

## Daniel Bernoulli (1738): evolution and economics under risk

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### 1. Daniel Bernoulli's reputation

An historian of science or physicist would probably say this about Daniel Bernoulli: "Ah, *Daniel Bernoulli*, one of the three great Basel Bernoullis, Johann's second son, Jakob's nephew; born in 1700. He died in 1782, never having married. He made fundamental contributions to hydrodynamics, including the basic principle that allows airplanes to fly and that governs the design of sails and boat hulls. He had a horrible time with his hyper-competitive father (who stole his work on hydrodynamics and published it under his own name in a book that Johann pre-dated by 10 years to make clear who had precedence). He took a degree in medicine but never abandoned his first love, mathematics, and was one of Leonhard Euler's best friends and constant supporters. After time with Euler and Goldbach in St. Petersburg in the golden days of the St. Petersburg Academy (1724–1732), he returned to Basel in 1732, where his lectures on mathematics and physics had exemplary clarity and profound impact. He was one of the great mathematical physicists and would have been an even greater experimental physicist had Basel given him the equipment he asked for. Of the Bernoullis he was the third best mathematician, that being fast company" (Merian 1860; Speiser 1939).

An economist or evolutionary biologist would, in contrast, emphasize the one paper on choice under risk in which he distinguishes between wealth and utility, a paper not often remembered by physicists or mathematicians. That paper (Bernoulli 1738, trans. 1954, written 1730–31) has profoundly influenced economic theory, portfolio theory, and operations research and has growing influence in evolutionary biology and behavioural ecology. Between 1983 and 1999 it was cited 36 times (according to the

Web of Science database) by people writing on decision theory, risk management, mathematical probability, expected utility, cognition and choice, ecology, evolutionary ecology, marketing, preference structures, and engineering design – not bad for a paper written by a mathematical physicist 262 years ago.

Here I sketch the basic principles of evolution under risk and show which were present in Bernoulli's 1738 paper – a small tribute to his extraordinarily clear mind in the 300th anniversary of his birth. Bernoulli taught us to measure risk with the geometric mean and recommended minimizing risk by spreading it across a set of independent events (bet-hedging). He also defined the situations in which one should avoid risk, from which it is a short step to recognizing those in which one should choose risk.

### 2. How to measure risk: the geometric mean

One type of evolutionary risk is temporal variance in fitness: increases in variance reduce long-term fitness. Measuring fitness as the *geometric mean* of per-generation reproductive success properly accounts for this kind of risk. The geometric mean is the  $n$ th root of the continued product of  $n$  terms, or the antilog of the arithmetic mean of the logarithms of the terms:

$$G = \text{geometric mean} = (\prod x_i)^{1/n} = e^{1/n \sum \ln x_i} \quad i = 1 \dots n.$$

We use the geometric mean to measure evolutionary fitness because fitness is multiplicative. If a genotype has reproductive success that is twice the average in this generation and three times the average in the next, then its fitness over those two generations is six times ( $2 \times 3$ ), not five times ( $2 + 3$ ) the average. If each of two children has

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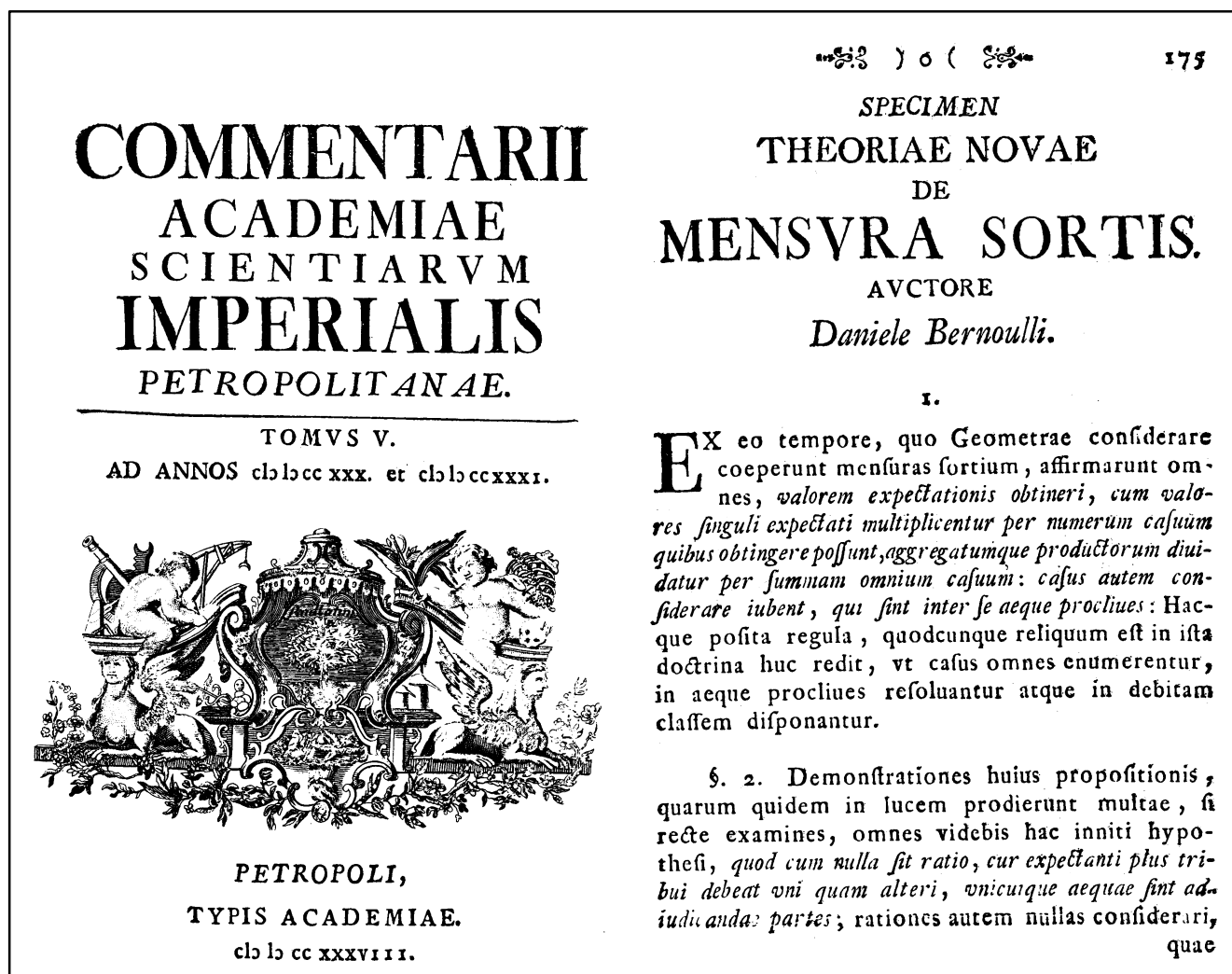
**Figure 1.** The portrait of Daniel Bernoulli aged 44 honouring his status as Professor of Anatomy and Botany in the medical faculty at Basel.

three grandchildren, then there are six, not five, grandchildren.

If we hold the arithmetic mean constant, it is easy to illustrate how the geometric mean decreases as variance increases. Consider two time series of per-generation fitness values with the same arithmetic mean (2.5) and different variances: (1) 2, 3, 2, 3, 2, 3, . . . ; (2) 1, 4, 1, 4, 1, 4, . . . . The second series has higher variance (2.25) than the first (0.25). The number of offspring left after 6 generations in the first is  $2^3 \times 3^3 = 8 \times 27 = 216$ ; in the second it is  $1^3 \times 4^3 = 64$ . The geometric mean for the first is 2.449, for the second 2.0. The geometric mean gives greater weight to low values than does the arithmetic mean. It penalizes variance.

The properties of the geometric mean have been thoroughly investigated in economics. Brieman (1960)

showed that a strategy that maximizes the geometric mean of returns has the highest probability of reaching, or exceeding, any given level of wealth in the shortest possible time, and it has the highest probability of exceeding any given level of wealth over any given period of time. Gillespie (1974, p 605) noted that "the advantage which a genotype gains through producing many offspring in a good year does not balance the disadvantage from producing few offspring in a bad year." Bulmer (1985, p 70) states, "The type with the higher geometric mean fitness will almost certainly predominate in the distant future." Geometric mean fitness implies that the probability of extinction increases with the variance in per-generation fitness (Lewontin and Cohen 1969). Those are all good reasons to use the geometric mean to measure fitness.



**Figure 2.** The title page of Bernoulli's seminal contribution, published in St. Petersburg in 1738, to the theory of risk. Those who prefer English to Latin are referred to the 1954 translation in *Econometrica* (see literature cited).

Maximizing geometric mean fitness may not always predict the distribution of strategies found in a population. When fitness has low variance and low values are not expected for a long time, then predictions based on maximizing the geometric mean may mislead (Samuelson 1971), for risk-prone strategies could outcompete risk-avoidance strategies for a fairly long time – hundreds or even thousands of generations depending on the parameters. This mistake can be avoided by working with invasion models with explicit dynamics. An analysis of risk-avoidance mutants invading a population of risk-prone residents could predict a mixture of risk-prone strategies tending toward arithmetic mean growth rate maximization, with a shorter time to extinction, and risk-averse strategies that maximize  $G$ , with a longer time to extinction, coexisting in the same population. If a single genotype can produce a distribution of offspring phenotypes, then there will be a unique such distribution that resists invasion (Sasaki and Ellner 1995).

Where did the idea of maximizing geometric mean fitness come from? In the biological literature, later workers suggest that Dempster (1955), Haldane and Jayakar (1963), Levins (1967), or Lewontin and Cohen (1969) introduced it as the appropriate measure for populations experiencing temporal variation. They thought the idea was obvious enough not to need attribution. In economics, discussions of  $G$  also cite modern authors who find it obvious. The earliest use I have found is in Bernoulli (1738, trans. 1954), in the context of analysing the relationship of utility to wealth:

*“Any gain must be added to the fortune previously possessed, then this sum must be raised to the power given by the number of possible ways in which the gain may be obtained; these terms should then be multiplied together. Then of this product a root must be extracted the degree of which is given by the number of all possible cases, and finally the value of the initial possessions must be subtracted therefrom; what then remains indicates the value of the risky proposition in question.”* (op. cit. p 28).

Bernoulli illustrated the geometric mean with an example of a merchant wondering whether he should purchase insurance on goods he is about to ship:

*“Suppose Caius, a Petersburg merchant, has purchased commodities in Amsterdam which he could sell for ten thousand rubles if he had them in Petersburg. He therefore orders them to be shipped there by sea, but is in doubt whether or not to insure them. He is well aware of the fact that that at this time of year of one hundred ships which sail from Amsterdam to Petersburg, five are usually lost. However, there is no insurance available below a price of eight hundred rubles a cargo, an amount which he considers outrageously high. The question is, there-*

*fore, how much wealth must Caius possess apart from the goods under consideration in order that it be sensible for him to abstain from insuring them? If  $x$  represents his fortune, then this together with the value of the expectation of the safe arrival of his goods is given by  $((x + 10000)^{95}x^5)^{1/100}$  in case he abstains. With insurance he will have a certain fortune of  $x + 9200$ . Equating these two magnitudes we get  $(x + 10000)^{19}x = (x + 9200)^{20}$  or, approximately, 5043. If, therefore, Caius, apart from the expectation of receiving his commodities, possesses an amount greater than 5043 rubles he will be right in not buying insurance. If, on the contrary, his wealth is less than this amount he should insure his cargo.”* (op. cit. p 30).

In evolutionary biology we can substitute fitness for fortune and define the number of possible ways in which a gain may be obtained as the reproductive success in each of a series of generations. We then see that Bernoulli gave us, in principle, a definition of geometric mean fitness.

### 3. Geometric mean approximations: Mean-variance analysis

The most widely used approximation for the geometric mean is  $G = m - s^2/2m$  where  $m$  is the arithmetic mean and  $s^2$  is the variance. There are many other approximations in the literature. Young and Trent (1969) tested the performance of 5 of them by calculating the geometric mean and each of the approximations for 233 time series of stock values 60 periods long. There were no significant differences in performance; all five approximations estimated  $G$  with much less than 1% error.

My search for the origin of the approximation of the geometric mean by the arithmetic mean minus a variance term suggested that many people do not read the literature and reinvent the wheel. A discovery thought important enough in evolutionary biology to be named a new evolutionary principle is considered trivial enough in mathematical statistics to be given as a problem for students to work out for themselves in the second chapter of *Kendall's advanced theory of statistics* (Stuart and Ord 1994).

### 4. Bet-hedging: don't put your eggs in one basket

Bernoulli (1738, 1954, p 30) wrote: “Another rule which may prove useful can be derived from our theory. This is the rule that it is advisable to divide goods which are exposed to some danger into several portions rather than to risk them all together.” This strategy of spreading risk was formalized in economics in Markowitz (1952), has often been applied in evolutionary biology (references in Sasaki

and Ellner 1995), and is what meant by “bet-hedging:” do not put your eggs in one basket. Note that the environment does not need to be variable or heterogeneous for selection to favour bet-hedging; it simply needs to create risk at all places and times.

### 5. Risk-prone and risk-averse behaviour

Traits are usually connected to fitness non-linearly in organisms, as is wealth to utility in classical economics. If the relationship of fitness (Y-axis) to trait (X-axis) is concave down, then *reducing* variance in the trait, being risk *averse*, will increase fitness. If the fitness-trait relation is concave up, then *increasing* variance in the trait, being risk *prone*, will increase fitness (figure 3).

The concept of concave-down, risk-averse utility was discovered by Bernoulli (1738). Its generalization to non-linear curves with proper probability theory is due to Hölder (1889) and Jensen (1906). One of their results, Jensen’s inequality, is a useful aid in interpreting the consequences of variation in nonlinear systems (Ruel and Ayres 1999). Tobin (1958), for example, applied it to choice under economic risk. Utility theory and the concave-up/down distinction have become pervasive in economics.

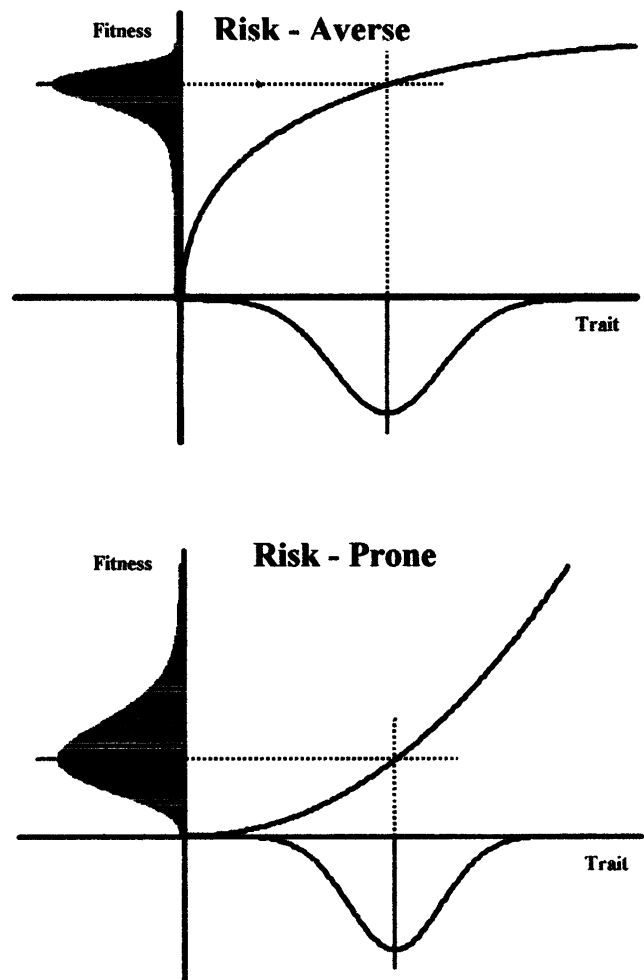
In evolutionary biology we think about the connection of traits to fitness rather than the connection of wealth to utility. When the relationship of trait to fitness is concave-up and risk-prone, increasing the variance of the trait increases fitness; when it is concave-down (the classic case) and risk-averse, increasing the variance of the trait decreases fitness (Stephens and Krebs 1986). This application has been developed by Real and Ellner (1992).

Bernoulli’s perspective on risk-prone and risk-averse behaviour can be applied with advantage to the analysis of several important contrasts in life-histories and evolutionary genetics, including the following: (i) the contrast between semelparity, or one reproductive event per lifetime (risk-prone), and iteroparity, or more than one reproductive event per lifetime (risk-averse); (ii) the contrast between local settlement of offspring in the parental habitat (risk-prone), and broad dispersal of offspring over a wide area (risk-averse); (iii) the contrast between asexual reproduction of genetically identical offspring (risk-prone), and sexual reproduction of genetically diverse offspring (risk-averse). This list is not exhaustive. It does suggest the rich diversity of the phenomena that can be partially united under Bernoulli’s perspective.

### 6. Mean-variance fitness isoclines

A second method of dealing with risk emerges when we consider several traits that affect reproductive perfor-

mance (or several investment instruments that affect long-term gains). Suppose several traits each contribute to fitness through a mean and a variance. A given fitness – a long-term geometric mean growth rate – can result from many combinations of means and variances of traits. Some components might contribute a low mean and a low variance, others a high mean and a high variance. We call the combinations that yield the same fitness value a mean-variance fitness isocline in multi-trait space. Investment should then be distributed across those fitness components



**Figure 3.** The distribution of a trait in the offspring of a focal individual is plotted as a normal distribution on the X-axis. The relationship of the trait to fitness is depicted as a curve. If the curve is concave-down (upper panel), the normal distribution of the trait is transformed into a left-skewed distribution of fitness on the Y-axis. Here normal variation of the trait creates greater penalties than it does rewards. Selection should act to reduce variation in the trait. If the curve is concave-up (lower panel), the normal distribution of the trait is transformed into a right-skewed distribution of fitness on the Y-axis. Here normal variation of the trait creates greater rewards than it does penalties. Selection should then act to increase variation in the trait.

to yield maximum fitness given the constraints on the organism.

Markowitz (1952) stated that investors should seek to minimize variance in return by diversifying their investments while maximizing mean return. He defined the efficient set of portfolios as those with the maximum mean return for a given variance and those with minimum variance for a given mean. He saw that there was a mean-variance tradeoff, and he suggested but did not formalize the concept of mean-variance isoclines of equal growth rate (cf. Ekbohm *et al* 1980; Real and Ellner 1992): “The portfolio with maximum expected return is not necessarily the one with minimum variance. There is a rate at which the investor can gain expected return by taking on variance, or reduce variance by giving up expected return” (Markowitz 1952, p 79).

Bernoulli (1738) did not contribute to the analysis of mean-variance tradeoffs and isoclines; that came later.

### 7. Invasion in the general case with frequency dependence and potential chaos

It is now standard to analyse the evolutionary process as a game in which strategies are tested by the invasion of alternatives, and to estimate the fitness of a strategy as its invasion exponent, the rate at which it reproduces when rare. In the general case this is the Lyapunov exponent (see next paragraph for a definition), which reduces to the geometric mean of the per-generation growth rates in the simple case of a series of generations whose growth rates are known. Framing evolution as an invasion process automatically reveals frequency-dependence if it is present. Invasibility is not the only relevant criterion – attainability is also critical, for not all parts of phenotype space can always be reached from all other parts. For more on this see Dieckmann (1997).

Ellner (1989) proved that the invasibility criterion for an analysis of evolutionarily stable strategies (ESSs) is geometric mean fitness. Ferrière and Gatto (1995) generalized this. They defined the Lyapunov exponent as follows: Let  $M_T$  be the transition matrix for the population (the Leslie matrix would be a particular case). Let  $A$  be an invader and  $R$  be a resident. Then  $s$ , the Lyapunov exponent, is defined for an invader with respect to a resident as

$$S_R(a) = \lim_{T \rightarrow \infty} 1/T \sum \log \mathbf{m}_T,$$

where  $T$  is time and  $\mathbf{m}_T$  is the dominant eigenvalue of the transition matrix, i.e.  $\lambda_T$  in the usual life-history notation. Here the Lyapunov exponent, the fitness measure for invasion, is given as the limit of the geometric mean of the per-year (or other time unit) growth rates defined by

the sequence of transition matrices characterizing the conditions in each year. Doebeli (1998) showed that success depends on the resident, for some invaders can even create the conditions for their own elimination.

### 8. Who knew what and when did they know it?

The economists generally got there first, but the biologists sometimes took it further. Among the biologists, Cohen (1966) notes the analogy to investment theory, and Lewontin and Cohen (1969) acknowledge a debt to economics. There is no trace of input from economics in Schaffer (1974) or Gillespie (1974). Concepts from portfolio theory enter biology explicitly in Real (1980), who notes that under uncertainty, a portfolio of behaviours is better than a single behaviour and that negative covariance of the fitness contributions of the behaviours in the portfolio is advantageous because it reduces the variance in fitness.

At least since Cohen started mean-variance analysis in biology, biologists have preferred to separate the arithmetic mean and the variance rather than to combine them in the geometric mean as a summary measure. This reflects a similar stance in economics, where leading textbooks on portfolio theory advocate the separation of mean and variance, to allow one to think about their separate effects, rather than using the geometric mean, which conflates their effects.

I do not wish to suggest that the analogy between economic and evolutionary risk is exact, but it is suggestive. We know that spatial and temporal variation contribute differently to evolutionary fitness (Gillespie 1974). In economics, investors certainly worry about variation in rates of return and risk in different countries, and they might want to look into the evolutionary analogy for some technical insights. A second complicating factor in evolution is the regular genetic recombination generated by sexual reproduction. This has a rough, certainly not a precise, analogy to the annual reshuffling of portfolios by fund managers who respread the risk regularly.

### 9. Some interesting recent insights into evolutionary risk

The train of thought started by Bernoulli in 1738 continues to spawn insights in evolutionary biology. For example, Lacey *et al* (1983) applied variance discounting to each trait separately. They found that both mean and variance contribute to fitness in empirical examples and found cases where negative covariances produced compensating impacts on fitness. Their work suggests the following idea: The phenotypic plasticities of the traits contributing to fitness should be so designed that the traits covary

negatively to minimize variance in fitness. This sees traits as stocks in a portfolio, and phenotypic plasticity as ideal management practice.

Up to this point, we have been discussing bet-hedging and risk-spreading strategies as though they were properties of asexual clones with perfect heritability. What happens with sexual reproduction and the potential for kin selection? A first step towards an answer was taken by Frank and Slatkin (1990). In a haploid, one-locus, two-allele model, they partition variance in reproductive success into parts attributable to individuals and parts attributable to correlations in reproductive success among individuals. When frequency-dependence is important – when variation in one individual's reproductive success induces variation in the reproductive success of other individuals – the geometric-mean principle may not predict which allele wins, although it does so in special cases. Bet hedging for genotypes means that a trait or behaviour produces a low correlation in reproductive success among individuals of the same genotype, in effect increasing the number of independent samples of reproductive success for that genotype. Bet hedging for individuals means reducing the correlations in reproductive success among offspring by putting eggs into different baskets.

Sasaki and Ellner (1995) asked how many different phenotypes can be maintained by environmental variance, and whether a strategy of producing those phenotypes with separate genotypes will win against a strategy that produces them all from a single genotype. They found that as the environmental variance increases, and all types play against all types, the number of phenotypes maintained increases, but those phenotypes are distributed in discrete blocks, not continuously. Genotypes that made several phenotypes – polyphenotypic strategies in which parents produce a variety of offspring – always invaded a polymorphic population of similar but genetically fixed phenotypes. They did so because of their bet-hedging advantage, for by producing a variety of progeny they reduced the temporal variance in per-generation fitness.

## 10. Phenotypic evolution under uncertainty and risk

### 10.1 *Diapause and dormancy*

Cohen (1966) concluded that variation in reproductive success and postbreeding adult survival would shape the optimal *fraction* of the population that should germinate or reproduce in a given year. “One obvious way to survive and reproduce in a risky environment is to spread the risk so that one failure will not be decisively harmful.”

### 10.2 *Iteroparity and reproductive effort*

Schaffer (1974) showed that for iteroparous organisms, adding variation in reproductive success favours reduced

reproductive effort, and adding variation in adult post-breeding survival favours increased reproductive effort. Lacey *et al* (1983) showed that *Daucus carota* is selected to be biennial over annual because of environmentally induced variation in cohort fitness.

### 10.3 *Sex versus asex in risky environments*

Robson *et al* (1999) showed that sexually reproducing organisms invade asexually reproducing populations more easily as risk (variance in reproductive success) increases. Leonard (1999) suggested that sexual reproduction was a form of individual bet-hedging, and Doebeli and Koella (1994) showed that sex dampens tendencies towards chaotic population dynamics. Their work suggests that we could look at sex from the point of view of a single gene that could influence the proportion of sexual or asexual reproduction. If it is living in an environment that selects for risk-spreading, then sexual reproduction has an advantage for the gene: it will find itself in the next generation in each of a number of genetically different offspring. To the extent that each offspring interacts with the environment independently, sex spreads risk (cf. Frank and Slatkin 1990; Sasaki and Ellner 1995).

## 11. Conclusion

In this 300th anniversary of Daniel Bernoulli's birth, this essay traces the influence of one of his works usually regarded by mathematicians and physicists as too minor to mention. From this source has flowed much of our understanding of how to deal with risk in economics and evolution. The concepts introduced by Bernoulli help us to think about the evolution of reproductive lifespan, dormancy and diapause, sexual versus asexual reproduction, and population dynamics. In economics they form the foundation of portfolio and insurance theory. The 1738 paper was definitely not minor.

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