**Bet-hedging simulation**

C.M. Lively, Indiana University, Honors Evolution

Consider a temporally variable environment. In some years, there are many resources, and all offspring survive. But in other years, resources are limited; not all offspring survive.

What to do? Here we consider two different strategies: Risky and Bet-hedging.

**Risky**. In the good years, the best strategy might be to make many, relatively small offspring, let's say the optimal number is 5. In good years, all 5 offspring survive. But in bad years, when resources are scarce, only 2 survive. If good and bad years alternate, then the expected number of offspring is (2+5)/2 = 3.5. Let's call this the risky strategy, because making few, small offspring is risky.

**Bet-hedging**. Consider now a bet-hedging strategy. The bet hedger does not know in advance whether the year will be good or bad for her offspring, so she makes fewer but larger offspring, say 4. These larger offspring have a better chance of survival during bad years. Let's say that 3 of the 4 survive in bad years. Still assuming that good and bad years alternate, the expected number of offspring over a 2-year period is (3+4)/2 = 3.5. So, the expected number of offspring is the same for the risky strategy and the bet-hedging strategy. (Here I am following Steve Stearn's foundational book, *The Evolution of Life Histories.*)

So, it would seem that the two strategies have the same average reproductive output. But, and this is important, selection does not operate on just the mean in temporally variable environments. Selection also operates on the variance. More specifically, selection would act to reduce the between-year variance. We can get a sense of this my looking by comparing the geometric mean to the arithmetic mean.

The geometric mean is simply the *N*th root of the product of *N* observations. For example, for 4 observations get $(x1\*x2\*x3\*x4)^{1/4}$. The geometric mean (GM) can also be helpfully approximated from the arithmetic mean $(\overbar{x})$ and the variance in $x$ (var($x$)).

$$GM = \overbar{x}-\frac{var(x)}{2\overbar{x}}$$

If the var(x) is zero, then the GM = arithmetic mean. But if the variance in x is greater than zero, the GM is less than the arithmetic mean. And, all else equal, the larger the variance, the smaller the GM. Steve Stearns wrote an excellent historical essay on this idea (Stearns, 2000).

Natural selection should operate to reduce the between-year variance, which increases the GM. Hence, we can think of it this way. Natural selection in temporally variable environments acts to maximize the geometric mean. This is true even increasing the geometric mean leads to a decrease in the arithmetic mean. This last idea is classic bet hedging (Philippi & Seger, 1989).

Some examples comparing different risky and bet-hedging strategies are given in Table 1. See example 1. The arithmetic means are the same, but the bet-hedging strategy has a low variance and a higher geometric mean. The bet hedger should win, right?

None of this is especially intuitive, so we will use a simulation to gain insight. Our prediction is that, in a competition between two strategies, the strategy with the highest geometric mean will eventually win. The simulation assumes asexual reproduction, and that all individuals only live for one year. The user can input the number of offspring produced in good and bad years for both strategies. The probability of a bad year is also a random variable that you can set. So for example, if you set the probability of a bad year at 0.4, then the year will be "bad" when a random number (between 0 and 1) is less than 0.4. Try out the different scenarios given in Table 1. Does the bet-hedger win when it has a higher GM?

Note that, in the simulation, the bet-hedger starts as the rare strategy. We want to know if the bet-hedger increases when rare, and if so, whether it replaces the risky strategy. Note too that the simulation is stochastic, as the type of year is random. So, each run will be different. Run the simulation 10 or more times for each combination of values. (Type "control +" to rerun the simulation.) Now summarize your findings. Focus on the main conclusions with respect to the hypothesis that the bet-hedging strategy will win when it has a higher geometric mean due to a lower between-year variance.

Table 1. Number of surviving offspring for two different strategies. Strategy 1 is Risky: make many relatively small offspring every year. Strategy 2 is a bet-hedger: make fewer, but larger, offspring to increase survival in bad years. The numeric entries in black font given the number of surviving offspring in good and bad years. Compare the arithmetic mean with the geometric means for the two strategies in each of the 4 examples. Which strategy would win? (Note in particular that the GM is zero for the risky strategy in Example 3.) Example 1 was chosen following Stearn's book, *The Evolution of Life Histories* (1992), Oxford University Press.

|  |  |  |  |
| --- | --- | --- | --- |
|  |  **Number of surviving offspring** |  |  |
|  |  |  |  |  | **Arithmetic** | **Variance** | **Geometric** |
|  | good yr | bad yr | good yr | bad yr | **mean** |  | **mean** |
| **Example 1**1. Risky | **5** | **2** | **5** | **2** | **3.50** | **2.25** | **3.16** |
| 2.BetHedge | **4** | **3** | **4** | **3** | **3.50** | **0.25** | **3.46** |
| **Example 2** |  |  |  |  |  |  |  |
| 1. Risky | **6** | **1** | **6** | **1** | **3.50** | **6.25** | **2.45** |
| 2.BetHedge | **4** | **2.5** | **4** | **2.5** | **3.25** | **0.56** | **3.16** |
| **Example 3** |  |  |  |  |  |  |  |
| 1. Risky | **7** | **0** | **7** | **0** | **3.50** | **12.25** | **0.00** |
| 2.BetHedge | **4** | **2.5** | **4** | **2.5** | **3.25** | **0.56** | **3.16** |
| **Example 4** |  |  |  |  |  |  |  |
| 1. Risky | **8** | **2** | **8** | **2** | **5.0** | **12.0** | **4.00** |
| 2.BetHedge | **5** | **4** | **5** | **4** | **4.5** | **0.33** | **4.47** |

**References**

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

Stearns, S. C. 2000. Daniel Bernoulli (1738): evolution and economics under risk. *Journal of Biosciences* **25**: 221-228.