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 Yoshimura[1,2,3]*~~,*~~, Yumi Tanaka[4], Tatsuya Togashi[2]~~2~~~~,~~, Shigehide Iwata[1] and Kei-ichi Tainaka[1]~~Yumi Tanaka[4],~~ ~~and Kei-ichi Tainaka[1]~~

~~Jin Yoshimura[1, 2, 3]*[#], Taro Hayashi[1]*, Kei-ichi Tainaka[1]~~ a~~And Chris Simon[4]~~

~~* Equally contributed.~~

~~[1]Department of Systems Engineering, Shizuoka University, Hamamatsu 432-8561, Japan.~~

~~[2]Marine Biosystems Research Center, Chiba University, Uchiura, Amatsu-Kominato, Chiba 299-5502, Japan~~

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

~~[4]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT~~

書式変更: 書式なし、行間 : 2 行
書式変更: 段落番号 : 現在の位置から開始
書式変更: フォント : (英) Times New Roman, 14 pt, 太字
書式変更: フォント : 14 pt
書式変更: フォント : 16 pt
書式変更: フォント : 16 pt, 太字
書式変更: 書式なし、行間 : 2 行, タブ位置: -5.39 字(なし) + -2.7 字 + 0 字 + 2.7 字 + 5.39 字 + 8.09 字 + 10.79 字 + 13.49 字 + 16.18 字 + 18.88 字 + 21.58 字 + 24.27 字 + 26.97 字 + 29.67 字 + 32.36 字 + 35.06 字 + 37.76 字 + 40.46 字 + 43.15 字
書式変更: 左揃え, 行間 : 2 行
書式変更: フォントの色 : 自動
書式変更: 上付き
書式変更: 行間 : 2 行

~~06269-3043 USA~~

~~# 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~~

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

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

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

[4]School 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)

書式変更: 左揃え，行間 ： 2 行，タブ位置： -5.39 字，左揃え + -2.7 字，左揃え + 0 字，左揃え + 2.7 字，左揃え + 5.39 字，左揃え + 8.09 字，左揃え + 10.79 字，左揃え + 13.49 字，左揃え + 16.18 字，左揃え + 18.88 字，左揃え + 21.58 字，左揃え + 24.27 字，左揃え + 26.97 字，左揃え + 29.67 字，左揃え + 32.36 字，左揃え + 35.06 字，左揃え + 37.76 字，左揃え + 40.46 字，左揃え + 43.15 字，左揃え

書式変更: 左揃え，行間 ： 2 行

書式変更: フォントの色 ： 自動

書式変更: 英語（米国）

~~*To whom correspondence should be addressed. jin@sys.eng.shizuoka.ac.jp~~

書式変更: フランス語（フランス）

書式変更: 行間 : 2 行

書式変更: フォント :（日）ＭＳ 明朝, フランス語（フランス）

書式変更: フランス語（フランス）

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

書式変更: フォントの色 : 自動

書式変更: フォントの色 : 自動

natural selection. ~~Environmental uncertainty can be expressed as a probability distribution. Probabilistic optimisation 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 ~~ty 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~~

書式変更: フォントの色 ： 自動

書式変更: フォント ： 太字, フォントの色 ： 自動

書式変更: フォント ： 10.5 pt, 英語（米国）

書式変更: フォント ： 10.5 pt

書式変更: フォント ： 10.5 pt, フォントの色 ： 自動

書式変更: フォント ： 10.5 pt

書式変更: フォント ： 10.5 pt, フォントの色 ： 自動

書式変更: フォント ： 10.5 pt

書式変更: 本文

書式変更: フォント ： 太字

書式変更: フォント ： 太字

書式変更: フォント ： 太字

~~**survival per year; clutch size; emergence success. Reproductive intervals from ten years to twenty years compete for survival in the simulations. The model makes threetwo 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~~

書式変更: フォント ： Times New Roman, 太字

書式変更: フォント ： 太字

書式変更: フォント ： Times New Roman, 太字

書式変更: フォント ： 太字

書式変更: フォント ： 太字

書式変更: フォント ： (日) ＭＳ 明朝

書式変更: フォント ： 太字

書式変更: 左揃え, 行間 ： 2 行

~~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 (Marlatt, 1907; 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

書式変更: フォント : 太字

書式変更: フォント : (日) ｩ

書式変更: 本文

コメント **[CS1]:** Marshall, D. C. 2001. Periodical cicada (Homoptera: Cicadidae) life cycle variations, the historical emergence record, and the geographic stability of brood distributions. Annals of the Entomological Society of America. Ann. Entomol. Soc. Amer. 94: 386-399.

書式変更: フォント : 太字

書式変更: フォント : (日) ｩ

書式変更: フォント : Times New Roman

書式変更: フォント : (日) ｩ

書式変更: フォント : Times New Roman

書式変更: フォント : (日) ｩ

書式変更: フォント : Times New Roman

書式変更: 左揃え, 行間 : 2 行

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~~theories~~ 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 ~~Next I will explain the~~ principles of probabilistic optimization in these categories are ~~:~~ all in ~~how uncertainty can be incorporated into optimality analyses. A canonical form of probabilistic optimization is a~~ some form of~~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

書式変更: フォントの色 : 赤

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.

書式変更: 行間 : 2 行

書式変更: フォント : 12 pt

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.

書式変更： フォント ： 斜体

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 $f_i(x,y)$ 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 $h_i(x)$ 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 $f_i(x,y)$ by their distribution $h_i(x)$ (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 $f_i(M, Y_d) = \max \quad f_i(M, y)$, where M (=50) is the expectation of x, i.e., $M = \int h_i(x)\, dx$ (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.

書式変更: フォント : 斜体

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).

書式変更: フォント : 斜体

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_{max} represents the trait that achieves the highest reproductive success in the environment, i.e., $f(Y_{max}) = \max f(y)$. In contrast, the genotypic optimum Z_{max} is the trait selected by natural selection, i.e., $w_p(Z_{max}) = \max w_p(z)$. In general, the two optima differ in their values. In this example, the genetic optimum Z_{max} is always smaller than phenotypic optimum Y_{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 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 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, 1998). 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).

書式変更: 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

~~2. THE PRINCIPLE OF OPTIMIZATION~~

~~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). 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 α and y β be individual and collective trait values, respectively. For example, if α x is a phenotype value, then β y is a genotype value associated with a distribution of phenotype value α x. Suppose $f(\alpha x, \beta y)$ is the fitness potential function of α x given β y. Then the canonical form of fitness $w(\beta y)$ is given as:~~

$$w(\beta)=\int f(\alpha,\beta)h(\alpha,\beta)d\alpha \qquad (1)$$

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

~~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~~

書式変更: 左揃え, 行間 : 2 行, タブ位置: 2.7 字, 左揃え + 1.71 字(なし)

書式変更: 左揃え, 行間 : 2 行

~~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 GOEMETRIC 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; Yoshimura and Clark, 1991).

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: $N_z(t+1) = r_z(t)\, N_z(t)$, for $t = 0, 1, 2, \ldots$, 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:

$$N_z(t) = r_z(0) r_z(1) \cdots r_z(t-1) N_z(t-1) = \left(\prod_{i=0}^{t-1} r_z(i) \right) N_z(0) \qquad (7)$$

The geometric mean fitness is then defined as an average population growth rate per generation: $G(z) = \prod_{i=0}^{t-1} r_z(i)^{(1/t)}$. Suppose that the population growth rate $r_z(i)$ is randomly drawn from a probability distribution $h_g(r, z)$ for a given genotype z. Then the geometric mean fitness is expressed by the probability distribution $h_g(r, z)$ as:

$$G(z) = \prod_{w} w^{h_g(w,z)} \qquad (8)$$

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 $f_g(r) = \log(r)$ (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).

書式変更: フォント : Times New Roman, 斜体, フランス語 (フランス) , 文字位置下げる 15 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 8 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 14 pt

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

$$P(r; m_z, \sigma_z) = \left(\frac{1}{r\sqrt{2\pi}\sigma_z}\right)\exp\left(-\frac{(\log(r) - m_z)^2}{2\sigma_z{}^2}\right) \qquad (9)$$

Where $P(r) = P(r; m_z, \sigma_z)$ is the probability distribution of r with mean m_z, and variance σ_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):

$$w_g(z) = \log G(z) = \log G(m_z, \sigma_z) = m_z = \mathrm{E}_z\{\log(r)\} \qquad (10)$$

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 $w_g(z) = \mathrm{E}\{\log(r)\}$. In this measure, variance and the shape of the probability distribution does not affect the overall fitness over generation time.

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 17 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 5 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 7 pt

書式変更: タブ位置: 35.79 字, 左揃え + 37.76 字(なし)

書式変更: フォント : 斜体 (なし)

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 $w_G(z)$ = $\mathrm{E}\{R\}$ (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.

~~4~~3. 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 ($\mathrm{E}\{\log(r)\}$ or $\mathrm{E}\{R\}$). ~~These uncertainties can be incorporated into the unified fitness at the generation level (Yoshimura and Shields, 1992).~~

書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 太字
書式変更: 左揃え, 行間 : 2 行
書式変更: フォント : 斜体
書式変更: フォント : 斜体

~~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~~

~~$f_Y v(y|y;x)$: fitness of an individual with phenotype x in environment y~~

~~$h_Y d(y)$: 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 *d*(*y*):~~

~~$$f(x)= \int_{x\in D(y\backslash x)} v(y;x)d(y)dy \qquad (2)$$~~

~~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)~~

書式変更: 下付き

書式変更: 下付き

書式変更: 英語（米国）

変更されたフィールド コード

~~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)*:~~

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

~~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:~~

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

~~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:~~

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

~~Here maximizing *G*(*z*) is same as maximizing its logarithm *g*(*z*) and the latter is equal to the discrete~~

書式変更: 左揃え, 行間 : 2 行, タブ位置: 13.49 字(なし)

書式変更: 左揃え, 行間 : 2 行

~~weighted average of the logarithmic fitnesses log (w) with their distribution $p(w;z)$:~~

~~$g(z)=\log G(z)=\sum_{w} p(w;z)\log(w)=\mathrm{E}\{\log(w)\}$ (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 optimization is then given as follows. Let α and β be individual and collective trait values, respectively. For example, if α is a phenotype value, then β is a genotype value associated with a distribution of phenotype value α. Suppose $f(\alpha, \beta)$ is the fitness potential function of α given β. Then the canonical form of fitness $w(\beta)$ is given as:

$$w(\beta)=\int f(\alpha,\beta)h(\alpha,\beta)d\alpha \qquad (11)$$

where $f(\alpha, \beta)$ and $h(\alpha, \beta)$ are the fitness potential and the probability distribution of trait values α and β, respectively. Depending on the situation given these two functions may be those of a single variable α, 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 = {$w_p(z)$*(number of adult) + (number of surviving adult)}/(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~~

書式変更: 左揃え, 行間 : 2 行, タブ位置: 2.7 字(なし)

書式変更: フォント : 斜体

書式変更: フォント : 斜体

書式変更: フォント : 斜体

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : 10.5 pt, (特殊) Times New Roman

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : 10.5 pt, (特殊) Times New Roman

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : 太字 (なし) , (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : 10.5 pt, 太字 (なし) , (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

~~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). 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).~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

~~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 $f(x)$ (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. 1d). 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~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)
書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

~~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~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フランス語 (フランス)

書式変更: 行間 : 2 行

書式変更: フォント : 10.5 pt, 太字 (なし) , (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, フランス語 (フランス)

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

~~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 (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 be a function of body size x, i.e., $f = f(x)$, 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) (equation (3)). Here the phenotypic optimum x_{max} represents the trait that achieves the highest reproductive success in the environment, i.e., $f(x_{max}) = \max f(x)$. In contrast, the genotypic optimum z_{max} is the trait selected by natural selection, i.e., $w(z_{max}) = \max w(z)$. In general, the two optima differ in their values. In this example, the genetic optimum z_{max} is always smaller than phenotypic optimum x_{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~~

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

~~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.~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: 行間 : 2 行

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: 左揃え, 行間 : 2 行

~~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).~~

~~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, 1969).~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : 10.5 pt, 太字 (なし) , (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

~~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: $N_z(t+1) = w_z(t)\, N_z(t)$, 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:~~

~~$N_z(t) = w_z(0)w_z(1)\cdots w_z(t\;\;1)N_z(t\;\;1) = \left(\prod_{i=0}^{t-1} w_z(i)\right) N_z(0)$ (7)~~

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

~~$G(z) = \prod_{i=0}^{t-1} w_z(i)^{(1/t)}$. Suppose that the population growth rate $w_z(i)$ is randomly drawn from a probability distribution $p(w, z)$ for a given genotype z. Then the geometric mean fitness is expressed by the probability distribution $p(w, z)$ as:~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

~~$G(z)=\prod_{w} w^{p(w;z)}$ (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:~~

~~$\log G(z)=\int p(w;z)\log(w)dw$ (9)~~

~~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 2x2x2 = 8 offspring. However, in changing environments we may expect, say, 2x1x3 = 6 offspring. In both environments, the mean fitness is same (i.e., (2+2+2)/3=(2+1+3)/3=2). But the geometric mean fitness is lower (($(2\text{x}1\text{x}3)^{1/3}$=1.82) in the variable environment, than in the constant environment (($(2\text{x}2\text{x}2)^{1/3}$=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.~~

書式変更: フォント：(特殊) Times New Roman

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: 左揃え, 行間：2 行, タブ位置：29.79 字, 左揃え + 31.79 字(なし)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: 左揃え, 行間：2 行

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント：(特殊) Times New Roman, フランス語 (フランス)

~~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 *w* 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~~

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：Times New Roman, フランス語（フランス）

書式変更: 行間： 2 行

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: 左揃え, 行間： 2 行

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

書式変更: フォント：(特殊) Times New Roman, フランス語（フランス）

~~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~~

~~$P(w;m_z,\sigma_z)=\left(\frac{1}{w\sqrt{2\pi}\sigma_z}\right)\exp\left(\frac{(\log(w)-m_z)^2}{2\sigma_z{}^2}\right)$ (10)~~

~~Where $P(w)=P(w;m_z,\sigma_z)$ is the probability distribution of w with mean m_z, and variance σ_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):~~

~~$\log G(z)=\log G(m_z,\sigma_z)=m_z=\mathrm{E}_z(\log(w))$ (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~~

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : (特殊) Times New Roman, フランス語 (フランス)

書式変更: フォント : Times New Roman, フランス語 (フランス)

書式変更: 行間 : 2 行

書式変更: フォント : 10.5 pt, 太字 (なし) , (特殊) Times New Roman, フランス語 (フランス)

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 10.5 pt, (特殊) Times New Roman, フランス語 (フランス)

~~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*,~~ $h(\alpha, \beta)$)~~*h*, and p(w;z)~~, e.g., variance and skew; see equations in Tables 1 and 2~~equations (1-6)~~). 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.

書式変更: フォント : (特殊) Times New Roman, 英語 (米国)

書式変更: フォント : (特殊) Times New Roman

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: $r(1)=1$, $r(2)=0.001$, $r(3)=1000$.

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 $w_g(z)=\mathrm{E}_z\{\log(r)\}=0$, 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.

変更されたフィールド コード

書式変更: フォント : Times New Roman, 斜体, フランス語 (フランス) , 文字位置下げる 5 pt

変更されたフィールド コード

変更されたフィールド コード

変更されたフィールド コード

書式変更: フォント : Times New Roman, 斜体, フランス語 (フランス) , 文字位置下げる 5 pt

書式変更: 左揃え, 行間 : 2 行

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.

書式変更: 左揃え, 行間 : 2 行

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" (uncertainty) and "necessity" in evolution. ~~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.~~

書式変更: 行間 : 2 行

~~↓これを入れないとダメらしいです↓~~

書式変更: フォントの色 : 赤

~~Acknowledgements~~

書式変更: 左揃え, 行間 : 2 行

~~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).~~

書式変更: 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

~~*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 Thebaud, Vincent Jansen and John Lawton provide helpful comments on the previous manuscript. This work was supported by grants-in-aids from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

書式変更: 行間 ： 2 行

書式変更

書式変更: フォント ：(特殊) Times New Roman, 英語 (米国)

書式変更: フォントの色 ： 赤, 英語 (米国)

書式変更: 左揃え, 行間 ： 2 行, タブ位置: -5.39 字(なし) + -2.7 字 + 0 字 + 2.7 字 + 5.39 字 + 8.09 字 + 10.79 字 + 13.49 字 + 16.18 字 + 18.88 字 + 21.58 字 + 24.27 字 + 26.97 字 + 29.67 字 + 32.36 字 + 35.06 字 + 37.76 字 + 40.46 字 + 43.15 字

書式変更: 左揃え, 行間 ： 2 行

References

Andrewartha, H.G., Birch, L.C., 1954. *The distribution and abundance of animals.* Chicago University Press, Chicago.

Boyce, M.S., Perrins, C.M., 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology* 68, 142-153.

書式変更: 左揃え, 行間 : 2 行

Bulmer, M., 1994. *Theoretical evolutionary ecology*. Sinauer Associates, Sunderland, MA.

書式変更: 左揃え, 行間 : 2 行

Caraco, T.~~hesson, P.L.~~, ~~Warner, R.R.,~~ 1980~~1~~. On foraging time allocation in a stochastic environment. ~~Environmental variability promotes coexistence in lottery competitive systems.~~ *Ecology*~~*Am. Nat.*~~ 61~~117~~, 119~~923~~-128~~943~~.

書式変更: フォント : 太字 (なし)

Caraco, T., Chasin, M., 1984. Foraging preferences: response: response to reward skew. *Anim. Behav.* 32, 76-85.

Caraco, T., Martindale, S., Whitham, T.S., 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim. Behav.* 28, 820-830.

書式変更: 左揃え, 行間 : 2 行

Chesson, P.L., Warner, R.R., 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117, 923-943.

Cohen, D., 1993. Fitness in random environments, in Adaptation in stochastic environments (Yoshimura, J. and Clark, C. W., eds.), pp. 8-25, Springer-Verlag, Berlin.

書式変更: 左揃え, 行間 : 2 行

Crow, J.F., Kimura, M., 1970. *An introduction to population genetics theory*. Harper and Row, New

York.

Darwin, C., 1859. *The origin of species*. John Murray, London.

DeWitt~~Ellner~~, T.J., 1998. Costs and limits of phenotypic plasticity: Tests with predator-induced morphology and life history in a freshwater snail. *Journal of Evolutionary Biology* 11: 465-480.

DeWitt, T.J., Scheiner, SM, Eds., 2004. *Phenotypic Plasticity. Functional and Conceptual Approaches*. New York: Oxford University Press.

DeWitt, T.J., Yoshimura, J. 1998. The fitness threshhold model: Random environmental change alters adaptive landscapes. *Evol. Ecol.* 12: 615-626.~~S., 1985. ESS germination strategies in randomly varying environments. I. Logistic-type models, *Theor. Pop. Biol.* 28, 50-79.~~

Ellner, S., 1985. ESS germination strategies in randomly varying environments. I. Logistic-type models, *Theor. Pop. Biol.* 28, 50-79.

Fisher, R.A., 1930. *The genetical theory of natural selection*. Dover, New York.

Frank, S., Slatkin, M., 1989. Evolution in a variable environment. *Am. Nat.* 136, 244-260.

Gillespie, J.H., 1977. Natural selection for variance in offspring numbers: a new evolutionary principle. *Am. Nat.* 111, 1010-1014.

Halley, J.M., 1996. Ecology, evolution and 1/*f*-noise. *Trends Ecol. Evo.* 11, 33-37.

Karlin, S., Taylor, H.M., 1975. *A first course in stochastic processes*. 2nd Ed. Academic Press, New

書式変更: フォント : 斜体

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 斜体

書式変更: フォント : 斜体

書式変更: フォント : 斜体

書式変更: フォント : 太字 (なし)

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 太字 (なし)

書式変更: フォント : 太字 (なし)

書式変更: フォント : 太字 (なし)

York.

Krebs, J.R., Davies, N.B., 1993. *An introduction to behavioural ecology.* 3rd Ed. Blackwell Scientific, Oxford, UK.

Lalonde, R.G., 1991. Optimal offspring provisioning when resources are not predictable. *Am. Nat.* 138, 680-686.

Lewontin, R.C., Cohen, D., 1969. On population growth in a randomly varying environment. *Proc. Natl. Acad. Sci.* USA, 62, 1056-1060.

Mangel, M., Clark, C.W., 1988. *Dynamic modeling in behavioral ecology.* Princeton University Press, Princeton, NJ.

McNamara, J., 1995. Implicit frequency dependence and kin selection in fluctuating environments. *Evol. Ecol.* 9, 185-203.

Monod, J., 1971. *Chance and necessity.* Vintage Books, London.

Mountford, M.D., 1968. The significance of litter-size. *J. Anim. Ecol.* 37, 363-367.

Parker, G.A., Maynard Smith, J., 1990. Optimality theory in evolutionary biology. *Nature* 348, 27-33.

Pettifor, R.A., Perrins, C.M., McCleery, R.H., 1988. Individual optimization of clutch size in great tit. *Nature* 336, 160-162.

Philippi, T., Seger, J., 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* 4, 41-44.

書式変更: フォント : 太字 (なし)

書式変更: フォント : 太字 (なし)

書式変更: フォント : 太字 (なし)

書式変更: 行間 : 2 行

書式変更: フォント : 太字 (なし)

書式変更: 左揃え, 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 太字 (なし)

Pigliucci, M., 2001. *Phenotypic Plasticity: Beyond Nature and Nurture.* Johns Hopkins University Press, Baltimore, MD.

Price, M.V., Waser, N.M., 1979. Pollen dispersal and optimal outcrossing in Delphinium nelsonii. *Nature* 277, 294-296.

Real, L.A., Caraco, T., 1986. Risk and foraging in stochastic environments. *Ann. Rev. Ecol. Syst.* 17, 371-390.

Roff, D., 1981. On being the right size. *Am. Nat.* 118, 405-422.

Roff, D.A., 1992. *The evolution of life histor~~ie~~y.* Chapman and Hall, New York.

Root, R.B. and Kareiva, P.M., 1984. The search for resources by cabbage butterflies (Pieris rapae): Ecological consequences and adaptive significance of markovian movements in a patchy environment. *Ecology* 65, 147-165.

Schmidt-Nielson, K., 1984 Scaling: why is animal size so important? Cambridge University Press, Cambridge, UK.

Sibly, R.M., Calow, P., 1986. *Physiological ecology of animals.* Blackwell Scientific, Oxford, UK.

Stearns, S.C., 1992. *The evolution of life histories.* Oxford University Press, Oxford, UK.

Stephens, D.W., Krebs, J.R., 1986. *Foraging theory.* Princeton University Press, Princeton, NJ.

Via, S. and Lande, R. 1985. Genotype-environmental interaction and the evolution of phenotypic plasticity. *Evolution*, 39, 505-522.

書式変更: フォント : 斜体

書式変更: 左揃え, 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 太字 (なし)

書式変更: フォント : 太字 (なし)

書式変更: フォント : 太字 (なし)

書式変更: 左揃え, 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

書式変更: 左揃え, 行間 : 2 行

書式変更: フォント : 斜体

Williams, G.C., 1992. *Natural selection:* domains, levels, and challenges. Oxford University Press, Oxford UK.

Yoshimura, J., 1995. Environmental uncertainty and natural selection, Japanese Journal of Ecology, 45, 185-190 (in Japanese).

Yoshimura, J., Clark, C.W., 1991. Individual adaptations in stochastic environments. *Evol. Ecol.* 5, 173-192, 430 (Corrigenda).

Yoshimura, J., Clark, C.W. (eds.), 1993. *Adaptation in stochastic environments (Lecture Notes in Biomathematics, Vol. 98).* Springer-Verlag, Berlin.

Yoshimura, J., Shields, W.M., 1987. Probabilistic optimization of phenotype distributions: a general solution for the effects of uncertainty on natural selection? *Evol. Ecol.* 1, 125-138.

Yoshimura, J., Shields, W.M., 1992. Components of uncertainty in clutch-size optimization. *Bull. Math. Biol.* 54, 445-464.

Yoshimura, J., Shields, W.M., 1995. Probabilistic optimization of body size: a discrepancy between genetic and phenotypic optima, *Evolution,* 49, 375-378.

Yoshimura, J., Jansen, V.A.A., 1996. Evolution and population dynamics in stochastic environments. Researches on Population Ecology 38, 165-182.

書式変更: 左揃え，行間 : 2 行

書式変更: 左揃え，行間 : 2 行，タブ位置: 2.7 字，左揃え

書式変更: フランス語（フランス）

書式変更: 左揃え，行間 : 2 行

書式変更: フォント : 太字（なし）

書式変更: フォント : 太字（なし）

書式変更: フォント : 太字（なし）

書式変更: フォント : 太字（なし）

書式変更: インデント : 左 : 0 mm，ぶら下げインデント : 5.66 字，行間 : 2 行，タブ位置: -5.39 字，左揃え + -2.7 字，左揃え + 0 字，左揃え + 2.7 字，左揃え + 5.39 字，左揃え + 8.09 字，左揃え + 10.79 字，左揃え + 13.49 字，左揃え + 16.18 字，左揃え + 18.88 字，左揃え + 21.58 字，左揃え + 24.27 字，左揃え + 26.97 字，左揃え + 29.67 字，左揃え + 32.36 字，左揃え + 35.06 字，左揃え + 37.76 字，左揃え + 40.46 字，左揃え + 43.15 字，左揃え

書式変更: フォント : 太字（なし）

書式変更: 左揃え，行間 : 2 行

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)):

$$\log G(r; m_z, \sigma_z) = \int_0^{\infty} \log(r) \left(\frac{1}{r\sqrt{2\pi}\sigma_z} \right) \exp\left(-\frac{(\log(r) - m_z)^2}{2\sigma_z{}^2} \right) dr \qquad \text{(A1)}$$

Let log(r) = y, r: 0→∞. Then, $dr = rdy$, y:−∞ →+∞ and we get

$$\log G(r; m_z, \sigma_z) = \int_{-\infty}^{\infty} y \left(\frac{1}{\sqrt{2\pi}\sigma_z} \right) \exp\left(-\frac{(y - m_z)^2}{2\sigma_z{}^2} \right) dy \qquad \text{(A2)}$$

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

$$\log G(r; m_z, \sigma_z) = a\left\{ \int_{-\infty}^{\infty} x \exp\left(-bx^2\right) dx + m_z \left(\int_{-\infty}^{\infty} \exp\left(-bx^2\right) dx \right) \right\} \qquad \text{(A3)}$$

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

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

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

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

And from $\int_0^{\infty} \exp\left(-bx^2\right) dx = \frac{\sqrt{\pi}}{2\sqrt{b}}$, we get

$$\int_{-\infty}^{\infty} \exp\left(-bx^2\right) dx = 2\int_0^{\infty} \exp\left(-bx^2\right) dx = \frac{\sqrt{\pi}}{\sqrt{b}}$$

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 5 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 17 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 17 pt

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 18 pt

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.

書式変更: フォント : Times New Roman, 斜体, 英語 (英国), 文字位置下げる 17 pt

書式変更: フォント : Times New Roman, 英語 (英国)

書式変更: 行間 : 2 行, タブ位置: -5.39 字, 左揃え + -2.7 字, 左揃え + 0 字, 左揃え + 2.7 字, 左揃え + 5.39 字, 左揃え + 8.09 字, 左揃え + 10.79 字, 左揃え + 13.49 字, 左揃え + 16.18 字, 左揃え + 18.88 字, 左揃え + 21.58 字, 左揃え + 24.27 字, 左揃え + 26.97 字, 左揃え + 29.67 字, 左揃え + 32.36 字, 左揃え + 35.06 字, 左揃え + 37.76 字, 左揃え + 40.46 字, 左揃え + 43.15 字, 左揃え

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

$f_p(y) = w_i(y)$: 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)

$$w_i(y) = \int_{y\in H_i(x)} f_i(x,y)h_i(x)dx \qquad (1)$$

$$w_p(z) = \int_{y\in H_p(y,z)} f_p(y)h_p(y,z)dy \qquad (2)$$

$$w_p(z) = \sum_{y\in H_p(y,z)} f_p(y)h_p(y,z) \qquad (3)$$

Note: the suffix i in equation (1) denotes the individual level (p: population level).

書式変更: フォント : 斜体

変更されたフィールド コード

書式変更: 英語（米国）

書式変更: フォント : 斜体

書式変更: フォント : 斜体

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

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

$$w_G(z) = \int_{e^R\in H_G(e^R,z)} RH_G(e^R,z)e^R dR \qquad (2)$$

書式変更：フォント：斜体

書式変更：フォント：斜体

書式変更：左揃え，行間：2 行

Figure Legends

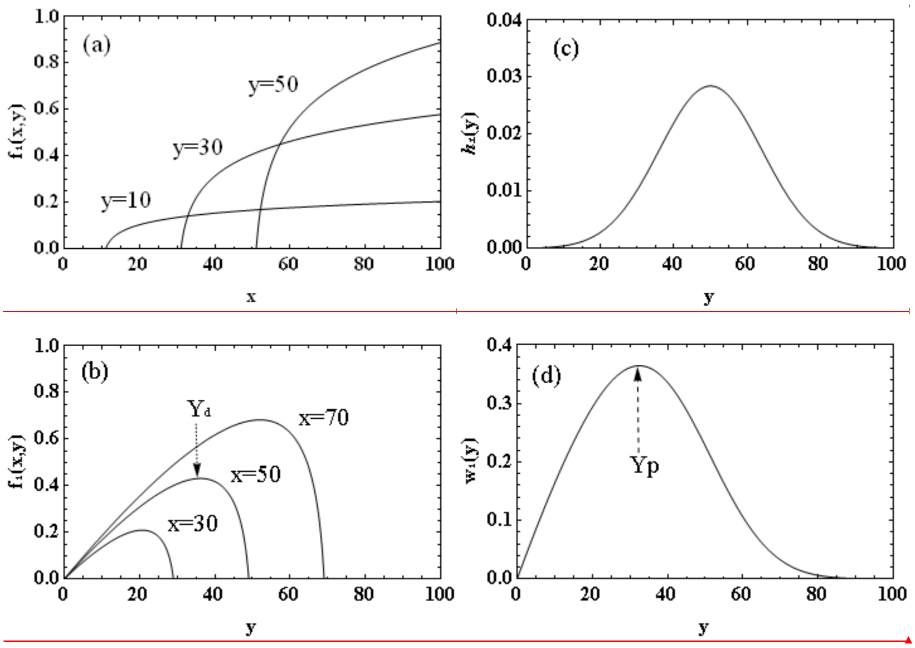
Fig. 1 - Probabilistic optimization of uncertain daily food amounts x~~y~~ for a given phenotype y~~x~~. (a) the fitness f_i~~v~~(x~~y~~, y~~x~~) of an individual with a phenotype y~~x~~ in environment x~~y~~. The phenotype y~~x~~ = 10 is adapted for bad environments, ~~x~~y = 30 for intermediate environments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

Fig. 2 - Probabilistic optimization of body size y~~x~~. (a) $w_i(y)$~~$f(x)$~~: the phenotypic fitness of body size (the dotted line); $w_p(z)$~~$w(z)$~~: 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_p(y~~x~~, 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~~$_{max}$.

Fig. 3 - Probabilistic optimization of population growth rates r over cross-generations. (a) $f_g(r)$ = 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: $z = z_1$, z_2 and z_3). (c) The log-transformed generational fitness $F_F(R) = F_F(\log r) = R$ plotted against R = log (r). (d) $h_G(r, z)$: probability distributions of log growth rate log (r) for three genotypes (transformed from (b)).

Fig. 4~~3~~ - Mean-variance approximation of geometric mean fitness: $G(r$~~w~~$)$ ~ ~~□~~ $\mu - \sigma^2/(2\mu)$, where μ and σ^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) is~~may be~~ better than that of high mean and high standard deviation (cross). ~~–~~On an isocline, two genotypes have equal geometric mean fitnesses.

書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: フォント : 斜体
書式変更: 下付き
書式変更: 下線
書式変更: 左揃え



書式変更: フォント : 0 pt, フォントの色 : 黒, (特殊) Times New Roman, (なし), 文字の倍率 : 0%, グリッドへ配置しない, 罫線 : : (罫線なし), 模様 : なし (黒)

Fig. 1.

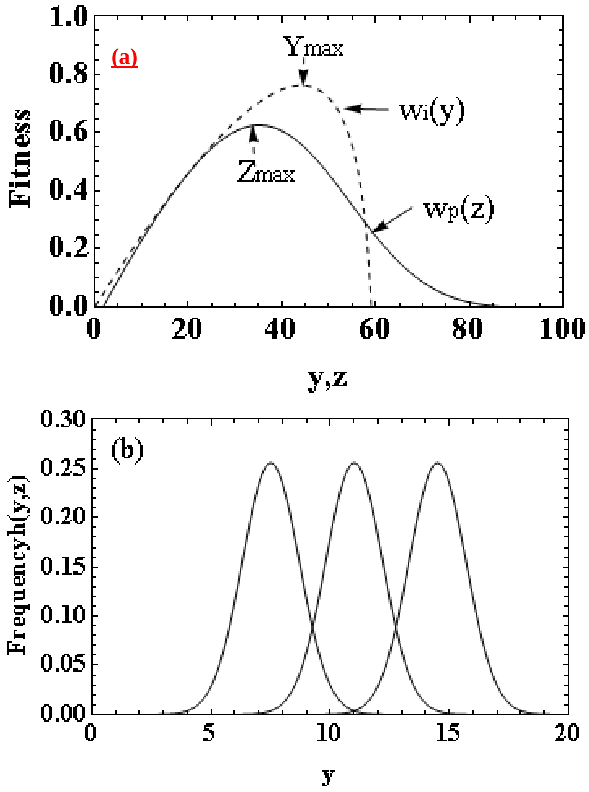


Fig. 2.

書式変更: インデント : 最初の行 : 5.39 字

書式変更: 左揃え

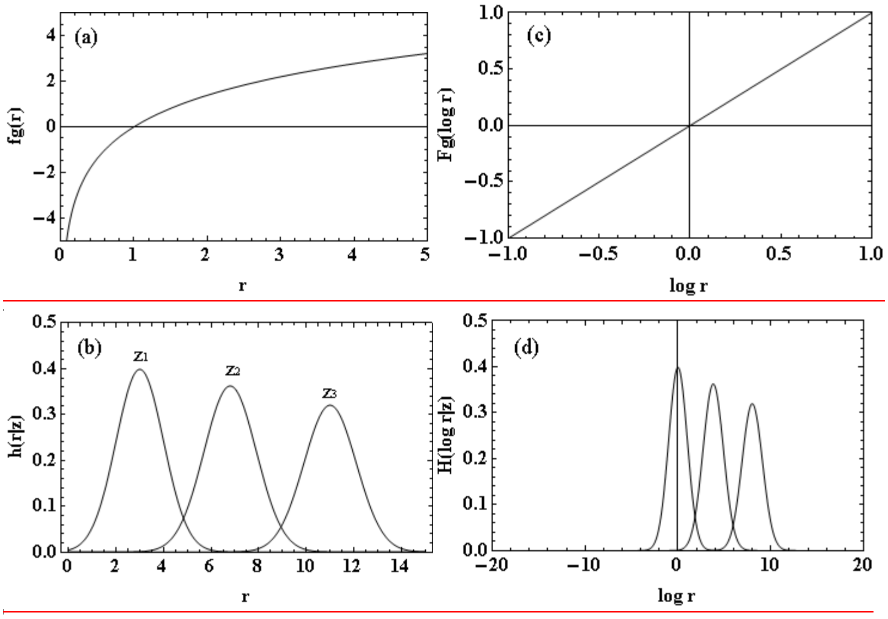


Fig. 3.

書式変更: 行間 : 2 行

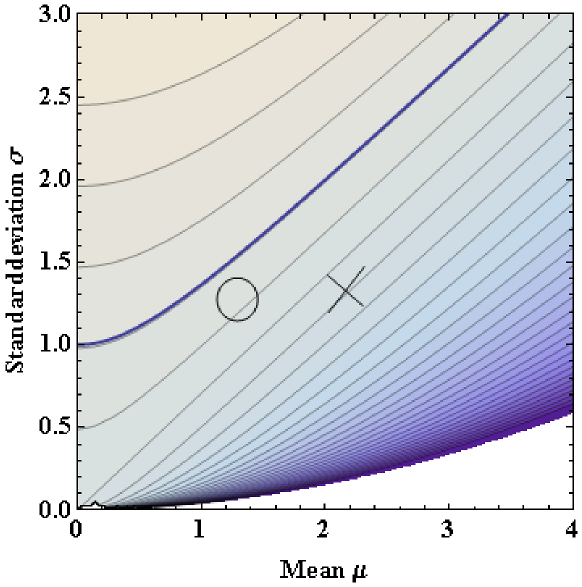
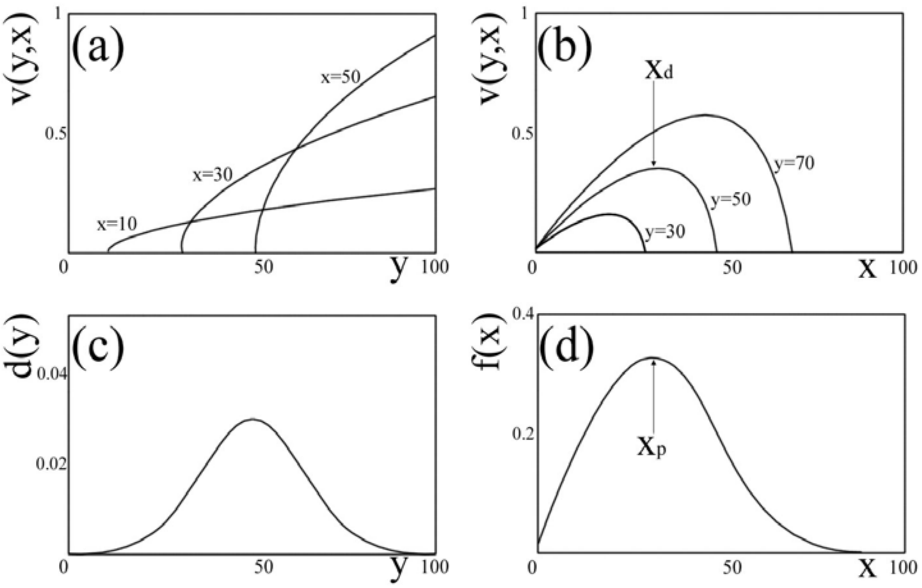


Fig. 4.

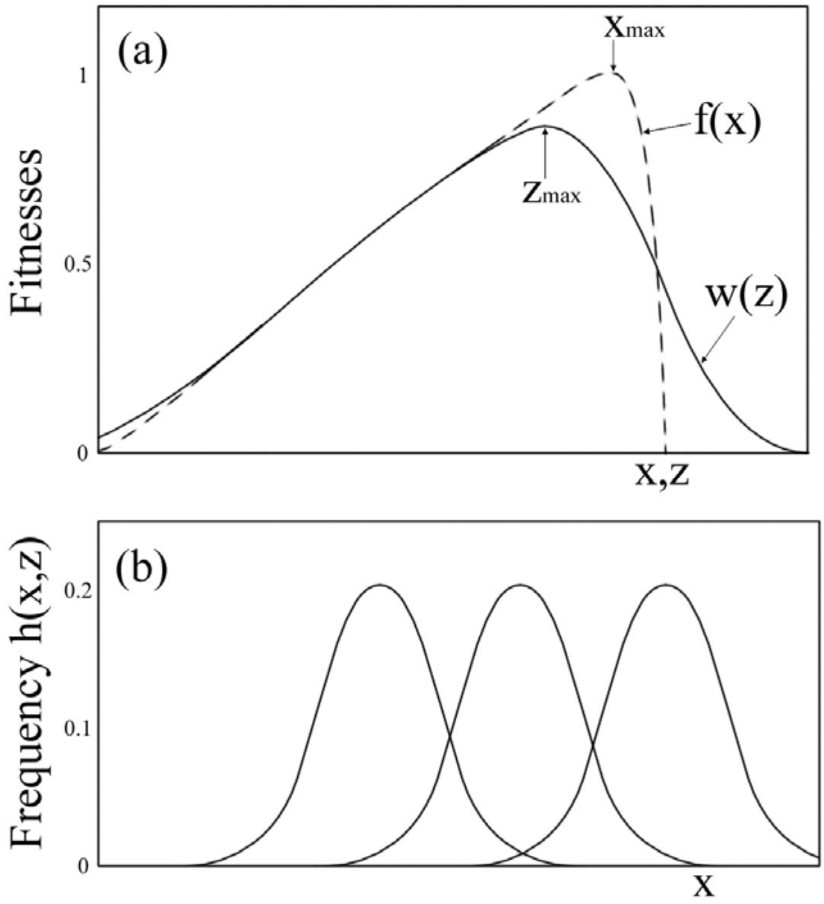
書式変更: フォント : Times New Roman, 12 pt, 太字, 英語 (英国)

書式変更: フォント : 10.5 pt

書式変更: 左揃え

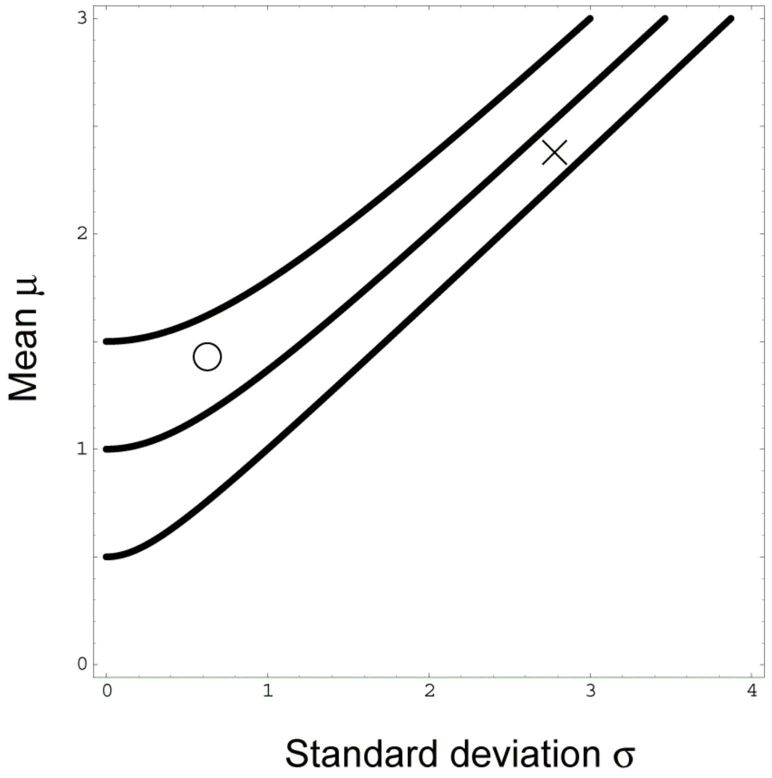

(a)
v(y,x)
1
0.5
x=50
x=30
x=10
0
50
y
100
(b)
v(y,x)
1
0.5
x_d
y=70
y=50
y=30
0
50
x
100
(c)
d(y)
0.04
0.02
0
50
y
100
(d)
f(x)
0.4
0.2
x_p
0
50
x
100

~~Fig. 1~~



~~Fig. 2~~

書式変更: 行間 : 2 行



~~Fig. 3~~~~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; Hoppenstead 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~~

書式変更: 両端揃え, インデント : 左 : 0 mm, ぶら下げインデント : 5.66 字, 行間 : 2 行, タブ位置: -5.39 字, 左揃え + -2.7 字, 左揃え + 0 字, 左揃え + 2.7 字, 左揃え + 5.39 字, 左揃え + 8.09 字, 左揃え + 10.79 字, 左揃え + 13.49 字, 左揃え + 16.18 字, 左揃え + 18.88 字, 左揃え + 21.58 字, 左揃え + 24.27 字, 左揃え + 26.97 字, 左揃え + 29.67 字, 左揃え + 32.36 字, 左揃え + 35.06 字, 左揃え + 37.76 字, 左揃え + 40.46 字, 左揃え + 43.15 字, 左揃え

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 10.5 pt, フォントの色 : 自動

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 10.5 pt, フォントの色 : 自動

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 10.5 pt, フォントの色 : 自動

~~(Lloyd and Dybas, 1966; Hoppensteadt and Keller, 1976). 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~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : 10.5 pt, フォントの色 : 自動

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 10.5 pt, フォントの色 : 自動

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 10.5 pt, フォントの色 : 自動

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (日) ＭＳ 明朝, (特殊) Century, 英語 (英国)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: 行間 : 2 行

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~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 gGenetics 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~~

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~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).~~

コメント **[CS2]:** One problem with this hypothesis that I have noted in the past is that current evidence suggests that periodical cicadas cannot live sympatricaly unless separated by at least four years in life cycle due to nymphal competition—but we don't need to mention this here. Perphaps nymphal competition was lower in the past and populations denisites not as high as in your model when populations are on the edge of extinction.

書式変更: フォント : Times New Roman

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~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 (1- S) 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 $i \leq j$. 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).~~

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: インデント : 最初の行 : 0 字, 行間 : 2 行

書式変更: 行間 : 2 行

~~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:~~

書式変更: フォント : Century

~~$N_{l,t}(i,j) = S \times N_{l,t-1}(i,j)$ (1)~~

変更されたフィールド コード

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~where *S* (0<*S*<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~~

~~$N_{A,t}(i,j) = E \times N_{l,t}(i,j)$ (2)~~

~~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:~~

~~$\text{Num. offspring} := \frac{1}{2} N_{A,t}(i,j) \times F(N_{A,t}(m,n)) \times C(\mathrm{y})$ (3)~~

~~where F is the frequency of the target brood, such that~~

~~$F(N_A(m,n)) = \frac{N_A(m,n)}{\sum N_A}$~~

~~where $\sum N_A$ is the sum of all co-emergent adults for a given year, and C is the clutch size and a function of the cycle:~~

~~$C(\mathrm{y}) = R \times \mathrm{y}$ (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~~

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：Century

書式変更: フォント：Century

~~example, the offspring brood size of genotype [*i,m*] follows:~~

$$N_{l,t}(i\,,m)=\sum_{x}\sum_{z}\left\{\frac{1}{2}N_{A,t}(i,x)\times F\left(N_{A,t}(m,z)\right)\times C(y)\right\} \qquad (5)$$

~~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 larva (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 ($N_{l,t}$ 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 * 0.955 = 955, whereas that of N_t= 100 becomes N_{t+1}= 100 * 0.955 = 95. This disadvantage of smaller brood sizes becomes larger when brood sizes decrease. In a small brood, the actual survival rate S becomes veryis relatively low. In extremity, when equation (3) is less than 4, the number~~

書式変更 ... [1]

書式変更 ... [2]

変更されたフィールド コード

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更 ... [3]

~~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 $[i, i]$ and $[j, j]$ ($i<j$) makes three genotypes (broods); $[i, i]$, $[j, j]$ and $[i, j]$. In our model, brood $[i, i]$ and brood $[i, j]$ co-emerge at i year. The brood $[i, j]$ reduces its population size considerably, and results in a huge disadvantage. On the other hand, brood $[i, i]$ and brood $[i, j]$ hybridize and make three genotypes (broods); $[i, i]$, $[i, j]$ and $[j, j]$. Brood $[i, i]$ and brood $[i, j]$ 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).~~

書式変更 ... [4]

書式変更 ... [5]

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~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 results 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. 3).~~

~~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~~

書式変更: フォント : Century

書式変更

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

~~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).~~

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~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~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~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. 3B), 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~~

コメント **[CS3]:** I would remove the sentence below because Okanagana synodica might have 19 year cycles in Canada.

書式変更: フォント : Times New Roman

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: 左揃え, 行間 : 2 行

~~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).~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: 行間 : 2 行

コメント **[CS4]:** Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686-693.

書式変更: フォント : Times New Roman

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~FurthermoreEarlier in the Pleistocene, prime number fixation might not be achieved by a single glacial period, but bemay have extended over a few glacial periods with . hHybridization might taketaking 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 interval dominance appears 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 referee for~~

書式変更: フォント : Century

書式変更: フォント : Century

コメント **[CS5]:** We do not believe that the origin of the new 13-year cicadas was a result of hybridization. That is what Cox and Carlton believe and we think that they are wrong as explained in Marshall et al. 2003. However, that is less relevant to this paper.

書式変更: フォント : Times New Roman

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

~~valuable comments. This work was supported by grants-in-aids from the Ministry of Education, Culture, Sports, Science and Technology of Japan.~~

~~REFERENCES~~

~~Alexander, R. D. and Moore, T. E. 1962. The evolutionary relationships of 17-year and 13- year cicadas and three new species (Homoptera, cicadidae, *Magicicada*). Miscellaneous Publications of the Museum of Zoology University of Michigan, 121: 1-59.~~

~~Allee, W. C. 1931. Animal Aggregations: A Study in General Sociology. Chicago : University of Chicago Press.~~

~~Bulmer, M. G. 1977. Periodical insects. Am. Nat. 111: 1099-1117.~~

~~Chapman, R. F. 1971. *The Insects: Structure and Function*. New York : American Elsevier.~~

~~Cooley, J. R., Simon, C. and Marshall, D. C. 2003. Temporal separation and speciation in periodical cicadas. Bioscience, 53: 151-157.~~

~~Cooley, J. R., Simon, C., Marshall, D. C., Slon, K., and Ehrhardt, C. 2001. Allochronic speciation, secondary contact, and reproductive character displacement in periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.): genetic, morophological, and behavioural evidence. Molecular Ecology, 10: 661-671.~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: インデント : 左 : 0 mm, 最初の行 : 0 字, 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: インデント : 左 : 0 mm, 最初の行 : 0 字, 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~Cox, R. T. 1992. A comment on Pleistocene population bottlenecks in periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). Evolution, **46**: 845-846.~~

~~Cox, R. T. and Carlton, C. E. 1988. Paleoclimatic influences in the ecology of periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). American Midland Naturalist, **120**: 183-193.~~

~~Cox, R. T. and Carlton, C. E. 1991. Evidence of genetic dominance of the 13-yeat life cycle in periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). American Midland Naturalist, **125**: 63-74.~~

~~Delcourt, P. A. and Delcourt, H. R. 1987. *Long-term Forest Dynamics of the Temperate Zone*. New York: Springer.~~

~~Dybas, H. S. and Davis, D. D. 1962. A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). Ecology, **43**: 432-444.~~

~~Ebert, D. 1992. A maturation size threshold and phenotypic plasticity of age and size at maturity in *Daphinia magna*. Oikos, **69**: 309-317.~~

~~Gates, D. M. 1993. *Climatic Change and its Biological Consequences*. Sinauer: Sunderland, Mass..~~

~~Hoppensteadt, F. C. and Keller, J. B. 1976. Synchronization of periodical cicadas emergences. Science, **194**: 335-337.~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~Karban, R. 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. Ecology, 63: 321-328.~~

~~Kuno, E. 1992. Competitive exclusion through reproductive interference. Researches on Population Ecology, 34: 275-284.~~

~~Lloyd, M. and Dybas, H. S. 1966. The periodical cicada problem. I. Population ecology. Evolution, 20: 133-149.~~

~~Lloyd, M. and Dybas, H. S. 1966. The periodical cicada problem. II. Evolution. Evolution, 20: 466-505.~~

~~Lloyd, M., G. Kritsky, and C. Simon. 1983. A simple Mendelian model for the 13- and 17-year life cycle of periodical cicadas, with historical evidence for hybridization between them. Evolution 37:1162–1180.~~

~~Marlatt, C. L. 1907. The periodical cicada. USDA Bureau of Entomology Bulletin 71.~~

~~Marshall, D. C. and Cooley, J. R. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. Evolution, 54: 1313-1325.~~

~~Martin, A. P. and Simon, C. 1988. Anomalous distribution of unclear and mitochondrial DNA markers in periodical cicadas. Nature, 336: 237-239.~~

~~May, R. M. 1979. Periodical cicadas. Nature, 277: 347-349.~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: インデント : 左 : 0 mm, 最初の行 : 0 字, 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

~~Rosenzweig, M. L. 1979. Three probable evolutionary causes for habitat selection. In *Contemporary Quantitative Ecology and Related Ecometrics* (G. P. Patil and M. L. Rosenzweig, eds.), pp. 49-60. International Co-operative Publishing House, Fairland, Maryland.~~

~~Simon, C.M., R. Karban, & M. Lloyd. 1981. Patchiness, mean crowding and relative density of allochronic, sympatric populations of 17-year cicadas. Ecology **62**:1525-1535.~~

~~Simon, C. 1988. Evolution of 13- and 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). Bulletin of the Entomological Society of America, **34**: 163-176.~~

~~Tainaka, K., Hayashi, T. and Yoshimura , J. 2006. Sustainable sex ratio in lattice populations. EUROPHYSICS LETTERS 74 (3), pp. 554–559.~~

~~Williams, K. and Simon, C. 1995. The ecology, behavior, and evolution of periodical cicadas (Hemiptera: Cicacidae: *Magicicada*). Annu. Rev. Entomol., **40**: 269-295.~~

~~Yoshimura, J. 1997. The evolutionary origins of periodical cicadas during ice ages. Am. Nat., **149**: 112-124.~~

~~Yoshimura, J. and Clark, C. W. 1994. Population dynamics of sexual and resource competitions. Theoret. Pop. Biol., **45**: 121-131.~~

書式変更: インデント : 左 : 0 mm, 最初の行 : 0 字, 行間 : 2 行

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century, 太字

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: 1 行の文字数を指定時に右のインデント幅を自動調整する, 行間 : 2 行, 日本語と英字の間隔を自動調整する, 日本語と数字の間隔を自動調整する

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : (英) Century

書式変更: フォント : Century

書式変更: フォント : Century

書式変更: フォント : Century, 太字

書式変更: フォント : Century

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: インデント : 左 : 0 mm, 最初の行 : 0 字, 行間 : 2 行

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝, 斜体 (なし)

書式変更 ... [6]

書式変更: 行間 : 2 行

~~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. Serrated 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~~

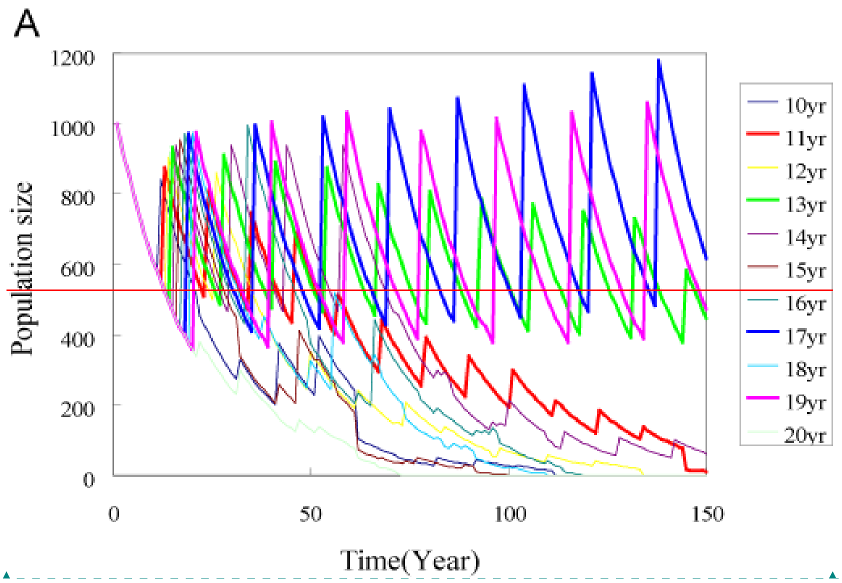
書式変更: フォント：(英) Century, (日) ＭＳ 明朝

書式変更: フォント：Century

~~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 tends to decreasing smoothly near the border of extinction (B), whereas those of smaller primer 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~~ ~~$S > 0.96$~~~~).~~

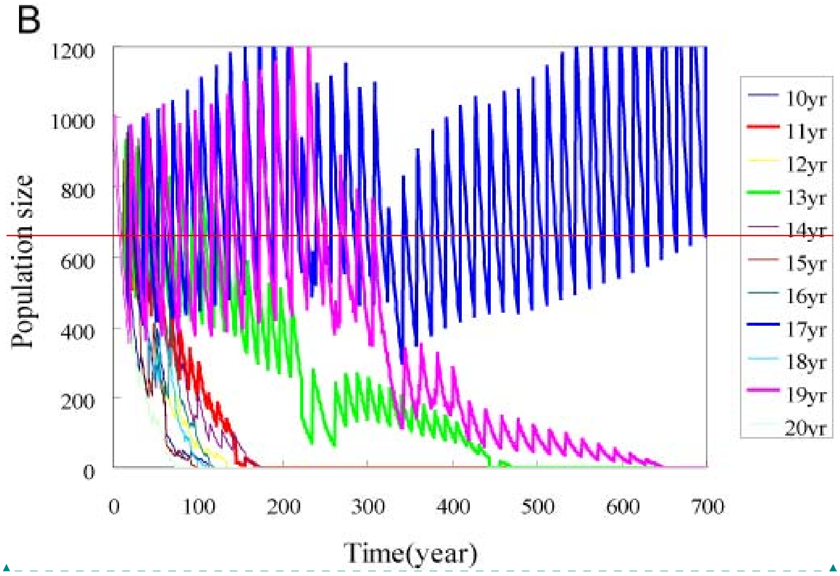
書式変更: フォント : (英) Century, (日) ＭＳ 明朝



~~Fig. 1A.~~

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

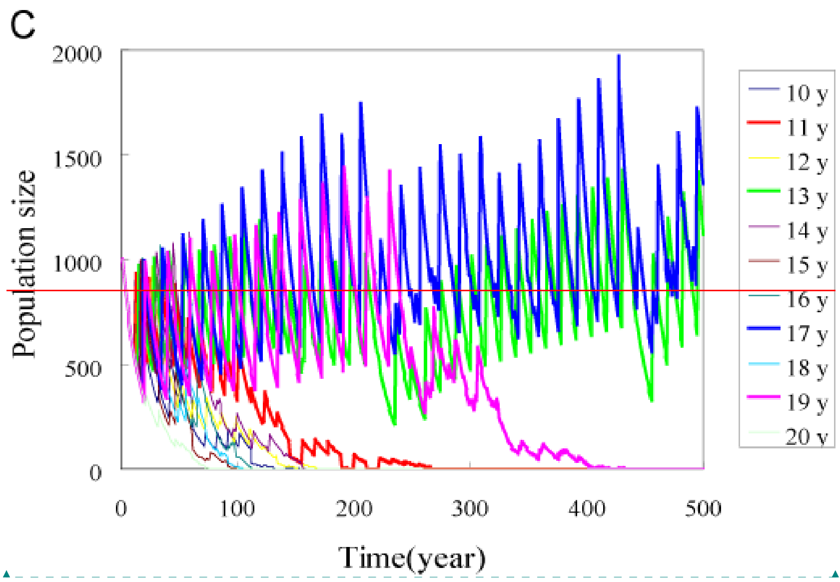
書式変更: フォント：（英）Century, （日）ＭＳ 明朝



~~Fig. 1B.~~

書式変更: フォント：（英）Century, （日）ＭＳ 明朝

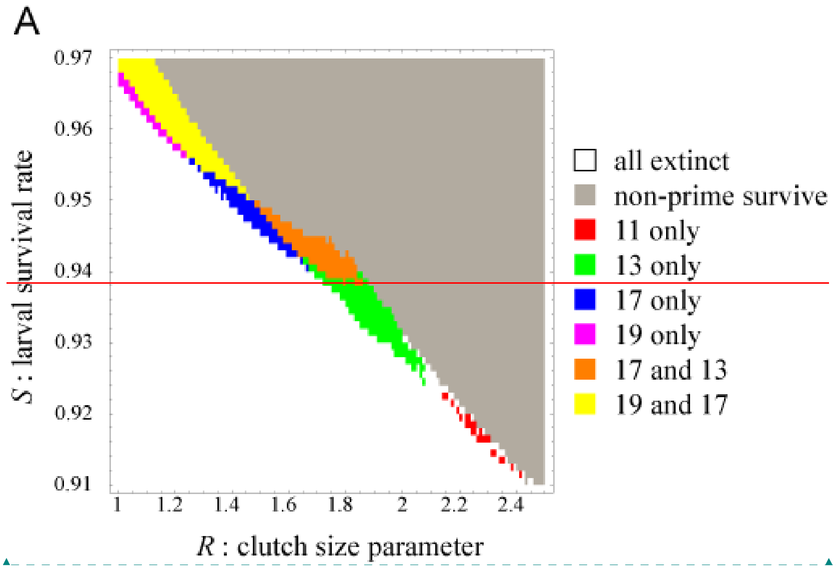
書式変更: フォント：（英）Century, （日）ＭＳ 明朝



書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

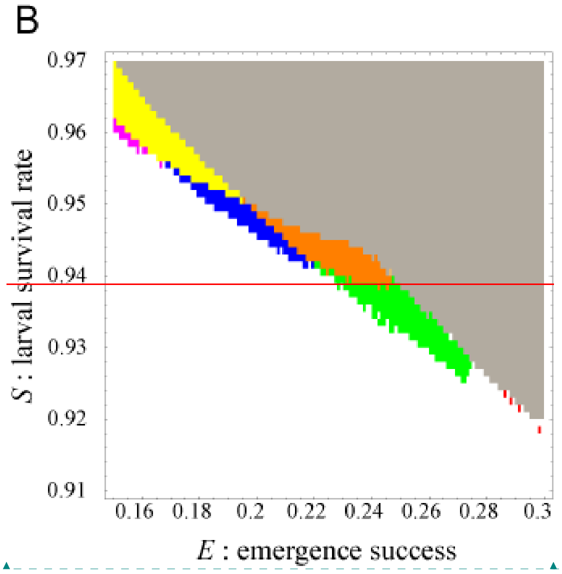
~~Fig. 1C.~~



書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

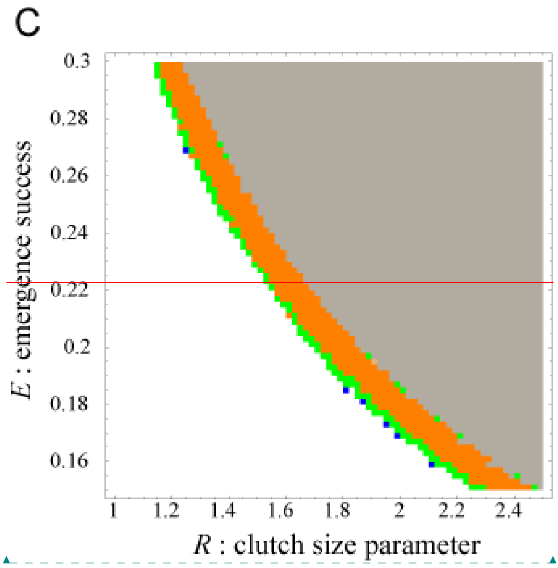
~~Fig. 2A.~~



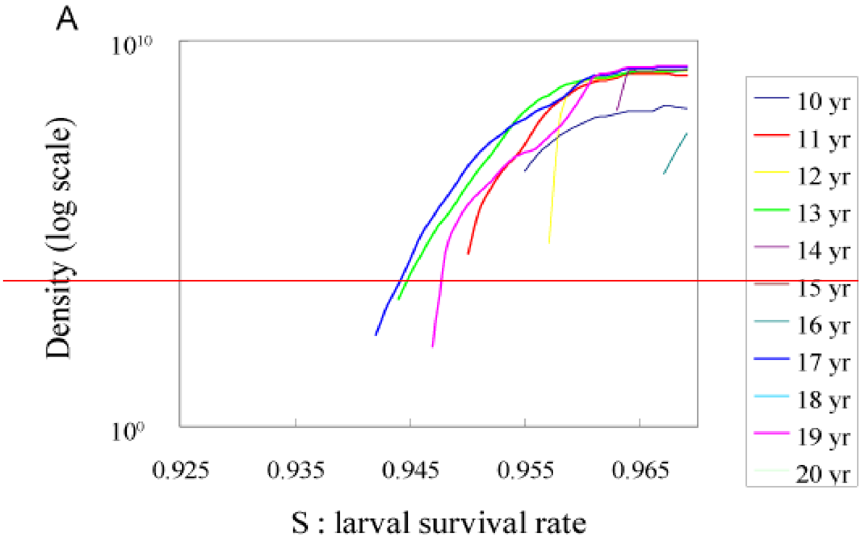
~~Fig. 2B.~~

書式変更: フォント : （英）Century, （日）ＭＳ 明朝

書式変更: フォント : （英）Century, （日）ＭＳ 明朝



~~Fig. 2C.~~



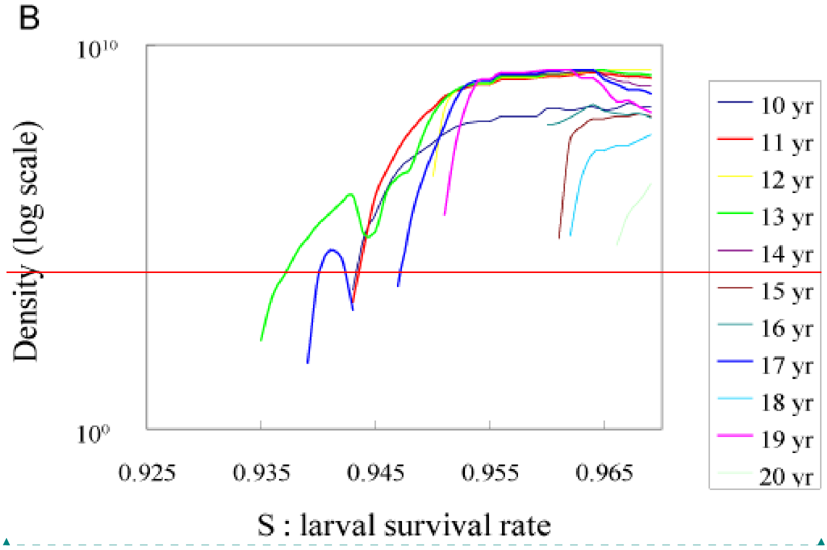
~~Fig. 3A.~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝



~~Fig. 3B.~~

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

書式変更: フォント : (英) Century, (日) ＭＳ 明朝

ページ 68: [1] 書式変更 Taro HAYASHI 2008/01/21 16:40:00

フォント ：Century, 斜体

ページ 68: [1] 書式変更 Taro HAYASHI 2008/01/21 16:40:00

フォント ：Century, 斜体

ページ 68: [1] 書式変更 Taro HAYASHI 2008/01/21 16:40:00

フォント ：Century, 斜体

ページ 68: [1] 書式変更 Taro HAYASHI 2008/01/21 16:40:00

フォント ：Century, 斜体

ページ 68: [2] 書式変更 Taro HAYASHI 2008/01/21 16:40:00

文字位置下げる 14 pt

ページ 68: [2] 書式変更 Taro HAYASHI 2008/01/21 16:40:00

文字位置下げる 14 pt

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 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 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 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 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 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 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 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 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

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

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

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: [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 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 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 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 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 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 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 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 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 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 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 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 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 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 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 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