the generational fitness can be averaged over generation as a simple average if the fitness is measured as the logarithm of the multiplicative growth rates.

43. DISCUSSION

MATHEMATICAL REPRESENTATION AND INTERGRATION OF UNCERTAINTY

We can classify environmental uncertainty into three categories based on the level of integration: (1) short-term temporal change experienced by an individual (individual level within a generation), (2) phenotypic variation among individuals (population level within a generation) and (3) population fluctuation across generations due to long-term environmental changes (cross-generation level). The principle of probabilistic optimisation appears as a form of weighted average (equation (1)) at three levels: individual, population and generation. The fitness at the cross-generation level is the simple average of log growth rates without a weight \( E\{\log(r)\} \) or \( E\{R\} \). These uncertainties can be incorporated into the unified fitness at the generation level (Yoshimura and Shields, 1992).
We first consider the fitness of an individual associated with a phenotype.

Denote the following variables and functions:

- $y$: an environmental factor for an individual
- $x$: the phenotype of an individual
- $f_I^v(y|x)$: fitness of an individual with phenotype $x$ in environment $y$
- $h_I^d(y)$: probability distribution of environment $y$
- $f(x)$: fitness of an individual with phenotype $x$

Then the fitness $f(x)$ of an individual associated with a phenotype $x$ is a weighted sum of all possible environmental fitnesses $v(y,x)$ with the distribution of the environments $h_I^d(y)$:

$$f(x) = \frac{\int_{D(y|x)} v(y,x) h_I^d(y) dy}{\int_{D(y|x)} h_I^d(y) dy}$$

where $D(y|x)$ is the domain of environments $y$ for a given phenotype $x$. This is a weighted average of fitness measures at the individual level.

Next we consider the fitness of an individual associated with a genotype from the fitness of phenotypes $f(x)$. Denote the following variable and functions:

- $z$: a genotype
- $h(x;z)$: probability distribution of phenotypes $x$ for a given genotype $z$
- $w(z)$: fitness of a genotype $z$ (within a generation)
The fitness of a genotype $w(z)$ is then the weighted sum of all the phenotypic fitnesses $f(x)$ multiplied by the distribution of phenotypes $h(x; z)$:

$$w(z) = \int_{x \in H(x; z)} f(x) h(x; z) dx$$  (3)

where $H(x; z)$ is the domain of phenotypes $x$ for a given phenotype $z$. If the phenotype $x$ is discrete, e.g., clutch size, then $w(z)$ becomes the summation:

$$w(z) = \sum_{x \in H(x; z)} f(x) h(x; z)$$  (4)

This is the weighted average of discrete phenotypes at the population level within a generation.

Lastly we consider geometric mean fitness as the long-term fitness of a genotype across generations.

Denote the following variable and functions:

- $w$: fitness per generation measured as multiplicative growth rates
- $p(w; z)$: the probability distribution of fitnesses $w$ for a genotype $z$
- $G(z)$: the geometric mean fitness of a genotype $z$
- $g(z)$: the logarithm of the geometric mean fitness

Then the geometric mean fitness of a genotype is the expected long-term growth rate for a given genotype:

$$G(z) = \sum_{w} w^p(w; z)$$  (5)

Here maximizing $G(z)$ is same as maximizing its logarithm $g(z)$ and the latter is equal to the discrete...
weighted average of the logarithmic fitnesses \( \log(w) \) with their distribution \( p(w; z) \):

\[
g(z) = \log G(z) = \sum_w p(w; z) \log(w) = \mathbb{E} \{ \log(w) \} \tag{6}
\]

This is the weighted average of fitnesses at the generation level.

The principle of probabilistic optimisation is a weighted average of fitnesses (or fitness potentials) according to their probability distributions (Yoshimura and Shields, 1992; Cohen, 1993). A canonical form of probabilistic optimisation is then given as follows. Let \( \alpha \) and \( \beta \) be individual and collective trait values, respectively. For example, if \( \alpha \) is a phenotype value, then \( \beta \) is a genotype value associated with a distribution of phenotype value \( \alpha \). Suppose \( f(\alpha, \beta) \) is the fitness potential function of \( \alpha \) given \( \beta \). Then the canonical form of fitness \( w(\beta) \) is given as:

\[
w(\beta) = \int f(\alpha, \beta) h(\alpha, \beta) d\alpha \tag{11}
\]

where \( f(\alpha, \beta) \) and \( h(\alpha, \beta) \) are the fitness potential and the probability distribution of trait values \( \alpha \) and \( \beta \), respectively. Depending on the situation given these two functions may be those of a single variable \( \alpha \), such that, \( f = f(\alpha) \) and \( h = h(\alpha) \).

In other words, the overall fitness is the expectation (weighted average) of all individual fitnesses (or fitness potentials) associated with each value (probabilistic optimum); this expectation is different from the fitness for the mean value (deterministic optimum). Weighted averages appear as an
underlying concept in any stochastic and probabilistic modelling for uncertainty, not only at the
individual level, but also at the population and generation levels.

We should also note that these uncertainties can be incorporated into the unified fitness at the
generation level (Yoshimura and Shields, 1992). The integration of the individual-level fitness into
the population-level fitness is given by $f_p(y) = w_i(y)$, in equations (1) and (2) of Table 1. The fitness
measure at the population level $w_p(z)$ should be transformed into the multiplicative population
growth rate $r$ for each generation. For example, if $w_p(z)$ is defined as the growth rate per individual
adult, then simply, $r = w_p(z)$. However, if it is measured as a number of offspring/adult individual, as
is often seen, then $r = w_p(z) \times \text{(number of adult)} + \text{(number of surviving adult)} / \text{(number of adult)}$ at
a generation.

We can also estimate the effect of uncertainty on the outcome of natural selection. How

4. LEVELS

OF UNCERTAINTY

4.1 UNCERTAINTY AT INDIVIDUAL LEVEL

An individual experiences temporal changes in environments. An individual lives in daily changing,
environments, unstable and unpredictable in many aspects. How an individual behaves, grows and
reproduces in such changing environments has often been dealt as a problem of optimisation in.
behavioral and physiological ecology (Krebs and Davies, 1993; Sibly and Calow, 1986; Mangel and Clark, 1988; Stephens and Krebs, 1986; Real and Caraco, 1986). Here the underlying principle can be illustrated as follows: individual animal forages for varying, and thus unpredictable amounts of food daily. Daily food amounts are then expressed as a probability distribution. The overall fitness of an individual associated with a given phenotype is a weighted sum of all the fitnesses of daily food intake during its lifetime (Yoshimura and Shields, 1992). The optimum based on the overall fitness is a probabilistic optimum that is different from the fitness at the average food intake, a deterministic optimum.

Daily uncertainty in foraging animals can be mathematically expressed as follows (Fig. 1). Let $y$ be daily food amounts as an environmental factor, where $y = 0$ in the worst environment and $y = 100$ in the best environment, and $v(y, x)$ be the fitness of an individual with a phenotype $x$ in environment $y$. Naturally, $v(y, x)$ is an increasing function of $y$ (Fig. 1a). The difference in phenotype $x$ indicates what kind of food environments an individual is adapted for: if $x = 10$, an individual is adapted for bad environments, i.e., fitness is fairly similar for bad and good environments ($10 < y < 50$ and $y > 50$).

However, if $x = 50$, an individual is adapted for good environments, i.e., fitness is low (zero) for bad environments ($y < 50$) and extremely high for good environments ($y > 50$). The fitness function $v(y,x)$ for phenotypes $x$ in a given environment $y$ is a function with a peak (Fig. 1b).
Suppose that the probability distribution of daily food abundance $d(y)$ is approximated by a distribution with mean $E(y) = 50$ (Fig. 1c). Then the fitness $f(x)$ of an individual associated with a phenotype $x$ is an weighted sum of all possible environmental fitnesses $v(y,x)$ by their distribution $d(y)$ (equation (2)). The probabilistic optimum $x_p$ is then defined on the phenotypic fitness $f(x)$ as:

$$f(x_p) = \max f(x) \text{ (Fig. 1d).}$$

In contrast, the deterministic optimum $x_d$ is the optimal phenotype in the average environment, that is $f(M,x_d) = \max f(M,x)$, where $M = 50$ is the expectation of $y$, i.e., $M = \int d(y) dy$ (Fig. 1b). In this case, the probabilistic optimum $x_p(=30.89)$ is always smaller than the optimum in the average environment $x_d(=33)$.

In foraging theories, the concept of risk-sensitivity has been specifically developed to deal with daily uncertainty in food acquisition by animals (Stephens and Krebs, 1986; Real and Caraco, 1986). This body of theory reveals that animals often show sensitivity to the variance and skewness of a temporal distribution of foods. This demonstrates that not only the mean, but also the entire distribution of food availability is important for the evolution of animal behaviour. The expected utility theory used in risk-sensitive foraging (Real and Caraco, 1986) is a specific form of weighted average, in which the fitness function is an increasing function of the amount of food. In dynamic programming, in every time step of decision-making, the overall fitness of an individual is calculated...
from the weighted average of individual fitnesses of all possible states (Mangel and Clark, 1988).

4.2 UNCERTAINTY AT POPULATION LEVEL

Phenotypic variation among individuals of a population is common in many traits, such as body size. Such individual variation arises because environments differ among individuals. Therefore, environmental uncertainty may also appear as phenotypic variation in a population. Most important cases are when phenotypic variation occurs as a result of cumulative effects of past environmental differences.

Here probabilistic optimization can be stated as follows (Yoshimura and Shields, 1987). Actual (observed) survivorship and reproduction is determined by the phenotype of an individual for a given environment. Therefore, phenotype is the criterion for realised (observed) fitness. Because of this, we often compare observed mean phenotypes with optimal phenotypes as a measure of achievement of optimality (adaptation) by natural selection (Price and Waser, 1979; Roff, 1981).

However, the comparison based on this (deterministic) phenotypic optimum is not valid if there is variation in phenotypes. The evolutionary criterion of fitness is the genotypes that are selected through natural selection. For a given genotype, phenotypic variation is expressed as a probability.
The fitness of a genotype is the weighted sum of the fitnesses of all the phenotypes associated with the genotype, the probabilistic genetic optimum \( \text{equation (3)} \). We can then compare the observed mean phenotype with this genetic optimum.

Phenotypic variation in body size is mathematically expressed as follows (Fig. 2). Let phenotypic fitness \( f = f(x) \), with a single peak (Fig. 2a: dotted line), and \( h(x, z) \) be a probability distribution of body size \( x \) for a given genotype \( z \). Suppose that genotype \( z \) controls the mean body size of a normal distribution with a constant variance (Fig. 2b: three genotypes are shown). We assume here that the mean body size can shift continuously by changing genotypes. Then the fitness of the genotype \( w(z) \) is the weighted sum of all the phenotypic fitnesses \( f(x) \) with their distribution \( h(x, z) \) (Fig. 2a: solid line) \( \text{equation (3)} \). Here the phenotypic optimum \( x_{\text{max}} \) represents the trait that achieves the highest reproductive success in the environment, i.e.,

\[ f(x_{\text{max}}) = \max_x f(x) \]

In contrast, the genotypic optimum \( z_{\text{max}} \) is the trait selected by natural selection, i.e.,

\[ w(z_{\text{max}}) = \max_z w(z) \]

In general, the two optima differ in their values. In this example, the genetic optimum \( z_{\text{max}} \) is always smaller than phenotypic optimum \( x_{\text{max}} \) (Fig. 1a).

The discrepancy between genetic and phenotypic optima can be illustrated as follows: Suppose that 2 meters is the optimum height for a man, but that if he is more than 2 meters tall (even slightly) be...
tends to kill himself by banging into the tops of door frames. A critical point is that genotypes
determine the height only on average, because their environments vary. We have to consider all the
individuals for a given genotype. For people associated with an average 2-meter genotype, nearly
half of them become more than 2 meters tall and are knocked out by the door frame. Therefore, the
optimal average height (genotype) is actually smaller than 2 meters. For this optimal genotype, most
people are suboptimal, but their loss of fitness is much less than killing themselves, and a very few
will be lost due to their being >2 meters in height. In other words, the deterministic optimum height
lies above the probabilistic genetic optimum.

More generally, it is well known that there is a discrepancy between phenotypic and genetic optima
in most genetic systems because of various genetic constraints, such as segregation, recombination,
and mutation (Crow and Kimura, 1970), and because of environmental variation (Mountford, 1968;
Lalonde, 1991). For example, in quantitative traits like body size, the phenotypes of offspring vary
from parental phenotypes.

The body-size example is a case when phenotypic variation appears on the target trait for which we
evaluate the optimality. However, it may also appear in correlated traits, which in turn affect the
optimality of the target trait. Here phenotypic correlation can be either positive or negative.
Allometry (e.g., in body size) is an example of a positive correlation (Schmidt-Nielsen, 1984).

Negative correlation is often known as a trade-off (Roff, 1992; Stearns, 1992). It is important that phenotypic variation in such correlated traits can affect the optimality of the target traits. For example, if there is a trade-off between current clutch size and future reproduction (via parental survivorship), anticipated variation in future reproduction should be accounted for through the current clutch size (Yoshimura and Shields, 1992; Lalonde, 1991).

4.3 UNCERTAINTY AT GENERATION LEVEL

Fitness varies over generation times. Natural populations often fluctuate widely due to long-term environmental changes in weather and other environmental factors (Andrewartha and Birch, 1954).

Similarly, the multiplicative growth rates of a genotype in a population should also vary according to environmental conditions. Here, variation in growth rates might play an important role in the evolution of many phenotypic traits (Philippi and Seger, 1989; Bulmer, 1994; Yoshimura and Clark, 1991). In order to assess the effect of the variation in growth rates on natural selection, we have to evaluate the long-term growth rate of a genotype. Here the appropriate concept of fitness is the average (expected) growth rate per generation. This average is called geometric mean fitness, because it is the geometric mean of multiplicative growth rates (Yoshimura and Clark, 1991; Lewontin and Cohen, 1960).
The principle of probabilistic optimisation (equation (1)) appears in the concept of geometric mean fitness, as follows. Variation in growth rates is expressed as a probability distribution, and geometric mean fitness is a specific form of weighted sum of all growth rates within the distribution (equation (5)). This becomes evident when we take the logarithm of the geometric mean fitness, which is the usual arithmetic mean of logarithmic growth rates (equation (6)).

Mathematically, geometric mean fitness can be derived from the population growth as follows.

Geometric mean fitness is a specific form of probabilistic optimization, where the fitness function is a logarithm of population growth rates. Consider the population dynamics of a given genotype \( z \) for an organism with discrete generations: 
\[
N_z(t+1) = w_z(t)N_z(t), \quad \text{for } t = 0, 1, 2, \ldots,
\]
where \( N_z(t) \) is the population size and the fitness of a genotype \( z \), \( w_z(t) \), is expressed as the population growth rate at generation \( t \). Then the population size at generation \( t \) is given by:
\[
N_z(t) = w_z(0)w_z(1)w_z(t-1)N_z(0) = \prod_{i=0}^{t-1} w_z(i)N_z(0) \quad \text{(7)}
\]

The geometric mean fitness is then defined as an average population growth rate per generation:
\[
G(z) = \prod_{i=0}^{t-1} w_z(i)^{1/t} \quad \text{Suppose that the population growth rate } w_z(t) \text{ is randomly drawn from a probability distribution } p(w_z) \text{ for a given genotype } z. \text{ Then the geometric mean fitness is expressed by the probability distribution } p(w_z) \text{ as:}
\]
Here genotypes with the highest geometric mean fitness (max $G(z)$) should be selected through natural selection. Taking logarithm of equation (8), we get:

$$ \log G(z) = \int_0^1 p(w;z) \log(w) dw $$

Here the probabilistic optimization (equation (1)) is a weighted average with the weight $f(w) = \log(w)$. As in the previous examples, geometric mean fitnesses lie below arithmetic mean fitnesses in variable environments. The difference between geometric mean and arithmetic mean fitnesses increases when environments fluctuates strongly, because variation in growth rates increases. Suppose that an organism produces two offspring on average in a generation. In stable environments, after three generations, we expect $2 \times 2 \times 2 = 8$ offspring. However, in changing environments we may expect, say, $2 \times 1 \times 3 = 6$ offspring. In both environments, the mean fitness is same (i.e.,

$$(2 \times 2 \times 2)/(2 + 1 + 3) = 0.82$$

But the geometric mean fitness is lower ($((2 \times 1) \times 3)^{1/3} = 1.82$) in the variable environment, than in the constant environment ($2 \times 2 \times 2)^{1/3} = 1.2$). Since the population reaches only 6 individuals after three generations, the average growth rate of 1.82 individual/generation is a correct measure of fitness. To reiterate, the probabilistic optimum is based on geometric mean fitness, and the deterministic optimum is based on arithmetic mean fitness.
This example indicates that variation in growth rates decreases geometric mean fitness. Because of this, the geometric mean fitness is often approximated with mean and variance using a variance-discount method (Fig. 3; Frank and Slatkin, 1989; Gillespie, 1977; Yoshimura and Clark, 1991). Such approximation clearly depicts the effect of variance. As in the previous calculus example, variance in population growth rate reduces the geometric mean fitness. Even if the mean $w$ is smaller, if the variance of $w$ is smaller, the geometric mean fitness can be higher (Fig. 3).

However, ironically such approximation concentrates only on the effects of mean and variance and ignores the entire distribution of growth rates. In addition, the approximation also assumes the normal distribution of growth rate with small variance (Yoshimura and Jansen, 1996). Therefore, it is not applicable to a case when variance is large or when extinction is a prominent possibility. This is evident from the logarithmic function in geometric mean fitness: the weight of negative growth is much higher than the weight of positive growth, because the logarithm drops faster on the negative side than increases in the positive side. In the limit, if fitness falls to zero in any generation, arithmetic mean fitness will still be positive, but geometric mean fitness will be zero.

What is the probability distribution best fit to the distribution of population growth rates? Growth
rate \( w \) is a nonnegative variable. Therefore, normal distribution that can take negative values is not appropriate. In this sense, lognormal distribution is more appropriate or at least applicable. Here we show the geometric mean fitness becomes extremely simple when the lognormal distribution is assumed in population growth rates. Let population growth rate \( w \) follows a lognormal distribution such that

\[
P(w; m_z, \sigma_z) = \frac{1}{w\sqrt{2\pi \sigma_z}} \exp\left(-\frac{(\log(w) - m_z)^2}{2\sigma_z^2}\right)
\]

(10)

where \( P(w; m_z, \sigma_z) \) is the probability distribution of \( w \) with mean \( m_z \) and variance \( \sigma_z \) for genotype \( z \). Then the logarithmic form of geometric mean fitness (equation (9)) can be solved analytically and reduces to the mean of the lognormal distribution \( m_z \), such that (see Appendix for derivation):

\[
\log G(z) = \log G(m_z, \sigma_z) = m_z = E_z(\log(w))
\]

(11)

It has been believed that variance is important in adaptation in stochastic environments. However, it may be an artefact of our use of multiplicative population growth rates. The correct measure may be the logarithmic population growth rates. The simple 'arithmetic' mean of the logarithmic growth rates is the fitness over generation time. In this measure, variance and the shape of the probability distribution does not affect the overall fitness over generation time.

5. EFFECTS OF UNCERTAINTY
How strong is the effect of uncertainty on natural selection? How large is the discrepancy between the deterministic and probabilistic optima for phenotypes, genotypes in a generation or genotypes across generations? This depends on two factors: (1) the fitness response to phenotypes or environmental conditions (the shape of functions $v$ and $f$ and the logarithm of geometric mean fitness) and (2) the degree of uncertainty (the shape of probability distributions $d(\alpha, \beta)$ and $p(w; z)$, e.g., variance and skew; see equations in Tables 1 and 2). Even though exact quantitative differences depend on the exact shape of individual fitness and probability distributions, in general, we can state that sharp fitness responses (steep functions) and large degrees of uncertainty (flat distributions) tends to lead to a large discrepancy between the deterministic and probabilistic optima (Yoshimura and Shields, 1995).

The variance-discount method is often used to estimate the discrepancy quantitatively, e.g., the $Z$-score model (Stephens and Krebs, 1986) in risk-sensitive foraging. However, we need to be aware that this approximation ignores the higher order terms of central tendency in probability distributions and may result in a large discrepancy from true probabilistic optima, as in the usual mean fitness approaches. As is discussed in the previous section, the limitation of variance-discount methods becomes clear when we apply them to geometric mean fitness.
Reinforcing and extending earlier generalisations, we should also note here that which direction the
probabilistic optimum shifts from the deterministic optimum can be simply identified (Figs. 1-3).

In the case of geometric mean fitness, it is always smaller than the arithmetic mean fitness (Figs. 3
and 4). Mathematically, this directionality can be often characterised by Jensen's inequality which
compares the expectation of values (here, probabilistic optimum) and the value of an expected factor
(here, deterministic optimum) (Karlin and Taylor, 1975).

Equation (10) has an important meaning for the strategy of species (see also equations (1) and (2) of
Table 2). As a thought experiment, we consider two typical species A and B. The reproduction rates
during three generations are assumed as follows:

Species A: \( r(1) = r(2) = r(3) = 1 \).

Species B: \( r(1) = 1, \quad r(2) = 0.001, \quad r(3) = 1000 \).

Species A has a safer strategy such as mammals, while species B takes a risky strategy like fish and
plankton. For both cases, equation (10) leads to \( w_g(z) = E_x \{ \log(r) \} = 0 \), so that the geometric
mean fitness takes the same value; the population size of each species is unchanged after three
generations. In contrast, the mean fitness for both species largely differs. The arithmetic mean fitness
for species B is much larger than that of species A. Most fish must release a huge amount of eggs to
cope with variable environments.
The empirical studies of geometric mean fitness is extremely difficult, because severe stochastic events are rare and not measurable (Yoshimura and Clark, 1991). This situation is also reflected in the empirical studies. Only few trial attempts are seen for the effects at the level across generations, e.g., the cabbage butterfly (Root and Kareiva, 1984) and the Great Tit (Boyce and Perrins, 1987).

However, these attempts are not inconclusive. In contrast, the effects of uncertainty is well documented at the level of an individual (for many empirical studies, see Stephens and Krebs, 1986; Real and Caraco, 1986) and few good examples are reported at the level of a population (e.g., Price and Waser, 1979; Yoshimura and Shields, 1995). The current analyses of geometric mean fitness may help empiricists to measure the effects of cross-generational uncertainty on natural selection.

As in Monod's famous essay (Monod, 1971) "Chance and necessity," chance (or uncertainty) may be equally as important in evolution as necessity (causality). **6. RESULT**

Chance and necessity governs the evolution of organisms (Monod, 1971). The traditional statistical theory of natural selection has been developed based mostly on mean fitness, one central tendency, and it describes the causal "necessity" of evolution. Only in a few case, variance, the second order measure, is included as a variance discount. In contrast, the current probabilistic theory covers an entire probability distribution of fitness and it elucidates the intertwining features of "chance".
As I showed, this basic principle applies to problems of uncertainty in all three major categories of uncertainty: (1) behavioural decision-making of an individual (individual level: e.g., risk-sensitive foraging and dynamic behaviour), (2) phenotypic adaptation of life-history and behavioral traits (population level: e.g., body size, dispersal strategy), and (3) population dynamics and evolution (cross-generation level: e.g., risk-spreading, bet-hedging).

As in Monod’s famous essay (Monod, 1971) “Chance and necessity,” chance (or uncertainty) may be equally as important in evolution as necessity (causality). It has been shown that environmental uncertainty often relates to many other issues in evolution and ecology (Yoshimura and Clark, 1993; Bulmer, 1994), e.g., game theory (Ellner, 1985), kin selection (McNamara, 1995), and community diversity (Chesson and Warner, 1981). However, we still have a very limited knowledge about the importance of uncertainty in the evolution of organisms. For example, we have only just started to characterise the basic property of randomness in fluctuating environments, such as 1/f-noise (Halley, 1996). I hope that this synthesis will promote better understanding of the probabilistic nature of natural selection.

Acknowledgements
I would like to thank Christoph Thebaud, Vincent Jansen and John Lawton for helpful comments on the previous manuscript.

Acknowledgements

Please include, at the end of the acknowledgements, a declaration that the experiments comply with the current laws of the country in which they were performed.

Example:

Acknowledgements. We thank the staff of the Los Tuxtlas Biological Station for their continuous support, and H. Lambers, E. van der Maarel, and M.J.A. Werger for their comments on an earlier draft of the manuscript. The IBM Scientific Center of Mexico and the Department of Experimental Plant Ecology of the Catholic University of Nijmegen, The Netherlands, kindly provided computer facilities. We were supported by grant nr. W84-204 of The Netherlands Foundation for the Advancement of Tropical Research (WOTRO).
Acknowledgments. Dale Roberts, Kristina Jones, Judy Anderson, Denise Stevenson and Dale Gardner assisted in the field. Mark Rausher supplied the hand-held computers. This research was supported by National Science Foundation Grant BSR-8506064. P. Turchin was supported by NSF Grant BSR-8605303. Christoph Thébaud, Vincent Jansen and John Lawton provide helpful comments on the previous manuscript. This work was supported by grants-in-aid from the Ministry of Education, Culture, Sports, Science and Technology of Japan.
References


York.


APPENDIX

We solve the logarithmic form of geometric mean fitness (equation (8) to derive equation (10) when

\[ P(r) = P(r; m_z, \sigma_z) \]

is a lognormal distribution (equation (9)):

\[
\log G(r; m_z, \sigma_z) = \int_0^\infty \log(r) \left( \frac{1}{r \sqrt{2\pi \sigma_z}} \right) \exp\left( -\frac{(\log(r) - m_z)^2}{2\sigma_z^2} \right) dr
\]

(A1)

Let \( \log(r) = y, r: 0 \to \infty \). Then, \( dr = r dy, y: -\infty \to +\infty \) and we get

\[
\log G(r; m_z, \sigma_z) = \int_{-\infty}^{\infty} y \left( \frac{1}{\sqrt{2\pi \sigma_z}} \right) \exp\left( -\frac{(y - m_z)^2}{2\sigma_z^2} \right) dy
\]

(A2)

Then, let \( y - m_z = x, \frac{1}{\sqrt{2\pi \sigma_z}} = a, \frac{1}{2\sigma_z^2} = b \), equation (A2) becomes

\[
\log G(r; m_z, \sigma_z) = a \left[ \int_{-\infty}^{\infty} x \exp(-bx^2) dx + m_z \left( \int_{-\infty}^{\infty} \exp(-bx^2) dx \right) \right]
\]

(A3)

Here let \( F(x) = \exp(-bx^2) \). Then we get \( \frac{dF}{dx} = -2bx \exp(-bx^2) \), which is transformed to

\[
xF(x) = -\frac{1}{2b} \frac{dF}{dx}
\]

Therefore, we get \( \int xF(x) dx = \left[ -\frac{1}{2b} F(x) \right]_a^b \)

The right-hand side of Equation (A3) is now calculated as follows.

\[
\int_{-\infty}^{\infty} x \exp(-bx^2) dx = \left[ -\frac{1}{2b} \exp(-bx^2) \right]_a^b = 0
\]

And from \( \int_{-\infty}^{\infty} \exp(-bx^2) dx = \frac{\sqrt{\pi}}{2\sqrt{b}} \), we get

\[
\int_{-\infty}^{\infty} \exp(-bx^2) dx = 2 \int_{0}^{\infty} \exp(-bx^2) dx = \frac{\sqrt{\pi}}{\sqrt{b}}
\]
Equation (A3) is then rewritten as

\[
\log G(r; m_z, \sigma_z) = a \left\{ 0 + m_z \times \frac{\sqrt{\pi}}{\sqrt{b}} \right\} = \frac{1}{\sqrt{2\pi\sigma}} \times m_z \times \sqrt{2\pi\sigma} = m_z
\]

Thus equation (10) is derived.
Table 1. Terms and equations for the fitness at the levels of an individual and a population.

- $x$: an environmental factor for an individual
- $y$: the phenotype of an individual
- $z$: a genotype
- $H$: The domain of a given distribution $h$
- $f_i(x,y)$: fitness of an individual with phenotype $y$ in environment $x$
- $h_i(x)$: probability distribution of environment $x$
- $f_p(y)$: fitness of an individual with phenotype $y$
- $h_p(y,z)$: probability distribution of phenotypes $y$ for a given genotype $z$
- $w_p(z)$: fitness of a genotype $z$ (within a generation)

\[
\begin{align*}
w_i(y) &= \int_{y \in h_i(x)} f_i(x,y)h_i(x) dx \quad (1) \\
w_p(z) &= \int_{y \in h_p(y,z)} f_p(y)h_p(y,z) dy \quad (2) \\
w_p(z) &= \sum_{y \in h_p(y,z)} f_p(y)h_p(y,z) \quad (3)
\end{align*}
\]

Note: the suffix $i$ in equation (1) denotes the individual level ($p$: population level).
Table 2. Terms and equations for the geometric mean fitness.

- $r$: fitness per generation measured as multiplicative growth rates
- $f_g(r) = R = \log r$: logarithmic fitness at a generation
- $h_g(r,z)$: probability distribution of fitness $r$ over generations for a given genotype $z$
- $w_g(z) = w_G(z)$: logarithmic geometric mean fitness of a genotype $z$
- $H_g(e^R,z)$: probability distribution (or domain) of $R$ for a genotype $z$ in log scale

$$w_g(z) = \int_{r \in h_g(r,z)} f_g(r) h_g(r,z) dr = \int_{r \in h_g(r,z)} \log r h_g(r,z) dr \quad (1)$$

$$w_G(z) = \int_{e^R \in H_g(e^R,z)} RH_g(e^R,z) e^R dR \quad (2)$$
**Figure Legends**

Fig. 1 - Probabilistic optimization of uncertain daily food amounts $x_y$ for a given phenotype $y_x$. (a) the fitness $f_i(x_y, y_x)$ of an individual with a phenotype $y_x$ in environment $x_y$. The phenotype $y_x = 10$ is adapted for bad environments, $x_y = 30$ for intermediate environments and $x_y = 50$ for good environments. (b) the fitness $f_i(x_y, y_x)$ for phenotypes $y_x$ in a given environment $x_y$. The deterministic optimum $Y_x (=33)$ is the optimal phenotype in the average environment $x_{mm} (=50)$. (c) the (Gaussian) probability distribution of daily food abundance $h_i(y_x)$ with the mean $E(x_y) = 50$. (d) The phenotypic fitness of an individual $w(f(x,y))$. The probabilistic optimum $Y_x (=30.89)$ is the maximum of $w(f(x,y))$ for $y_x$. The probabilistic optimum $Y_x (=30.89)$ is different from the deterministic optimum $Y_x (=33)$.

Fig. 2 - Probabilistic optimization of body size $y_x$. (a) $w_i(y_x)f(x)$: the phenotypic fitness of body size (the dotted line); $w_p(z)$: the genotypic fitness of mean body size (the solid line); $Y_{x_{max}}$ represents the optimal phenotype (individual body size); and $Z_{z_{max}}$ represents the optimal genotype (mean body size). (b) $h_{ij}(x_y, z)$: probability distributions of body size $y_x$ for a given genotype $z$. The normal distributions are assumed with a constant variance and genotypic mean body sizes $z$ (three genotypes are shown). The genetic optimum $Z_{z_{max}}$ is different from the phenotypic optimum $Y_{x_{max}}$. 

---

53
Fig. 3 - Probabilistic optimization of population growth rates $r$ over cross-generations. (a) $f(r) = \log(r)$: the log population growth rate plotted against multiplicative growth rate $r$. (b) $h_g(r, z)$: probability distributions of multiplicative growth rate $r$ for three genotypes. The log normal distributions are assumed with a constant variance and genotypic mean body sizes $z$ (three genotypes are shown: $z_1, z_2$ and $z_3$). (c) The log-transformed generational fitness $F(R) = F(\log(r)) = R$. (d) $h_g(\log(r), z)$: probability distributions of log growth rate $\log(r)$ for three genotypes (transformed from (b)).

Fig. 4 - Mean-variance approximation of geometric mean fitness: $G(r_w) \sim \mu - \sigma^2/2\mu$, where $\mu$ and $\sigma^2$ are mean and variance of population growth rates $r_w$, respectively. Isoclines indicate several three different level of $G(r_w)$ with grey scale (from top: 1.5, 1 and 0.5). The combination of low mean and low variance (circle) may be better than that of high mean and high standard deviation (cross). On an isocline, two genotypes have equal geometric mean fitnesses.
Fig. 1.
Fig. 2
Fig. 3.
Fig. 4.
Fig. 1
Fig. 2
Numerous hypotheses have been advanced to explain the evolution of long perfectly synchronized life cycles, e.g., predator satiation and asynchronization with predator cycles (Lloyd and Dybas, 1966; Hoppensteadt and Keller, 1976), and larval competition (Bulmer, 1977). These arguments are summarized and synthesized in Williams and Simon 1995, Table 1. Two major hypotheses compete to explain the evolution of prime number reproductive intervals (life cycles) among periodical cicadas. The anti-predator hypothesis claims that prime number intervals help to protect cicadas from being overwhelmed by their predators.
This hypothesis can explain the origins and maintenance of periodical cycles, but it cannot explain why prime number cycles of periodical cicadas are have originated in the first place (May, 1979). The hybridization hypothesis claims that prime numbers greatly reduce the chance of hybridization among cicada broods (Cox and Carlton, 1988; Cox and Carlton, 1991; Yoshimura, 1997).

In the hybridization hypothesis, the origin of periodicity is due to environmental cooling during the Pleistocene Ice Ages. Apart from the timing of adult emergence, ancestral periodical cicadas are assumed to be very similar to typical members of the Cicadidae, emerging annually and spending 5-9 years in the larval stages based on the life history of Okanagana rimosa, a closely related species. Their determinant of maturation is cumulative temperature because their growth depends on that of the host plants, trees, (Yoshimura, 1997). Periodicity is originally caused by global cooling at the onset of the Pleistocene. Cooling causes a large delay in larval growth and additional mortality before emergence, resulting in a massive decrease in the adult density (Cox and Carlton, 1988; Cox, 1992; Yoshimura, 1997). The synchronization of cycles or periodicity is strongly selected at this stage owing to the adult densities approaching extinction.
The determinant of maturation switches from temperature to time (periodicity).

The selection of prime number intervals follows the evolution of periodicity and long intervals (Cox and Carlton, 1988; Yoshimura, 1997). Initially, a variety of incipient periodical cicada brood life-cycle lengths exist. Within a brood, females produce offspring on different lengths. By chance, some broods emerge concurrently; these hybridize randomly. The genetics of hybrids are unknown, but from the current periodical cicadas, it is likely to be Mendelian inheritance with shorter or longer cycle dominance.

These hybrids are eliminated because of their small population sizes and lack of coordinated intervals. Such co-emergence is highly disadvantageous and leads to the extinction of broods. Here, the frequency of co-emergence depends on intervals. Note that the lowest common multiplier (L.C.M.) of a prime number is usually large in contrast with those of non-prime numbers. Prime number intervals less frequently co-emerge with other intervals than non-prime number intervals. Non-prime number intervals suffer serious hybridization loss. Once the density of non-prime number broods decreases, selection against hybridization increases exponentially because of frequency-dependent mating between different broods (Yoshimura and Clark, 1994).

Yoshimura, 1997). Through frequent hybridization and elimination of non-prime number...
intervals, only prime number intervals sustain population densities and all other intervals are wiped out completely.

The hybridization hypothesis shows the advantage of prime number intervals in hybridization. However, the hypothesis does not confirm the evolution of prime number intervals, eliminating all other intervals, because this advantage of prime number intervals depends on both population size (density) and frequency of all intervals. The loss of fitness by hybridization varies depending on both population sizes and frequencies. When two cycles co-emerge, the cycle with the larger population size has a small loss of offspring by hybridization, while that with the smaller population size has a large loss, because of frequency-dependent hybridization. Thus the evolution of prime number intervals depends on the trade-off between disadvantage of hybridization, population sizes, frequency of intervals and growth conditions which affect the latter two. In this paper, we test the hybridization hypothesis using a deterministic simulation model. We show that prime number intervals persist while all other cycles go extinct under certain conditions, i.e., marginal (near extinction) environmental conditions, as suggested by Yoshimura (Yoshimura, 1997).
MODELS

In our model, we assume identical population sizes of insects with various established cycles (10-20 year cycles). We assume that survival (mortality) rate $S(t)$ per year is constant. The larval population size decreases with a constant survival rate $S$/year. (Karban, 1982) This means that the cicadas with longer intervals suffer higher mortalities. The clutch size $C$ of a copulated adult female with interval $y$ is assumed to be an increasing function of interval (growth period) $y$, such that $C(y) = Ry$, where $R$ is a constant. It is because reproductive output (clutch size) in insects often correlates with effective cumulative temperature (Chapman, 1971). This means that longer intervals (growth period) have larger clutch sizes, but suffer higher mortality per emergence.

Note that there is a trade-off between intervals with respect to overall juvenile survival rate and clutch size $C$ per cycle. In contrast, successful emergence rate $E(0 < E < 1)$ is kept constant, assuming emergence failure is independent from intervals. Emergence failure in cicadas is frequently seen in nature.
The allele controlling life cycle follows a single-locus Mendelian inheritance system with shorter cycle dominance, such that genotype \((i,j)\) corresponds to phenotype \(i\) (years) if \(i < j\). For example, when 12- and 15-year life cycle genotypes co-emerge, all the hybrid offspring \([12,15]\) appear after 12 years (Cox and Carlton, 1991; Lloyd et al., 1983). The number of hybrid individuals is assumed to be proportional to the relative population sizes of co-emergent broods (Ebert, 1992).

We build a discrete population model consisting of three major parameters: survival rate \(S\), emergence rate \(E\), and clutch size factor \(R\). We keep track the population sizes of all the broods with respect to interval genotypes including hybrids and birth year with larval and adult stages. For genotype \([i,j]\) of a given birth year, the larval population size of a brood at time \(t\) \((N_{l,t})\) follows the equation:

\[
N_{l,t}(i,j) = S \times N_{j,t}(i,j) \tag{1}
\]

where \(S(0 < S \leq 1)\) is survival rate at \(t\) (year). \(S\) is constant, because all broods occupy the same habitat. Adult brood size \(N_{A}\) (only appear in emergence year) is
where \( E(0 < E < 1) \) is a constant emergence rate. The offspring (larval) brood size between \([i, j]\) and \([m, n]\) is then assumed to be a function of interval \((y)\), such that:

\[
\text{Num. offspring} = \frac{1}{2} N_{ij}(i,j) \times F(N_{ij}(m,n)) \times C(y) \tag{3}
\]

where \( F \) is the frequency of the target brood, such that

\[
F(N_{ij}(m,n)) = \sum N_{ij},
\]

where \( \sum N_{ij} \) is the sum of all co-emergent adults for a given year, and \( C \) is the clutch size and a function of the cycle:

\[
C(y) = R \times y \tag{4}
\]

where \( R (R > 0) \) is a yearly increase rate of clutch volume.

The genotype of offspring between \([i, j]\) and \([m, n]\) has 4 pattern: \([i, m]\), \([i, n]\), \([j, m]\) and \([j, n]\). So, the offspring brood size at each genotype is determined for the sum of eq.(3). For...
example, the offspring brood size of genotype \([i,m]\) follows:

\[
N_{t+1}(i,m) = \sum_{x} \sum_{z} \left[ \frac{1}{2} \cdot N_{t}(i,x) \cdot F(N_{t}(m,z)) \cdot G(y) \right]
\]

(5)

As for the other genotypes, it is similar.

To avoid introducing an advantage to any specific cycle, we keep the initial conditions of all intervals identical. In the initial settings, we start 11 pure broods with a 10-20 yr intervals. All the initial brood sizes /cycle are 1000 first-instar larvae (the first year). We will test whether prime number intervals (11, 13, 17 and 19) are selected for within 10-20 yr intervals and in what conditions.

In order to introduce the selection on small population sizes (Yoshimura 1997), we measure the abundance of cicada \((N_{t} \text{ and } N_{A})\) by the number of individuals (integers). It leads disadvantages for smaller broods. For example, suppose that survival rate \(S = 0.955\). The brood size of \(N_{t} = 1000\) becomes \(N_{t+1} = 1000 \times 0.955 = 955\), whereas that of \(N_{t} = 100\) becomes \(N_{t+1} = 100 \times 0.955 = 95.5\). This disadvantage of smaller brood sizes becomes larger when brood sizes decrease. In a small brood, the actual survival rate, \(S\), becomes very relatively low. In extremity, when equation (5) is less than 4, the number
of offspring (eq. (5)) is evaluated to zero, because the number of offspring for each genotype (4 patterns) becomes less than 1 individual. Thus, smaller broods have a disadvantage, when the population size is counted as an integer.

The hybridization yields a small brood size of mostly hybrids (Yoshimura, 1997). The hybridization between genotype \([i, j]\) and \([i, j]\) makes three genotypes (broods): \([i, i]\), \([i, j]\), and \([j, j]\). In our model, brood \([i, j]\) and brood \([i, j]\) co-emerge at \(t\) year. The brood \([i, j]\) reduces its population size considerably and results in a huge disadvantage. On the other hand, brood \([i, j]\) and brood \([j, j]\) hybridize and make three genotypes (broods): \([i, i]\), \([i, j]\), and \([j, j]\). Brood \([i, j]\) and brood \([j, j]\) then also reduce their population sizes.

RESULTS AND DISCUSSION

We simulate the population dynamics of cicadas from eleven pure broods at 10-20 yr intervals. Figure 1 shows a case where only prime number cycles survive. All non-prime number cycles are eliminated within 200 years (Fig. 1A). In contrast to the elimination process of non-prime number intervals, the subsequent selection among prime numbers lasts many hundreds of years (Fig. 1B). Furthermore, in some conditions, coexistence is possible at least within a couple thousand years (Fig. 1C).
Next we evaluate the parameter sensitivity for all three parameters: (1) larval (nymphal) survival rate $S$, (2) clutch size parameter $R$, and (3) emergence success $E$ (Fig. 2). Only the prime number cycles survive, but at the edge of survival limits. We find no region in which only non-prime cycles eliminate all other cycles. This suggests that the advantage of prime number cycles prevails specifically at the verge of extinction. In the $S-R$ and $S-E$ phase planes, prime number cycles are aligned along the edge of survival limits: shorter cycles with low $S$ and high $R$ or $E$ and longer cycles show the reverse pattern (Figs. 2A and B). The coexistence regions of two prime numbers are usually located slightly inside of the single-prime number regions, forming a shell structure in the $R-E$ phase plane (Fig. 2C). Thus, under a specific combination of the three parameters, $S$, $R$, and $E$, we find the dynamics result in the survival of only 13- and/or 17-year cycles (Fig. 2). Furthermore, the density reduction along the environmental (parameter) cline shows that the advantage of prime number appears sporadically (often discontinuously) at the verge of extinction (Fig. 2C).

Disadvantage of small broods is a prerequisite of Yoshimura's hypothesis (Yoshimura, 1997). In reality, a population size is finite and integer. The stability of a small
population is inferior to that of a large population in the same environment. Using the number of individuals (integer) as the abundance of population (brood), we include the innate disadvantage of small populations without additional assumptions. We should note that the Allee effect is expected to be much stronger in the small populations of periodical cicadas during ice ages. The variability in predation pressures and/or mate encounters should lead to an additional huge disadvantage on a small population, resulting in the quick elimination of small broods (see e.g., Tainaka, Hayashi and Yoshimura, 2006). It is important that we did not introduce any additional Allee effect, but the subtle effects of integer are sufficient for the selection of prime numbers.

Introduction of additional Allee effects may strengthen the selection of prime numbers, as well as increase the area of convergence (Fig. 2).

Our results demonstrate that the hybridization breakdown associated with co-emergence can indeed lead to the selection of prime number cycles. A brood under frequent hybridization tends to suffer reduced population size and this process is accelerated as the population size decreases owing to the frequency dependence of random mating (Fig. 1). (Kuno, 1992; Yoshimura and Clark, 1994). The density profiles also indicate the superiority of prime numbers near the extinction borders (Fig. 3). Almost
all non-prime number cycles disappear when the survival rate is slightly lowered.

Interestingly, the lower prime number cycles tend to have a separate density peak at
the edge of extinction (Fig. 2B), whereas density profiles are smoothly decreasing in
higher prime numbers (Fig. 3A).

Our results also indicate that prime number selection is a very rare event, occurring at
the verge of extinction (Figs. 2 and 3). This is probably why the evolution of prime
number periodicity was likely only in what is now the central and eastern United States,
where glacial advances created many refugia during the Pleistocene glaciation (Delcourt,
and Delcourt, 1987; Gates, 1993).

Our model is a deterministic simulation model without random numbers. The simulated
results are numerical calculations derived from set initial conditions; thus the selection
of prime number cycles is numerically shown. We also run simulations with variable
initial conditions. The results are almost same with those of identical initial conditions.

Which prime number cycles are established depends simply on the combination of three
key parameters—larval survival $S$, clutch size parameter $R$ and emergence rate $E$.

Figure 2 shows that there is a relatively broad range of environmental conditions in.
which both 13- and 17-year cycles are only fixed. In contrast, the range of 11-year.

interval is very narrow. The temporal isolation benefit of prime number reduces with.

shorter intervals. The advantage of shorter reproductive cycles seems to dominate in.

shorter intervals. Our results also show that 19-year intervals are plausible. We.

speculate that larva could not survive nineteen years in the soil or host trees cannot.
survive under such conditions.

There is one very important aspect of the biology of periodical cicadas that must be.
reconciled with the theory of the origination of prime-numbered life cycles presented in.
this paper and elsewhere (Yoshimura 1997; Cox and Carleton 1988, 1991) and that is.
the four-year acceleration hypothesis. There is strong evidence that four-year shifts in.
life cycle are common in the evolution of periodical cicadas: 1) the largest year classes.
broods of periodical cicadas are separated in time by four years, these are the only.
broods that overlap geographically (Lloyd and Dybas 1966, Lloyd and While 1976); 2) in.
the large, overlapping 17-year cicada broods, lagging broods seem to be increasing.
historically while leading broods, four years later, seem to be diminishing in numbers of.
populations (Kritsky 1988); 3) forests seem to be able to support more cicadas if they are.
separated into two year-classes spaced four years apart (Simon et al. 1981); 4) 17-year.
cicadas differ from 13-year cicadas in their nymphal growth patterns in possessing a.
4-year dormancy period in the second instar; if this dormancy period is lost, 17-year cicadas would be transformed into 13-year cicadas (White and Lloyd 1975). 5) Long Island, NY is a microcosm of periodical cicada evolution possessing independently derived populations of cicadas that appear in the same years as broods I, V, IX, and X in addition the native brood XIV (Simon and Lloyd 1982). 5) In the Midwestern US, the northern third of the distribution of 13-year cicadas is recently derived from 17-year cicadas that permanently switched their life cycle to 13 years and joined two different year classes of pre-existing 13-year cicadas (Martin and Simon 1988, Martin and Simon 1990, Simon et al. 2000, Marshall and Cooley 2000). Lloyd and Dybas (1966) suggested that 13-year cicadas evolved first and gave rise to 17-year cicadas when they acquired their 4-year dormancy period.

Our model is relatively simple and the actual evolution of periodical cicadas may have been more complicated. Selection pressures related to inferior hybrids between different life cycles could have resulted in the formation of 13-year cicadas as described by this model while the 17-year life cycle could have evolved via four-year accelerations from the 13-year cycle later in the Pleistocene when glaciation intensified (Zachos et al., 2001).
Furthermore, earlier in the Pleistocene, prime number fixation might not be achieved by a single glacial period, but may have extended over a few glacial periods. Hybridization might have taken place during interglacial periods. We should also note that the short-year-dominance genetic system is not essential for the selection of prime number intervals. The prime number intervals also appear under longer year-dominance or a genetic system in which the hybrids are immediately removed (unpublished data). Our results indicate that the disadvantage in hybridization resulting in prime number intervals appears under severe environmental conditions (at the verge of extinction), while coexistence of many intervals with shorter intervals under good environmental conditions...

Our model only deals with the origins of periodical cicadas under glacial environmental conditions (Cox and Carlton, 1988; Yoshimura, 1997). The current maintenance of the extremely high densities of cicada populations is a different problem (May, 1979). A newly recognized 13-year brood and 17-year type genotypes in 13-year cicadas are suspected to
have arisen from a relatively recent hybridization event after the onset of the most
recent interglacial period. (Martin and Simon, 1988; Marshall and Cooley, 2000; Cooley et al.,
2001; Cooley et al., 2003). Here the complete dominance of 13-year broods is suspected in
this hybridization process. Our results demonstrate that the Mendelian genetic system
is indeed enough to extinct all non-prime number intervals. Thus we have shown:
mathematically that co-emergence hybridization is indeed a plausible mechanism for
the evolution of prime number intervals. (to Chris: please rewrite the paragraph and
add the whole acceleration hypothesis jin)

The hybridization hypothesis of periodical cicadas is a temporal version of rendezvous
habitat selection (Rosenzweig, 1979). Rendezvous habitat selection is niche separation due
to the mating at specific host plants. In the case of periodical cicadas, niche separation
is achieved by emergent years, thus temporal separation, instead of spatial separation.
In both cases, the evolution of this kind of phenomenon is achieved by severe frequency
dependence in mating (Rosenzweig, 1979; Kuno, 1992; Yoshimura and Clark, 1994).

Acknowledgements

We thank Donald G. Miller, III, Michael L. Rosenzweig and anonymous referees for.
valuable comments. This work was supported by grants-in-aid from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

REFERENCES


<table>
<thead>
<tr>
<th>Page</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1303</td>
<td></td>
</tr>
<tr>
<td>1305</td>
<td></td>
</tr>
<tr>
<td>1307</td>
<td></td>
</tr>
<tr>
<td>1309</td>
<td></td>
</tr>
<tr>
<td>1311</td>
<td></td>
</tr>
<tr>
<td>1313</td>
<td></td>
</tr>
<tr>
<td>1315</td>
<td></td>
</tr>
<tr>
<td>1316</td>
<td>Sunderland, Mass.</td>
</tr>
<tr>
<td>1317</td>
<td></td>
</tr>
<tr>
<td>1319</td>
<td></td>
</tr>
</tbody>
</table>


Figure legends

Fig. 1. Population dynamics of 11 pure broods, 10-20yr intervals. Parameters are
$S=0.948$, $R=1.45$ and $E=0.2$. (A) The first 200 years in the case of only 17-year brood
survival. (B) The continuation of (A) up to 700 years. (C) 600 years in the case of both
13- and 17-year co-survival. Parameters are $S=0.943$, $R=1.63$ and $E=0.2$. Thick lines are
the populations of prime number broods. Thin lines are those of non-prime numbers.
Serated lines show a decrease in larval to adult stages and an increase by the egg-
laying. Irregular serrations are produced by a time lag caused by hybrid mating. All
non-prime number broods go to extinct during the first few hundred years.

Fig. 2. Thousand-year survival phase planes of prime numbers only (colored), both
prime and non-prime numbers (grey) and all extinction (white) for the three main
parameters. (A) Plane for larval survival rate $S$ and clutch size parameter $R$. The other
parameter is $E=0.2$. (B) Plane for larval survival rate $S$ and emergence success $E$. The
other parameter is $R=1.8$. (C) Plane for clutch size parameter $R$ and emergence success
$E$. The survival of only prime number broods appears at the edges of extinction. The
other parameter is $S=0.94$. The non-prime numbers (grey) means most phenotypes.
including hybrids and prime number intervals.

Fig. 3: Density profiles (log scale) for larval survival rate $S$, when emergence success is $E = 0.2$ and clutch size parameter is (A) $R = 1.6$ and (B) $R = 1.8$. The density profiles of larger prime number intervals tend to decreasing smoothly near the border of extinction (B), whereas those of smaller prime number intervals tend to have a separate peak near the border of extinction (B). The population sizes are measured at 1000 years unless exploded (calculations are terminated when $S > 0.96$).
Fig. 1A.
Fig. 1B.
Fig. 1C.

Fig. 2A.
Fig. 2B.
Fig. 2C.

Fig. 3A.
Fig. 3B.
<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤
<table>
<thead>
<tr>
<th>ページ 68: [3] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
<tr>
<td>フォント：Century,</td>
<td></td>
<td>フォントの色：赤</td>
</tr>
<tr>
<td>フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
ページ 68: [3] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 68: [3] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 68: [3] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 68: [3] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 68: [3] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 69: [4] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 69: [4] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 69: [4] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 69: [4] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤

ページ 69: [4] 書式変更  Taro HAYASHI  2008/01/21 16:40:00
フォント：Century, フォントの色：赤
フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤

フォント：Century, フォントの色：赤
<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ページ 69: [5] 書式変更</th>
<th>Taro HAYASHI</th>
<th>2008/01/21 16:40:00</th>
</tr>
</thead>
<tbody>
<tr>
<td>フォント：Century, フォントの色：赤</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
ページ 69: [5] 書式変更  Taro HAYASHI  2008/01/21 16:40:00

フォント: Century, フォントの色: 赤

ページ 69: [5] 書式変更  Taro HAYASHI  2008/01/21 16:40:00

フォント: Century, フォントの色: 赤

ページ 80: [6] 書式変更  Taro HAYASHI  2008/01/21 16:40:00

フォント: (英) Century, (日) MS明朝