Storage for Good Times and Bad: Of Rats and Men

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1 Introduction

Fabulists, from Aesop to Walt Disney, have employed animal characters to play human-like roles in their stories. The success of these stories suggests that people are willing to take a sharper look at the foibles of their own species if they pretend to see them in other creatures. In this paper, I confess a similar motivation. The paper is motivated by the evolution of food-hoarding behavior in rats, squirrels, and other creatures, but I have found that thinking along these lines makes it easier to take a fresh look at the way that human preferences toward wealth-acquisition and risk-taking may have evolved. Unlike the fables of Aesop and Disney, this paper is inspired by the work of behavioral ecologists who have studied real animals [1] and I hope that it may be a useful contribution to the understanding of animal behavior as well as a fable for economists.

2 Models of Storage and Survival

Let us begin to hone our intuition about the evolution of strategies for acquisition and survival in a risky example by looking at an example that is so simple that we can almost solve it in our heads.

2.1 A Really Simple Example

An animal must store food in order to survive through the winter. If it does not store enough food, it will surely die without reproducing. If it stores enough food to last the entire winter, it may survive and reproduce. The length of winters are variable and unpredictable. Storing larger amounts of food is costly, exposing the animal to risks of predation.

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[1] *Food Hoarding in Animals* by Stephen Vander Wall [4] is an admirable survey of the large and fascinating empirical literature amassed by biologists on food storage by rodents, carnivores, birds, insects, and spiders.

- There are two kinds of winters, long and short.

- The climate follows a cyclical pattern with cycles of length $k = k_1 + k_2$. In each cycle, there are k_1 short winters and k_2 long winters.

- Animals can pursue one of two possible pure strategies. Strategy 1 is to store enough food to last through a short winter, but not enough to last through a long winter. Strategy 2 is to store enough food to last through a long winter.

- The probability that an animal will *not* be killed by a predator while storing food is v_1 if it pursues Strategy 1 and v_2 if it pursues Strategy 2, where $v_1 > v_2$.

- Reproduction is asexual. Except for rare mutations, each individual has the same genetic makeup as its mother.

Pure and Random Strategies

If each animal is genetically programmed to pursue the same pure strategy that its parent did, then in the long run, the population will consist almost entirely of animals that pursue Strategy 2. This is the case because every time that there is a long winter, all animals that pursue Strategy 1 will be wiped out. If long winters are very rare, but very severe, this means that evolution would select genes that mandate an extremely conservative and very expensive strategy, which is "wasteful" most of the time.

Suppose that it is possible for genes to induce induce randomized strategies. In this case, a gene may be carried by some individuals who store for a long winter, but also by some who store for a short winter. As we will show, a population of genes that mandate Strategy 2 can be invaded by genes that induce individuals to randomize between Strategies 1 and 2, with appropriate probabilities. The intuitive reason for the success of this strategy is quite simple. In a large population, a randomizing gene will not be entirely eliminated during the long winters, since some carriers of the gene will pursue Strategy 2. On the other hand, in the years with short winters, the randomizing gene will do better than genes for Strategy 2, since some carriers of the random gene will enjoy the smaller risks of predation that accompany Strategy 1.

Our task here is to solve for the randomizing gene that in the long run will reproduce most rapidly. Let π_1 be the probability that a gene assigns to Strategy 1 and $\pi_2 = 1 - \pi_1$ be the probability that it assigns to Strategy 2. In a large population, the fraction of carriers of this gene who pursue Strategy i will be close to π_i. In a year with a short winter, all animals that are not taken by predators will have enough food to survive the winter. Therefore in a year with a short winter , animals following Strategy 1 will survive predation with probability v_1 and those following Strategy 2 will survive with probability $v_2 < v_1$. It follows that in a short winter, the fraction of carriers of this randomizing gene who survive will be approximately $S_1 = \pi_1 v_1 + \pi_2 v_2$. In a long winter,

all of the animals pursuing Strategy 1 will die of starvation, while those who pursue Strategy 2 and are not eaten by predators will survive. Therefore the fraction of all carriers of the randomizing gene who survive a long winter will be close to $S_2 = \pi_2 v_2$.

Finding the most successful mixed strategy

Over the course of an entire climatic cycle, there will be k_1 short winters and k_2 long winters. Therefore if an individual has genes that mandate a randomizing strategy with probabilities π_1 for Strategy 1 and π_2 for Strategy 2, her expected number of surviving offspring after a full climatic cycle will be $S_1^{k_1} S_2^{k_2}$. In the long run, after a sufficiently large number of climatic cycles, the population will consist mainly of animals who use random strategies with probabilities π_1 and π_2 very close to the values that maximize $S_1^{k_1} S_2^{k_2}$ subject to the constraint that $\pi_1 + \pi_2 = 1$ and $\pi_i \geq 0$ for $i = 1, 2$.

Since $S_2 = \pi_2 v_2$ and $S_1 = \pi_1 v_1 + \pi_2 v_2$, we can write

$$\pi_2 = \frac{1}{v_2} S_2 \qquad \text{and} \qquad \pi_1 = \frac{1}{v_1}(S_1 - S_2). \tag{1}$$

Therefore we can state the constrained maximization problem entirely in terms of the variables S_1 and S_2. Specifically, the problem is: Maximize

$$S_1^{k_1} S_2^{k_2} \quad \text{subject to} \quad \frac{1}{v_1} S_1 + \left(\frac{1}{v_2} - \frac{1}{v_1} \right) S_2 = 1 \quad \text{and} \quad S_1 \geq S_2. \tag{2}$$

Let us define $\alpha_i = k_i/(k_1 + k_2)$ for $i = 1, 2$. Ignoring the constraint $S_1 \geq S_2$, the solution to the maximization problem (2) is

$$S_1 = \alpha_1 v_1 \quad \text{and} \quad S_2 = \alpha_2 \frac{v_1 v_2}{v_1 - v_2}. \tag{3}$$

Since $\alpha_1 + \alpha_2 = 1$, simple calculations show that $S_2 \geq S_1$ if and only if $\alpha_1 \geq v_2/v_1$. Therefore if $\alpha_1 \geq v_2/v_1$, the constraint $S_1 \geq S_2$ does not bind and the solution for S_1 and S_2 is as above. The randomizing probabilities that lead to this outcome are

$$\pi_1 = \frac{\alpha_1 v_1 - v_2}{v_1 - v_2} \quad \text{and} \quad \pi_2 = \alpha_2 \frac{v_1}{v_1 - v_2}. \tag{4}$$

If, on the other hand, $\alpha_1 < v_2/v_1$, the solution to the constrained optimization problem will be the pure strategy in which $\pi_2 = 1$, and $\pi_1 = 0$.

Implications of this Model

This simple model implies the following:

- Evolution will favor genes that result in mixed rather than pure strategies if the fraction of all years that have short winters is larger than the ratio of the survival rate in years with short winters of animals who store enough for a long winter to that of those who store only enough for a short winter.

- In an optimizing population of mixed strategists, we have

$$\frac{S_2}{S_1} = \frac{\alpha_2}{\alpha_1} \left(\frac{v_2}{v_1 - v_2} \right).$$

This means that the ratio of the expected number of survivors over a long winter will be inversely proportional to the probability of a long winter.

2.2 A More General Example

Let the length of winter be governed by a stochastic process in which there are N possible lengths of winter. Each year, the length of winter is determined by a random draw that is statistically independent of the length of previous winters. The probability that the length of winter is t days is α_t and $\sum_{t=1}^{N} \alpha_t = 1$. For $t = 1, \ldots, N$, an animal who pursues strategy t will either be eaten by a predator or will collect enough food to survive a winter of t days. The probability that an animal pursuing Strategy t is not eaten by a predator is v_t, where $v_t \geq v_{t+1}$. An animal who pursues Strategy t will survive through the winter if it is not eaten by a predator and if the length of the winter is no longer than t.

If all animals pursued pure strategies inherited from their parents, then eventually the only survivors in the population would be those animals who stored enough food for a winter of the maximal length N. All other genotypes would eventually encounter a winter that would wipe them out.

Suppose that a gene mandates that its carriers pursue a mixed strategy such that the probability that a carrier pursues Strategy t is given by π_t for each t. If the winter lasts for w days, the expected number of surviving carriers of this gene will be

$$S_w = \sum_{t=w}^{N} \pi_t v_t. \tag{5}$$

In the long run, the proportion of all years in which the winter is of length w will be α_w. The long run growth rate of the population of randomizers will with very high probability be very close to

$$\prod_{t=1}^{N} S_t^{\alpha_t} \tag{6}$$

where the S_t's are determined by the randomizer's choice of probabilities π_t. In the long run, the population will be dominated by genes for a mixed strategy in which the probabilities π_t are chosen so as to maximize the expression in Equation 6 subject to the constraint that

$$\sum_{t=1}^{N} \pi_t = 1. \tag{7}$$

From Equation 5 it follows that

$$S_N = \pi_N v_N \quad \text{and for all} \quad t < N, \ S_t - S_{t+1} = \pi_t v_t. \tag{8}$$

Therefore

$$\pi_N = S_N/v_N \quad \text{and} \quad \pi_t = (S_t - S_{t+1})/v_t \quad \text{for } t = 1, \ldots, N-1 \qquad (9)$$

From (9) it follows that the constraint in (7) is equivalent to

$$S_1 \frac{1}{v_1} + \sum_{t=2}^{N} S_t \left(\frac{1}{v_t} - \frac{1}{v_{t-1}} \right). \qquad (10)$$

The mixed strategy that maximizes the long run reproductive effort is therefore one that yields S_i's that maximize the expression in (6) subject to the constraint in equation (10) and subject to the additional constraint that

$$S_t \geq S_{t+1} \quad \text{for all} \quad t = 1, \ldots, N-1 \qquad (11)$$

Ignoring the inequality constraints in (11), the constrained maximization problem of maximizing (6) subject to the constraint expressed in (10) is of the familiar Cobb-Douglas form and has the solution

$$S_1 = \alpha_1 v_1 \quad \text{and} \quad S_t = \alpha_t \frac{v_t v_{t-1}}{v_{t-1} - v_t} \quad \text{for } t = 2, \ldots, N \qquad (12)$$

If for all $t < N.$, the solutions to equations (12) all have the property that $S_t > S_{t+1}$, then these equations (12) describe the constrained maximization problem of maximizing (6) subject to (10) and (11). If, however, the expressions in (12) do not satisfy these inequalities, then we must use Kuhn-Tucker methods to characterize the solution. In general, the the optimal mixed strategy may assign zero probability to storing enough food to last exactly t days for some values of $t < N$. So long as $\alpha_N > 0$, it must be that the optimal mixed strategy assigns positive probability to storing enough food for N days. Let T be the set of all pure strategies that are assigned positive probability by the optimal mixed strategy and let $A = \sum \alpha_{t \in S}$. Then for all $t \in T$, the optimal mixed strategy satisfies

$$S_t = \frac{\alpha_t}{A} \frac{v_t v_{t-1}}{v_{t-1} - v_t} \qquad (13)$$

Example 1

An instructive example is the case where $v_t = 1/t$ for $t = 1, \ldots, N$. In this case, the solution in (12) reduces to

$$S_t = \alpha_t \quad \text{for } t = 1, \ldots, N. \qquad (14)$$

These survival rates are achieved by a random strategy in which for $t = 1, \ldots, N$

$$\pi_t = t(\alpha_t - \alpha_{t+1}) \qquad (15)$$

The inequalities in (11) are then equivalent to the condition that $\alpha_t \geq \alpha_{t+1}$. Consider the case where the distribution of length of winter is single-peaked,

with modal length of winter being w^*. Let A^* be the probability that the winter is longer than the modal length. Then the constrained maximum of (6) subject to conditions (10) and (11) is

$$S_t = \frac{\alpha_t}{A^*} \tag{16}$$

for all $t \geq w^*$ and $S_t = S_{w^*}$ for all $t < w^*$.

In this example, no animal would store only enough food for a winter that occurs with less than the modal frequency. For winters longer than the modal length, the fraction of animals who survived through the winter would be proportional to the frequency of winters of that length.

Example 2

Suppose that every day's worth of consumption that an animal stores subjects it to a constant additional risk of being eaten by predators. Thus the probability that an animal who stores t days worth of food will *not* be eaten by predators will be $v_t = \rho^t$ where $0 < \rho < 1$. In this case, the solution to Equations 12 is

$$S_t = \frac{\alpha_t \rho^t}{1 - \rho} \tag{17}$$

The inequality constraints in (11) will hold for t such that $\alpha_t \geq \rho \alpha_{t+1}$. If the distribution of lengths of winter is single peaked with modal length w^*, then positive probability will be assigned to storage for all winters longer than ρw^*.

2.3   Do Genes Program for Random Strategies?

Richard Levins [1] presents a clear theoretical explanation of how it can be that in variable environments it may be advantageous for a gene to take a mixed strategy by producing more than one phenotype. The phenotypes produced by a given genotype may be determined by environmental cues, or may be stochastically determined. Levins cites many examples, including the determination of sexual versus asexual eggs in rotifera, the period of dormancy in many seed plants, the production of winged and wingless aphids, and clutch size in birds. The case of spadefoot toad tadpoles is another interesting example of phenotypic variability among individuals with the same genetic inheritance. These tadpoles live in ephemeral ponds, where the length of time before a pond dries up varies greatly from year to year. [2] The tadpoles develop into one of two morphs, a large, rapidly developing carniverous morph and a smaller, more slowly developing omniverous morph. If the pool dries up quickly, the carniverous type are more likely to survive than the omnivores, if the pool dries up slowly the omnivores are more successful. Both types have the same genetic inheritance. Morph frequency within a pond is stabilized at an equilibrium by frequency dependent morph reversals by individuals.[2]

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[2]An extra source of drama is provided by the fact that the omnivores frequently cannibalize their carniverous siblings.

In principle, phenotypic diversity in a population could be maintained either by an essentially monomorphic genetic population of randomizers or by genetic variation in the population. According to Vander Wall, "The genetics of hoarding is virtually unknown in wild animals, and only an incomplete picture ... is available in laboratory animals. " Vander Wall cites some experimental evidence that the ratio of genotypic variation to total phenotypic variation of hoarding in laboratory-bred mice ranges from 0.25-0.55. This seems to leave quite a lot of room for randomizing behavior as well as for genetic polymorphism.

Whether variation in food storage strategies is the result of randomization or of genetic variation, there appears to be a large amount of variation in the amount of food stored by different members of the same species. According to Vander Wall [4]

> "The hoarding performance of animals in both the wild and in controlled experiments is typified by great phenotypic variability. Pika (*Ochotona princeps)*[3] hay piles at one site in the Rocky Mountains ranged in size from 400-6,000 grams... and red squirrel middens contained from 280-4360 cones... Individual laboratory rats and Syrian golden hamsters differ so greatly in their propensity to store food that subjects often have been categorized as hoarders and nonhoarders ..." p 112.

It seems that a fairly straightforward empirical test would distinguish between the hypothesis of randomization by identical genes and that of genetic heterogeneity. One would simply want to compare the behavior of the next generation of an animal population after an unusually hard winter or dry season. If individual genes randomize, then the distribution of offspring of survivors of a long winter are expected to be genetically no different from those who did not survive. Since variation of phenotypes is the result of random draws, the offspring of the survivors would randomize with the same probability distribution as the parent generation. Hence the distribution of behaviors would not change. If on the other hand, phenotypic variation is maintained by genetic polymorphism, then in the year after a harsh winter, we would expect the survivors to store more food than they did in the previous generation. Vander Wall (pp 63-65) cites several studies that show that animals of the same species living in harsher climates store more than those living in milder climates (a result that is hardly surprising). However, he does not mention any studies that consider the ratio between survival rates under harsh conditions and the relative frequency of these harsh conditions.

Another testable implication of the theory that we have discussed is the following. Consider populations of the same species living in geographical areas with different climates, but where the predation costs of gathering food are similar. Now suppose that we were able to observe winters of length t and t' in each of the two places and that we were able to observe the number of survivors in each place. From equation 13 the theory predicts that in each of the two

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[3]These are guinea pig-like animals.

geographical areas,

$$\frac{S_t}{S_{t'}} = \frac{K\alpha_t}{\alpha_{t'}} \tag{18}$$

where, given that predation costs are the same in the two places, the constant K is the also the same in the two areas. Thus the ratio of the relative survival rates in the two places, will be the same as the ratio of the relative frequencies of winters of these lengths in the two places.

The hoarding example sharply focusses a difference between evolutionarily formed attitudes toward *idiosyncratic risk* and *aggregate risk* that is emphasized by Arthur Robson [3]. In this example, as in Robson's theory, it might be said that evolution selects genes that act so as to maximize the *arithmetic* mean success when faced with statistically independent faced by individuals carrying the gene and they seek to maximize the geometric mean reproduction rate when faced with risks like the length of winter, which influence the fate of the entire population of carriers of the gene.

3   Casino Gambling

In human societies, when property rights are reasonably well established, it is possible for individuals to achieve randomness in their incomes by means of "casino gambling" rather than by randomly choosing the amount of effort that they put into wealth accumulation. In particular, we will assume that individuals are able to make any "actuarially fair" gamble.[4] This may not be so easy for other animals to achieve, though it is interesting to consider the consequences of allowing such gambles. As we will show, where the risks of predation are as in the previous section, the optimal strategy for each animal is to collect a fixed number of days worth of food Y and then randomize its income by casino gambling. An animal who initially collects Y days worth of food and survives can gamble to achieve any probability distribution of days' worth of food, $(\pi_1, \ldots, \pi_N)$ such that

$$\sum_{t=1}^{N} t\pi_t = Y. \tag{19}$$

An animal who collects Y days food will escape predation with probability v_Y. It will survive to reproduce if and only if its stock of food after gambling is large enough to last at least as many days as the length of the winter. Therefore the number of individuals who survive a winter of length t will be

$$S_t = v_Y \sum_{w=t}^{N} \pi_w. \tag{20}$$

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[4]A gamble is actuarially fair if the expected payoff in the gamble is the same as the expected cost of entering the gamble.

From Equation 20, it follows that $S_t - S_{t-1} = v_Y \pi_t$ and therefore

$$\pi_t = \frac{S_t - S_{t-1}}{v_Y}. \tag{21}$$

Equation 19 can therefore be rewritten as

$$\sum_{t=1}^{N} t(S_t - S_{t-1}) = v_Y Y. \tag{22}$$

But Expression 22 simplifies to

$$\sum_{t=1}^{N} S_t = v_Y Y. \tag{23}$$

The requirement that gambles must be actuarially fair, therefore imposes the constraint in Equation on the election of S_ts. In addition, since the probabilities, π_t must all be non-negative, we see from Equation 3 that feasibility also requires that

$$S_{t+1} \le S_t \tag{24}$$

for $t = 1, \ldots, N - 1$. It follows that a gene would maximize its long run reproduction rate by inducing its carriers to take gambles in such a way as to maximize

$$\prod_{t=1}^{N} S_t^{\alpha_t} \tag{25}$$

subject to the constraints in Expressions 23 and 24. Ignoring the inequality constraint 24 and maximizing Expression 25 subject to the equality constraint 23, we find the solution:

$$S_t = \alpha_t v_y Y \tag{26}$$

for $t = 1, \ldots, N - 1$. We see, that this expression satisfies the inequality constraint 24 if and only if $\alpha_t \le \alpha_{t+1}$.

In general, we can account for the inequality constraints using methods known to economists as Kuhn-Tucker conditions. In general finding and characterizing solutions may be quite complex, but here we will look at an interesting special case where this characterization is easy. Recall that α_t is the probability that the winter is of length t and suppose that the length of winter is "single-peaked", where the modal length of winter is w^* and where $\alpha_{t+1} < \alpha_t$ if $t < w^*$ and $\alpha_{t+1} > \alpha_t$ if $t > w^*$. In this case, it is not hard to show that the unique solution to the constrained maximization problem is that every animal will save at least enough for a winter of length w^* and for all $t \ge w^*$,

$$S_t = k \alpha_t v_Y Y \tag{27}$$

where

$$k = \sum_{t=w^*}^{N} \alpha_t \tag{28}$$

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Looking at Expression 27, one sees that the solution for the best amount of food to collect will be the value of Y that maximizes $v_Y Y$, which is the expected amount of food collected by an animal that endeavors to collect Y days worth of food, when account is taken of the probability that the animal fails to collect this food because it is eaten by a predator.

Implications of the Casino Model

The casino model has implications that are especially interesting if we believe that human preference toward risk and acquisition of wealth may have evolved in an environment where storage and gambling were important features of economic life.

The model predicts that instead of randomizing on the amount of effort they devote to accumulation, individuals would accumulate the amount that maximizes expected payoff, taking into account the costs of effort. The model predicts that evolution would produce that individuals who earn a fixed, non-stochastic income would crave opportunities to gamble at actuarially fair odds, and if actuarially fair odds were not available they would still want to gamble at unfair odds. Perhaps compulsions to gamble are not maladaptive to the genes of the gamblers, but instead allow the gene to diversify the portfolio of genotypes who carry it.

The presence of the casino lottery option allows the economy to run more efficiently since with the casino lottery individuals can achieve variance in their payoff outcomes while pursuing the accumulation strategy that maximizes expected their expected accumulation. If there were no lottery available, individuals would seek to achieve random final incomes by randomizing on their strategy for accumulation of wealth. This randomization would mean assigning some probability to activity levels that did not maximize expected payoffs.

References

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