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On the evolution of hoarding, risk-taking, and wealth distribution in nonhuman and human populations

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This paper applies the theory of the evolution of risk-taking in the presence of idiosyncratic and environmental risks to the example of food hoarding by animals and explores implications of the resulting theory for human attitudes toward risk.

evolutionary bet hedging | storage | gambling | geometric mean | squirrel's dilemma

Fabulists, from Aesop to Disney, have used animal characters to play human-like roles in their tales. The popularity of these fables suggests that readers 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 of rats and squirrels, but thinking along these lines may help us to take a fresh look at human preferences toward wealth acquisition and risk-taking. Unlike the fables of Aesop and Disney, this paper is inspired by the work of behavioral ecologists who have studied real animals,[†] and I hope it may be of interest to those who study animal behavior as well as to economists.

This paper examines the implications of evolutionary bet hedging by organisms that store food supplies during periods of abundance to survive through periods of scarcity. Individuals face idiosyncratic predation risks as they accumulate food supplies, while the entire population faces environmental risks that the winter or the dry season may last so long as to exhaust their stored supplies. The theory leads to interesting predictions about the distribution across the population of stocks of stored food and about the relation between survival rates in harsh conditions to the frequency of such conditions.

Evolutionary biologists are aware that in a stochastically variable environment, natural selection is likely to favor a gene that randomizes its phenotypic expression. Because reproduction is multiplicative, the long-term average rate of reproduction of a gene will be the geometric mean of the reproduction rates of the generations that carry this gene. If an entire population is affected by environmental effects that vary over time, a genotype that induces random variation in the phenotypes who carry it will have a higher expected long-run growth rate than one that produces a single type. Seger and Brockmann describe this effect as "bet-hedging." In their words, "a bet-hedging strategy must be realized as the variable phenotypic expression of a *single* genotype, not as a genetic polymorphism" (ref. 2, p. 186).

Cooper and Kaplan (3) use a story of an animal seeking camouflage to illustrate this effect, which they call "adaptive coin-flipping." The animal must decide whether to grow a white or a brown coat for winter. If the winter is snowy, white is the better color, but if there is no snow, brown is better. They show that a gene that randomizes the colors of the animals that carry it has a higher expected long-run reproductive rate than one that mandates either single color. Cohen (4) developed a simple bet-hedging model to explain delayed seed germination, while Levins (5) explored applications of this theory to sexual versus asexual eggs in rotifera, the period of dormancy in seed plants, the production of winged and wingless aphids, and clutch size in birds. Childs et al. (6) survey recent theoretical contributions and empirical evidence of evolutionary bet hedging by plants and animals.[‡]

Robson (8) draws on a branch of probability theory known as branching theory (9) to develop this theory thoroughly and rigorously. In Robson's model, natural selection operates on types that are committed to specific strategies. These strategies may either be pure strategies that dictate a specific response to one's environment or mixed strategies that randomize among two or more pure strategies. The number of offspring of an individual of given type is a random variable that depends partly on statistically-independent, idiosyncratic risks and partly on environmental risks that affect all individuals of the same type uniformly. In this model, parents give birth to offspring that are most likely be of their own type, but there is a small probability that any type can mutate to any other type. In each period, the state of the environment is an independent and identically distributed (i.i.d.) random variable, drawn from a fixed finite set of possible states $(1, \ldots, S)$, where the probability of state s is π^s. The number of surviving offspring of a type i individual in environmental state s is a random variable with expected value $m^i(s)$. Robson shows that if mutation rates are small, in the long run the population will consist predominantly of individuals of the type i that has the highest value of

$$\sum_s \pi^s \ln m^i(s). \qquad [1]$$

Thus, evolution selects for a type that maximizes the log of the geometric mean across environmental states of the arithmetic mean number of descendants within each state.

A Squirrel's Dilemma: Simple Model

A squirrel must store nuts to survive through the winter, but does not know how long the winter will be. Collecting and storing food is costly because it exposes the animal to predation. However, collecting too few nuts to last the winter is fatal. There are two possible lengths of winter: short and long. The probability of a short winter is p_1 and that of a long winter is $p_2 = 1 - p_1$. A squirrel must choose either to gather enough nuts for a short winter or enough for a long winter. A squirrel that uses the short-winter strategy will avoid predators with probability v_1, and will survive a short winter, but not a long winter. Thus, a short-winter strategist has survival probability $v_1 p_1$. Storing enough nuts for a long winter rather than

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a short winter exposes a squirrel to additional hazard h of being eaten by predators. Therefore, a long-winter strategist will avoid predators with probability $v_2 = v_1(1-h)$. If not eaten by predators, the long-winter strategist will survive a winter of either length. Hence the probability that a long-winter strategist avoids predation and survives through the winter is $v_2 = v_1(1-h)$.

Can we expect natural selection to result in a population of squirrels with strategies that maximize their survival probabilities? Suppose that all squirrels who survive through the winter reproduce at the same positive rate. The survival probability of a short-winter strategist will exceed that of a long-winter strategist if $v_1 p_1 > v_1(1-h)$, or equivalently, if $h > 1 - p_1 = p_2$.

Although a short-winter squirrel is more likely to survive than a long-winter squirrel, if a squirrel's offspring must behave as its parent did, then whenever there is a long winter, the entire population of short-winter strategists will be wiped out. Thus, natural selection would produce a population consisting almost entirely long-winter strategists, despite the fact that they have lower survival probability than short-winter strategists. This would be the case, even if long winters are rare, and the hazard incurred in gathering a long winter's supply is great. Can Mother Nature improve on such an inefficient outcome?

The paradoxical conclusion that short-winter squirrels would eventually lose the evolutionary race, even though they have higher survival probability than long-winter squirrels, is a consequence of the fact that winter's length is an environmental risk that affects all squirrels in the same way, while the risk of being eaten by predators is faced independently by each squirrel. If all risks were independent, it would indeed be true that the strategy with higher survival probability would eventually dominate the population. However, with the correlated risks resulting from weather, this is not the case. In the long run, a gene that "puts all of its eggs in one basket" by dictating a single pure strategy will, in general, reproduce less rapidly than a gene that diversifies its portfolio of phenotypes by inducing some of its carriers to use one pure strategy and others to use another.

Suppose that the genes that regulate squirrel behavior can induce squirrels to randomize their behavior, using a mixed strategy $\pi = (\pi_1, \pi_2)$, such that with probability π_1, they attempt to gather enough nuts for a short winter and with probability $\pi_2 = 1 - \pi_1$ they attempt to gather enough nuts for a long winter. Let $S_1(\pi)$ and $S_2(\pi)$ be the conditional probabilities that a squirrel that carries a gene that induces the mixed strategy π will survive, respectively, through a short winter and a long winter. If the winter is long, a squirrel that carries the gene for mixed strategy π will survive only if it selects the long-winter strategy and is not eaten by predators. This happens with probability

$$S_2(\pi) = \pi_2 v_2. \qquad [2]$$

If the winter is short, the squirrel will survive as long as it is not eaten by predators. This probability is

$$S_1(\pi) = \pi_1 v_1 + \pi_2 v_2. \qquad [3]$$

Maximizing Expected Long-Run Growth Rate

Suppose that the annual reproduction rate of all squirrels that survive the winter is ρ and suppose that over a time period of T years, there are T_1 short winters and T_2 long winters. Because reproduction is multiplicative, it must be that the average annual growth rate of the population of π-strategists is

$$\left(\rho^T S_1(\pi)^{T_1} S_2(\pi)^{T_2} \right)^{1/T} = \rho S_1(\pi)^{T_1/T} S_2(\pi)^{T_2/T}. \qquad [4]$$

Then by the strong law of large numbers, for a sufficiently long time interval T, the random variables T_1/T and $T_2/2$ almost

certainly converge to the probabilities p_1 and p_2. Therefore, the logarithm of the average annual growth rate is close to

$$\ln \rho + p_1 \ln S_1(\pi) + p_2 \ln S_2(\pi). \qquad [5]$$

The mixed strategy that has the highest long-run average growth rate will therefore be the solution to the constrained maximization problem here below.

Maximization Problem 1. *Find* $\pi = (\pi_1, \pi_2)$ *to maximize*

$$p_1 \ln S_1(\pi) + p_2 \ln S_2(\pi),$$

subject to the constraints that

$$\pi_1 + \pi_2 = 1, \quad and \quad \pi_1 \geq 0, \quad and \quad \pi_2 \geq 0.$$

A convenient way to solve *Maximization Problem 1* is to make a change of variables that restates the problem entirely in terms of the survival rates S_1 and S_2. From Eqs. **2** and **3**, it follows that

$$\pi_1 = \frac{S_1(\pi) - S_2(\pi)}{v_1} \quad and \quad \pi_2 = \frac{S_2(\pi)}{v_2}. \qquad [6]$$

The constraint $\pi_1 + \pi_2 = 1$ can be expressed as

$$\frac{S_1}{v_1} + S_2\left(\frac{1}{v_2} - \frac{1}{v_1}\right) = 1. \qquad [7]$$

Since $v_2 = (1-h)v_1$, simple algebra shows that Eq. **7** is equivalent to

$$S_1 + S_2\frac{h}{1-h} = v_1. \qquad [8]$$

Therefore, *Maximization Problem 1* can be reformulated as the following.

Maximization Problem 2. *Find* S_1, S_2 *to maximize*

$$p_1 \ln S_1 + p_2 \ln S_2,$$

subject to

$$S_1 + S_2\frac{h}{1-h} = v_1, \quad with \quad S_2 \geq 0 \quad and \quad S_1 - S_2 \geq 0.$$

The Mixed Strategy Solution. If constrained *Maximization Problem 2* has an interior solution $(\overline{S}_1, \overline{S}_2)$, such that $\overline{S}_1 > \overline{S}_2 > 0$, then it must be that

$$\overline{S}_1 = p_1 v_1 \quad and \quad \overline{S}_2 = p_2 v_1 \frac{(1-h)}{h} \qquad [9]$$

and

$$(\overline{\pi}_1, \overline{\pi}_2) = \left(\frac{\overline{S}_1 - \overline{S}_2}{v_1}, \frac{\overline{S}_2}{v_2}\right) = \left(1 - \frac{p_2}{h}, \frac{p_2}{h}\right). \qquad [10]$$

The inequality constraints $\overline{S}_1 > \overline{S}_2 > 0$ needed for an interior solution will be satisfied if and only $p_2 < h$.

If $p_2 \geq h$, then the constraint $S_1 \geq S_2$ is binding and the solution to *Maximization Problem 2* is $\overline{S}_1 = \overline{S}_2 = v_2$, with $\overline{\pi}_1 = 0$ and $\overline{\pi}_2 = 1$. In this case growth is maximized if all squirrels pursue the long-winter strategy.

This simple example reveals patterns that will reappear in more general environments. If long winters are sufficiently rare, evolution will favor genes that pursue a bet-hedging strategy, such that some squirrels save only enough nuts for a short winter

and some save enough for a long winter. This is true despite the fact that short-winter strategists have higher survival probability than long-winter strategists. We also see that in the equilibrium population, the fraction of squirrels using the long-winter strategy will be proportional to the probability of a long winter.

A Squirrel's Dilemma: More Generally

Additional interesting patterns emerge when we allow for many possible lengths of winter. Suppose that the number of days of winter is a random variable, statistically independent of the length of previous winters, with the longest possible winter lasting for W days. Let p_t be the probability that the winter lasts for exactly t days and let $P_t = \sum_{i=0}^{t} p_i$ be the probability that the winter is no longer than t days.

A squirrel will survive through a winter of length t if and only if it is not eaten by predators and collects enough nuts to last at least t days. A squirrel that has gathered $j-1$ days' worth of nuts and attempts to collect one more day's supply is exposed to an additional hazard h_j of being eaten by predators. Thus, a squirrel that attempts to gather sufficient nuts to last through a winter of length t will survive predation with probability

$$v_t = v_0 \prod_{j=1}^{t} (1 - h_j). \qquad [11]$$

Let $\pi = (\pi_0, \ldots, \pi_W)$ be the mixed strategy, such that with probability π_t, a squirrel attempts to gather enough nuts to last through a winter of exactly t days. If the winter is of length w, then a squirrel that is not eaten by predators will survive to reproduce if it has saved at least w days' worth of nuts. This implies that, conditional on the event that the winter is of length w, a squirrel that uses mixed strategy π will survive and reproduce with probability

$$S_w(\pi) = \sum_{t=w}^{W} \pi_t v_t. \qquad [12]$$

The geometric mean growth rate across environmental states for a gene that uses strategy π is

$$V(\pi) = \rho \prod_{t=1}^{W} S_t(\pi)^{p_t}. \qquad [13]$$

If mixed strategies breed true and the environmental state is determined by an i.i.d. random process over a long period, then the population will be dominated by the genotype that uses the mixed strategy $\bar{\pi}$ that maximizes the geometric mean $V(\pi)$. Maximization of $V(\pi)$ is equivalent to maximization of $\ln V(\pi)$ and hence $\bar{\pi}$ must be a solution to the following constrained maximization problem.

Maximization Problem 3. *Find* $\pi = \bar{\pi}_0, \ldots, \bar{\pi}_W$ *to maximize*

$$\sum_{t=0}^{W} p_t \ln S_t(\pi), \qquad [14]$$

subject to

$$\sum_{t=0}^{W} \pi_t = 1 \quad and \quad \pi_t \geq 0 \quad for \quad t = 0, \ldots, W. \qquad [15]$$

A transformation of variables allows us to restate the constraints of *Maximization Problem 3* in terms of the contingent survival probabilities S_t. As is shown in *Appendix*, there is a one-to-one correspondence between mixed strategy vectors π and the

resulting vector of survival probabilities $S = (S_1, \ldots, S_W)$, such that *Maximization Problem 3* is equivalent to the following problem.
Maximization Problem 4. *Find* $\bar{S} = (\bar{S}_1, \ldots, \bar{S}_W)$ *to maximize*

$$\sum_{t=0}^{W} p_t \ln S_t, \qquad [16]$$

subject to

$$\frac{S_0}{v_0} + \sum_{t=1}^{W} \frac{h_t}{v_t} S_t = 1 \quad and \quad 0 \leq S_t \leq S_{t-1} \quad for \quad t = 1, \ldots, W. \quad [17]$$

In general, the solution to *Maximization Problem 4* may have complicated patterns of time intervals during which the inequality constraints $S_{t+1} \leq S_t$ bind and do not bind. Given some reasonable assumptions on the distribution of winter lengths and on the hazard rates of collecting additional nuts, the solution is greatly simplified. This paper will use two properties of discrete distributions: strict unimodality and a stronger condition, log concavity, which is also known as strong unimodality.[§]

A discrete strictly unimodal distribution is single-peaked in the sense that there is some modal value m, such that the probabilities p_t are strictly increasing in t when $t < m$ and strictly decreasing in t when $t \geq m$. Thus

Definition 1: A discrete probability distribution p defined on the set of integers is strictly unimodal about mode m if $p_t > p_{t-1}$ for $t \leq m$ and $p_t < p_{t-1}$ for $t \geq m+1$.

Definition 2: A discrete probability distribution p with support S, where S is a connected set of integers is log concave if the sequence $\{p_t/p_{t+1}, t \in S\}$ is nonincreasing in t. It is strictly log concave if the sequence $\{p_t/p_{t+1}, t \in S\}$ is decreasing in t.

An (11) and Balabdaoui et al. (12) show that the class of discrete log-concave distributions is very large and includes most of the familiar discrete parametric distributions, including the binomial, negative binomial, geometric, hypergeometric, uniform, Poisson, and Skellam distributions.

Assumption 1: Where p_t is the probability that winter lasts for exactly t days, the distribution of winter length is strictly log concave, with support equal to the integers from 0 to W, and with mode m where $0 < m < W$.

Assumption 2: The probability that a squirrel survives predation while gathering t days' supply of nuts is $v_t = v_0(1 - h)^t$, where $p_1/(p_1 + p_0) > h$ and $p_W < h$.

A squirrel that attempts to collect t days' supply of nuts will survive the winter if it is not eaten by predators and if the winter is no longer than t days. Thus, the survival probability of a squirrel that attempts to collect t days' supply of nuts is $v_t P_t$. From *Assumptions 1* and *2*, it follows that there is a unique effort level k that maximizes the survival probability for any squirrel. Thus, we define the following.

Definition 3: The privately optimal storage quantity is k, such that $v_k P_k \geq v_t P_t$ for all t, such that $0 \leq t \leq W$.

Lemma 1, which is proved in *Appendix*, shows that under our assumptions, the privately optimal storage quantity is uniquely determined and the distribution of winter's length has the properties listed.

Lemma 1: Given *Assumptions 1* and *2*, there exists a unique privately optimal storage quantity k, such that

i) $p_t/P_t \geq h$ for all $t \leq k$ and $p_t/P_t < h$ for all $t > k$.
ii) For all $t \geq k$,

$$\frac{p_{t+1}}{p_t} < \frac{1}{1-h}.$$

Our assumptions imply that in the mixed strategy, which maximizes a gene's expected long-term growth rate, every squirrel seeks to gather at least the privately optimal storage quantity. The following lemma is proved in *Appendix*.

Lemma 2: *Given* Assumptions 1 *and* 2, *where* k *is the privately optimal storage quantity, if* $\overline{S}$ *solves* Maximization Problem 4, *it must be that* $\overline{S}_t = \overline{S}_0$ *for all* $t \leq k$.

In the mixed strategy that maximizes long-run expected growth rates, some squirrels will attempt to gather more nuts than the privately optimal storage quantity. Where k is the privately optimal quantity, the number of squirrels who gather exactly t days' supply of nuts for $t > k$ is proportional to the product of the probability of a winter of exactly t days and the probability v_t of escaping predation for those who attempt to collect exactly t days' supply nuts.

Proposition 1. *If the distribution function of winter length satisfies Assumption 1 and probabilities of evading predators satisfy Assumption 2, then the privately optimal storage quantity* k *is uniquely determined and the solution to constrained* Maximization Problem 4 *is* $\overline{S}$ *where for* $t \leq k$,

$$\overline{S}_0 = \overline{S}_t = \overline{S}_k = P_k v_0 (1-h)^k,$$

while for $k < t \leq W$, $\overline{S}_t$ *is strictly decreasing in* t *with*

$$\overline{S}_t = \frac{v_0}{h} p_t (1-h)^t.$$

While *Proposition 1* describes the predicted survival rates for winters of each possible length, we can find the corresponding probability mix of strategies by invoking the transformations shown in expression **23**. This leads us to the following result.

Corollary 1. *The distribution of effort levels that maximizes the expected long-run growth rate is* $\overline{\pi} = (\overline{\pi}_0, \ldots, \overline{\pi}_W)$, *where* $\overline{\pi}_t = 0$ *for* $t < k$, $\overline{\pi}_k = P_{k+1} - (p_{k+1}/h)$, *and* $\overline{\pi}_t = p_t + ((1/h) - 1)(p_t - p_{t+1})$ *for* $k < t < W$, *and* $\overline{\pi}_W = p_W/h$.

Proposition 1 and its corollary tell us that if the distribution of winter length is log concave and the hazard rate for gathering additional nuts is constant, then the mixed strategy that maximizes long-run expected growth rate has a simple and interesting structure. There is a privately efficient level of food supply k, such that squirrels who attempt to gather k days' food supply have higher survival probabilities than those who attempt to gather any other quantity. No squirrel will attempt to gather less than this quantity, however some squirrels will gather enough nuts for each possible winter's length. In equilibrium, the survival rate of squirrels diminishes with the length of winter so that the expected survival rate for a winter of t days is the product of the frequency of winters of t days and the probability of avoiding predators if one stores exactly enough nuts for a t-day winter.

Redistribution by Lottery or Theft

In the discussion so far, each squirrel could consume only the nuts that it has gathered. The only way to achieve diversity of resource holdings was to have individuals collect different amounts. In this section we consider the possibility that resources, once acquired, can be redistributed. Redistribution might take the form of theft, accidental redistribution, or of voluntary participation in a lottery process.

Let us consider a process in which all squirrels who survive predation collect the same amount of nuts. Each squirrel deposits these nuts in a central cache, from which a redistributive

lottery determines the allotment of each squirrel. The resulting income distribution will determine the survival rates for each possible winter's length. Here we determine the income distribution that maximizes the expected long-run growth rate of the population.

Suppose that the length of winter is a random variable that ranges from 1 to W days, where the probability that winter lasts for exactly t days is p_t, and the probability that winter is no longer than t days is $P_t = \sum_{i=0}^{t} p_i$. Consider a population of N squirrels, each of which has collected Y days' worth of food. The total supply of food is reallocated among the N squirrels in such a way that N_t squirrels receive t days' worth of food, for each $t = 0, \ldots, W$. Since the total number of days' supply of nuts collected is NY, it must be that for a feasible allocation,

$$\sum_{t=0}^{W} t N_t = NY. \qquad \textbf{[18]}$$

Let $\lambda_t = N_t/N$ be the fraction of squirrels that receive t days' worth of food. Then this feasibility condition can be written as

$$\sum_{t=0}^{W} \lambda_t t = Y. \qquad \textbf{[19]}$$

A squirrel will survive a winter of t days if it receives at least t days' worth of food. Therefore, the fraction of the population that survives a winter of t days is

$$S_t(\lambda) = \sum_{i=t}^{W} \lambda_i. \qquad \textbf{[20]}$$

The distributional lottery that maximizes the geometric mean of survival probability is the probability distribution of income measured in days' supply of food that solves the following constrained maximization problem.

Maximization Problem 5. *Find* $\overline{\lambda} = (\overline{\lambda}_0, \overline{\lambda}_1, \ldots, \overline{\lambda}_W)$ *to maximize*

$$\sum_{t=0}^{W} p_t \ln S_t(\lambda),$$

subject to

$$\sum_{t=0}^{W} \lambda_t t = Y, \quad \sum_{t=0}^{W} \lambda_t = 1 \quad and \quad \lambda_t \geq 0, \quad for \; all \quad t = 1, \ldots W.$$

Maximization Problem 5 can be restated in terms of the survival rates S_t by means of a one-to-one transformation. We have

$$\lambda_t = S_t - S_{t+1} \quad for \quad t = 0, \ldots, W-1 \quad and \quad \lambda_W = S_W. \qquad \textbf{[21]}$$

Then

$$\sum_{t=0}^{W} t \lambda_t = \sum_{t=1}^{W-1} t(S_t - S_{t+1}) + W S_W = \sum_{t=1}^{W} S_t. \qquad \textbf{[22]}$$

Our constraints require that $S_0 = \sum_{i=0}^{W} \lambda_i = 1$. Thus, $\ln S_0 = \ln 1 = 0$ and $\sum_{t=0}^{W} p_t \ln S_t = \sum_{t=1}^{W} p_t \ln S_t$. Therefore, *Maximization Problem 5* is equivalent to the following.

Maximization Problem 6. *Find* $\overline{S} = (\overline{S}_1, \ldots, \overline{S}_W)$ *to maximize*

$$\sum_{t=1}^{W} p_t \ln S_t,$$

subject to

$$\sum_{t=1}^{W} S_t = Y,$$

with $S_{t+1} \leq S_t$ for $t = 1, \ldots, W-1$ and $S_1 \leq 1$.

We assume that the distribution of winter's length is strictly unimodal and that winters of the longest possible length are less likely than they would be if the distribution of winter lengths were uniform on $[0, W]$. *Assumption 3* states this formally.

Assumption 3: The distribution of winter length is strictly unimodal, with modal length $m < W$ and with $p_W < 1/W$.

A squirrel that is allotted t days' worth of food will survive all winters that are no longer than t days and hence has a survival probability of P_t. The average food cost per unit of survival probability for a squirrel that receives t days' food supply is therefore t/P_t. If one views food as an input into the production of survival probability, the following definition is natural.

Definition 4: The food supply that minimizes average cost per unit of survival probability is v, where $v/P_v \leq t/P_t$ for all $t = 1, \ldots W$.

Lemma 3, which is proved in *SI Appendix*, relates average and marginal costs of survival probability in a way that is reminiscent of the familiar U-shaped cost curves in economists' theory of the firm. In particular, average cost per unit of survival probability is decreasing in the number of days' storage and exceeds the marginal cost of increased survival probability for $t < v$, while these inequalities are reversed for $t > v$. *Lemma 3* states this formally.

Lemma 3: If the distribution of winter length satisfies *Assumption 3* with mode m, there is a unique average-cost-minimizing food supply $v > m$ that minimizes the average cost, $t/P(t)$. For $1 \leq t < v$, $P_t - tp_t < 0$ and for $v < t \leq W$, $P_t - tp_t > 0$.

Much as a profit-maximizing competitive firm will never produce output in quantities, such that average cost exceeds marginal cost, an income distribution that solves *Maximization Problem 6* will not assign positive probability to incomes in the range between 0 and v. Thus, squirrels will receive either no food or enough food to survive a winter of at least v days. The following result is proved in *SI Appendix*.

Lemma 4: Where v is the average-cost-minimizing food supply and $\overline{S}$ solves *Maximization Problem 6*, it must be that $\overline{S}_t = \overline{S}_1$ for all $t \leq v$.

In *SI Appendix* we show that *Lemmas 3* and *4* can be used to prove the following.

Proposition 3. *If the distribution of winter length is strictly unimodal and v is the average-cost-minimizing food supply, then the solution $\overline{S}$ of Maximization Problem 6 is as follows*:

i) *If $Y < v/P_v$, then $\overline{S}_t = (P_v/v)Y < 1$, where $1 \leq t \leq v$, and $\overline{S}_t = p_t Y$, where $v < t \leq W$.*

ii) *If $Y \geq v/P_v$, then for some $r \geq v$, $\overline{S}_t = 1$, where $t \leq r$ and*

$$\overline{S}_t = \frac{p_t}{1 - P_r}(Y - r),$$

where $r < t \leq W$.

Applying the correspondence between solutions to *Maximization Problems 5* and *6*, we have the following.

Corollary 2. *Given the assumptions of Proposition 3, the distribution of income $\overline{\lambda} = (\overline{\lambda}_0, \ldots, \overline{\lambda}_W)$ that maximizes the expected long-term growth of a population is as follows:*

i) *If $Y < v/P_v$, then $\overline{\lambda}_0 = 1 - (P_v/v)$, $\overline{\lambda}_t = 0$ for $0 < t < v$, $\overline{\lambda}_v = \left(\frac{P_v}{v} - p_{v+1}Y\right)$ and $\overline{\lambda}_t = (p_t - p_{t+1})Y$ for $v < t \leq W$.*

ii) *If $v/P_v \leq Y < W$, then for some $r \geq v$, $\overline{\lambda}_t = 0$ for all $t \leq r$ and*

$$\overline{\lambda}_t = (p_t - p_{t+1})\left(\frac{Y - r}{1 - P_r}\right)$$

for all t, such that $r < t \leq W$.

Proposition 3 and its corollary imply that if the distribution of winters' length is univalent, then the structure of the income distribution that maximizes the expected long-run reproduction rate has the following profile. There is some number of days' food supply v that minimizes food cost per unit of survival probability. In an optimal distribution, no individual receives a positive amount of food smaller than v. If the amount of food Y available per squirrel is small, so that $P_v Y < v$, then in this optimal distribution, some individuals will receive no wealth at all and will surely starve. Of the remainder, some receive exactly v units and for each t, such that $v < t \leq W$, some will receive exactly t days' supply, where the number receiving t days' supply is proportional to the probability of a winter of length t. Where Y is large enough so that $P_v Y \geq v$, there is some quantity $r \geq v$, such that all individuals receive at least r days' food supply, while for any number of days, $t > r$, the fraction receiving exactly t days' supply is proportional to the probability of a winter of length t.

Discussion

Storage with Predation Hazard. Our treatment of the squirrel's dilemma illustrates the principle that when a population is subjected to a common environmental hazard, a gene maximizes its long-run reproduction rate by diversifying the portfolio of phenotypes who carry it. Assuming a log-concave distribution of winter's length and constant hazard rates for gathering additional food, no squirrel would collect less than the privately optimal stock of r days' supply of food. Those who collect exactly r days' supply of food will have higher survival probability than squirrels who consume any other amount. Nevertheless, some squirrels would collect enough food to last for more than r days. For a winter of any length greater than r days, the survival rate of the squirrel population will be proportional to the frequency of winters of that length, multiplied by the probability of avoiding predation if one attempts to store enough food for such a winter.

This theory suggests that natural selection would favor the emergence of a gene that randomizes the behavior of its carriers with the same probabilities persisting in every generation. In their survey of empirical evidence for evolutionary bet hedging, Childs and coworkers (6) state that

> we believe there is now abundant empirical evidence for the role of bet-hedging in simple plant systems. . . . Numerous theoretical models also predict that bet-hedging should evolve in more complex life histories but at the moment empirical evidence for this is almost completely lacking.

Vander Wall (1) reports wide variation in the amount of food stored by animals of the same species in the wild.

> The hoarding performance of animals in both the wild and in controlled experiments is typified by great phenotypic variability. Pika (*Ochotona princeps*)[¶] hay piles at one site in the Rocky Mountains ranged in size from 400–6,000 grams . . . and red squirrel middens contained from 280–4,360 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 . . ." (ref. 1, p. 112).

While some of the diversity in the size of food caches may be the result of differences in availability, Vander Wall reports that similar diversity of cache size is found in laboratory experiments where availability is under control of investigators.

[¶]These are guinea pig-like animals that store food in small haystacks.

The studies reported by Vander Wall do not offer decisive evidence that the observed diversity in storage behavior is a consequence of evolutionary bet hedging as defined by Seger and Brockmann (2), rather than a consequence of genetic diversity in the population. For example, there might be dominant genes that mandate storing the privately efficient quantity and recessive genes that mandate storing greater amounts. Seger and Brockmann observe that it is difficult to determine whether observed diversity of behavior in a population arises from randomization by genetically identical individuals or from genetic differences resulting from immigration of individuals who are optimized for environmental conditions in a different geographical region.

Our theoretical predictions suggest empirical tests that could be helpful in determining whether observed diversity arises from evolutionary bet hedging by genetically identical individuals or from diversity of genetic endowments. The bet-hedging model predicts that, regardless of the length of the previous winter, the size distribution of observed food caches should be roughly the same from year to year. If on the other hand, diversity of amounts of stored food result from a genetically diverse population of genes, each of which mandates a determinant food strategy, then the genetic composition of the surviving population would depend on the length of the previous winter. After a long winter one would expect to find a greater proportion of large caches than after a short winter. The evolutionary bet-hedging theory also makes specific predictions about the shape of the distribution of food cache sizes. The theory predicts that there is a minimum cache level, which all population members would attempt to reach. It also predicts that the frequency distribution of food cache sizes that exceed this minimum would be inversely proportional to the frequency of winters for which such a food cache would be needed.

The model presented here is highly simplified and ignores some effects that must interact with evolutionary bet hedging in important and subtle ways. A gene can diversify its portfolio not only by varying the phenotypes of its carriers, but also by dispersing the locations of its carriers in such a way that not all face the same environment in any year. This possibility is discussed by Cohen and Levin (13) and further studied by Vitalis et al. (14). The interaction between variable environments and frequency dependence is also likely to have a major effect on the form that bet hedging will take (15). For example, when there are limited resources available, a large population surviving through a short winter faces severe competition for food in the following year, while survivors of a harsh winter have relatively few competitors for resources.[||]

Our model has focused on the behavior of squirrels, but the decision problems that the squirrels face are not unlike those confronted by our human ancestors. Like squirrels, humans must store food and other resources when they are available, because they face long and variable time periods during which little food can be harvested. More generally, stores of food and other resources become critical sources of livelihood in the event of many kinds of unpredicted vicissitudes. While the nature of risks for humans may be more complex than for squirrels, the structure is roughly similar. Thus, it is interesting to see that the theory of evolutionary bet hedging predicts that individuals with identical genetic endowments might differ greatly in their inclination to accumulate wealth and that the resulting wealth distributions are related to the frequency of occasions on which these amounts of wealth are critical to survival.

[||]A monograph by Clutton-Brock and Pemberton describes population cycles in an isolated but much-studied population of wild sheep (16) in the St. Kilda archipelago. This population faces highly variable winter conditions and is subject to intense competition for limited grazing resources when the population gets large.

Redistributive Lotteries. Although squirrels occasionally steal from each other, it is unlikely that they redistribute wealth to the extent required to maximize long-term expected reproduction rates. Our own species, with its greater capacity for theft and coercion and with its ability to implement voluntary lottery and insurance contracts, has managed to achieve highly unequal wealth distributions and in some communities provides safety nets to guarantee a minimum level of income.

Could the evolutionary theory that we have discussed shed any light on wealth distributions in human populations? Our discussion used the metaphor of a random "winter's length" to represent an environmental risk that affects the survival requirements of an entire population. The variable length of seasons quite literally played this role for our hunter–gatherer and peasant ancestors. However, for human populations, there are many other random events that simultaneously affect all members' need for accumulated wealth. Among such events are drought and flood, diseases of crops and cattle, war, conquest, and pestilence. While the probability distributions of such events are not as regular as those of the length of winter, these risks share many qualitative features with the winter's length model.

Quite generally, it will be true that in the presence of environmental risks affecting the survival requirements of an entire population, a bet-hedging gene that manages to diversify the wealths of those who carry it will reproduce more rapidly than a gene that mandates the same behavior whenever it appears. One way in which a gene could arrange for itself to be found in a diverse portfolio of individuals with differing wealth holdings would be to assign a variety of different savings propensities and risk preferences to the individuals who carry it.

Psychiatrists consider compulsive hoarding and compulsive gambling to be well-defined psychological disorders. A review article by Pertusa et al. (17) indicates that up to 5% of the US population are afflicted by a compulsive hoarding disorder, which they define as "excessive collection and failure to discard objects of apparently little value, leading to clutter, distress and disability." A review by Shaffer et al. (18) reports that about 1.5% of the US population suffer from pathological gambling problems while another 4.8% have subclinical levels of gambling problems, where the official definition of pathological gambling is "persistent and recurring maladaptive gambling behavior that disrupts personal, family or vocational pursuits."

The prevalence of these two disorders suggest that they may not be simple biological malfunctions, but rather genetically determined propensities that have been preserved by natural selection. Although each of these disorders is likely to reduce expected reproductive success of those who have them, it may be that in the ancestral past, compulsive hoarders would be more likely than others to survive through extreme winters and famines. Likewise, it may be that those compulsive gamblers who experienced good luck would acquire sufficient wealth to survive in lean years when more conservative individuals would surely starve.

Thus, it may be that compulsive hoarding and compulsive gambling can be at least partially explained by evolutionary bet hedging. In its strictest form, if diverse gambling and hoarding behaviors were the result of randomized phenotypic realizations of a single genotype, we would not expect to see any influence of heredity in these behaviors. In fact, available evidence suggests that the appearance of these disorders is at least partially sustained by genetic diversity rather than by random phenotypic realizations.

Zyphur et al. (19) administered questionnaires to pairs of monozygotic (identical) and dizygotic (nonidentical) twins to study the inheritance of risk preferences. Using the standard twin-study methodology of behavioral genetics, they conclude that that "risk preferences appear to be two-thirds genetically and one-third environmentally determined." However, they found that "there was no effect of shared environmental factors but a

sizable influence of unshared environmental factors." A recent study by Iervolino et al. (20) used observations of monozygotic and identical twins to estimate the "genetic and environmental components" of compulsive hoarding behavior. This study finds that ∼50% of the observed variance of compulsive hoarding is genetically determined and 50% is due to either "unshared environmental factors" or measurement error.

These studies, adhering to the usual convention in twin studies of inheritance, partition observed phenotypic differences into genetic and environmental differences by means of the assumption that any phenotypic differences found in identical twins must be the result of unshared environmental factors. The fact that these studies find substantial genetic components of behavior suggests that differences in hoarding and gambling behavior are partially the result of genetic diversity in the population. On the other hand, the large proportion of differences in behavior that cannot be explained by genetic differences and cannot be attributed to observed environmental differences may well be an indication that evolution has resulted in human genes that randomize their phenotypic realizations, much as the theory of evolutionary bet hedging suggests.

Appendix

Equivalence of *Maximization Problems 3* and *4*. Eq. **12** implies that

$$\pi_W = \frac{S_W}{v_W} \quad \text{and} \quad \pi_t = \frac{S_t - S_{t+1}}{v_t} \quad \text{for} \quad 0 \le t < W. \qquad [23]$$

The constraints that

$$\sum_{t=0}^{W} \pi_t = 1 \quad \text{and} \quad \pi_t \ge 0 \quad \text{for} \quad t = 1, \dots, W \qquad [24]$$

can then be written as

$$\sum_{t=0}^{W-1} \frac{S_t - S_{t+1}}{v_t} + \frac{S_W}{v_W} = 1 \quad \text{and} \quad 0 \le S_t \le S_{t-1} \quad \text{for} \quad t = 1, \dots, W, \qquad [25]$$

which is also equivalent to

$$\frac{S_0}{v_0} + \sum_{t=1}^{W} \frac{h_t}{v_t} S_t = 1 \quad \text{and} \quad 0 \le S_t \le S_{t-1} \quad \text{for} \quad t = 1, \dots, W. \qquad [26]$$

Properties of Log-Concave Distributions. Continuous probability distributions with log-concave density are frequently assumed in economic applications (11, 21). A continuous univariate probability distribution f with log-concave density has the property that $(\ln f(t))'' \le 0$ for all t in its support. This implies that $f'(t)/f(t)$ is nonincreasing in t. To see that *Definition 2* is a natural extension of log concavity for continuous distributions, we observe that the discrete analog of nonincreasing $f'(t)/f(t)$ is

$$\frac{p_{t+1} - p_t}{p_t} \le \frac{p_t - p_{t-1}}{p_{t-1}}.$$

This is equivalent to $p_{t+1}p_{t-1} \le p_t^2$ and thus to

$$\frac{p_{t+1}}{p_t} \le \frac{p_t}{p_{t-1}}.$$

The following result, which is proved in ref. 11, is the analog to the theorem that for continuous distributions, log concavity of

the density function implies log concavity of the cumulative distribution function.

Lemma 5: If the discrete distribution p_t is strictly log concave, then p_t/P_t is strictly decreasing in t.

Proofs of *Proposition 1* and Related Lemmas

Proof of Lemma 1: *Assumption 2* requires that $p_1/P_1 = p_1/(p_1 + p_0) > h$ and $p_W/P_W = p_W < h$. *Assumption 1* (log concavity) implies that p_t/P_T is a decreasing function of t (*Lemma 5*). Therefore, there must be some k between 1 and W, such that $p_t/P_t \ge h$ for all $t \le k$ and $p_t/P_t < h$ for all $t > k$. We note that

$$P_{t+1}(1-h)^{t+1} - P_t(1-h)^t = (1-h)^t(P_{t+1} - hP_{t+1} - P_t) \\ = (1-h)^t(p_{t+1} - hp_{t+1}). \qquad [27]$$

Since $p_t/P_t \ge h$ for all $t \le k$ and $p_t/P_t < h$ for all $t > k$, it must be that the expression in Eq. **27** is positive if $t < k$ and negative if $t \ge k$. Therefore, $P_t(1-h)^t$ is maximized at $t = k$. This proves *Assertion i of Lemma 1*.

To prove *Assertion ii of Lemma 1*, note that $p_k \ge hP_k$ and $p_{k+1} < hP_{k+1} = hP_k + hp_{k+1}$. Therefore, it must be that $p_{k+1} < p_k + hp_{k+1}$, which implies that

$$\frac{p_{k+1}}{p_k} < \frac{1}{1-h}.$$

Since the distribution of winter's length is log concave, it must be that p_{t+1}/p_t decreases with t. It follows that $p_{t+1}/p_t < 1/(1-h)$ for all $t \ge k$.

Proof of Lemma 2: Let t be the smallest number, such that $\overline{S}_{t+1} < \overline{S}_t$. Consider the perturbed survival probability distribution $S(x)$, such that $S_i(x) = \overline{S}_i - xh/(1-h)$ for all $i \le t$, $S_{t+1} = \overline{S}_{t+1} + x$ and $S_i(x) = \overline{S}_i$, where $t + 1 < i \le W$. For x sufficiently small, $S(x)$ satisfies all of the constraints of *Maximization Problem 4*. Therefore, it must be that

$$\sum_{i=0}^{W} p_i \ln S_i(x) \le \sum_{i=0}^{W} p_i \ln \overline{S}_i,$$

and hence the derivative of $\sum_{i=0}^{W} p_i \ln S_i(x)$ must be nonpositive at $x = 0$. This implies that

$$\frac{p_{t+1}}{S_{t+1}} - \frac{P_t}{S_t} \frac{h}{1-h} \le 0,$$

which implies that

$$\frac{p_{t+1}}{P_t} \frac{1-h}{h} \le \frac{S_{t+1}}{S_t} < 1.$$

If this is the case, we have $(1-h)p_{t+1} < hP_t$, and hence $p_{t+1} < h(p_{t+1} + P_t) = hP_{t+1}$. This implies that $p_{t+1}/P_{t+1} < h$. Since, according to *Lemma 1*, $p_t/P_t \ge h$ for all $t \le k$, it must be that $t > k$. Therefore, $\overline{S}_t = \overline{S}_0$ for all $t \le k$.

Proof of Proposition 1: According to *Lemma 2*, $\overline{S}_i = \overline{S}_0$ for all $i \le k$, where k is the privately optimal storage quantity. Given that this is the case, constrained *Maximization Problem 4* is equivalent to the following problem.

Find $(\overline{S}_k, \overline{S}_{k+1}, \dots, \overline{S}_W)$ to maximize

$$P_k \ln S_k + \sum_{k < i \le W} p_i \ln S_i, \qquad [28]$$

subject to the constraints $S_{t+1} \leq S_t$ for all $k \leq t < W$ and

$$\sum_{k \leq i < W} \frac{S_i - S_{i+1}}{v_i} + \frac{S_W}{v_W} = 1. \qquad [29]$$

Now

$$\sum_{k \leq i < W} \frac{S_i - S_{i+1}}{v_i} + \frac{S_w}{v_W} = \frac{S_k}{v_k} + \sum_{k < i < W} S_i \left(\frac{1}{v_i} - \frac{1}{v_{i-1}} \right). \qquad [30]$$

Since we assume that $v_i = v_0(1-h)^i$, it must be that

$$\frac{1}{v_i} - \frac{1}{v_{i-1}} = \frac{h}{(1-h)^i},$$

and therefore the constraint in Eq. **29** is equivalent to

$$\frac{S_k}{v_0(1-h)^k} + \sum_{k < i < W} S_i \frac{h}{v_0(1-h)^i} = 1. \qquad [31]$$

If the inequality constraints are ignored, the maximum of expression **28**, subject to the constraint in Eq. **31** has a solution $S^* = (S_k^*, S_{k+1}^*, \ldots, S_W^*)$, such that $S_k^* = P_k v_0(1-h)^k$ and $S_t^* = (1/h) p_t v_0(1-h)^t$ for $k < t \leq W$. We now show that S^* satisfies the inequality constraints $S_{t+1}^* \leq S_t^*$ for all $k \leq t < W$, and hence S^* maximizes expression **28**, subject to the required constraints.

For $k < t < W$, we see that

$$\frac{S_{t+1}^*}{S_t^*} = \frac{p_{t+1}(1-h)}{p_t}.$$

According to *Lemma 1*, for all $t > k$, $p_{t+1}/p_t < 1/(1-h)$. It follows that $S_{t+1}^*/S_t^* < 1$. It remains to be shown that $S_k^* \geq S_{k+1}^*$. We have

$$\frac{S_{k+1}^*}{S_k^*} = \frac{p_{k+1}}{P_k} \frac{1-h}{h}. \qquad [32]$$

Lemma 1 implies that $p_{k+1}/P_{k+1} < h$. Therefore, $p_{k+1} < h P_{k+1} = h(P_k + p_{k+1})$, which, in turn, implies that $p_{k+1}/p_k < h/(1-h)$, and hence

$$\frac{S_{k+1}^*}{S_k^*} = \frac{p_{k+1}}{P_k} \frac{1-h}{h} < 1. \qquad [33]$$

Therefore, the vector S^* maximizes **[28]** subject to **[29]**. It follows that $\overline{S}$ solves constrained *Maximization Problem 1*, where $\overline{S}_t = P_k v_0(1-h)^k$ for all $t \leq k$ and

$$\overline{S}_t = \frac{v_0}{h} p_i (1-h)^t$$

for all $t > k$. Thus, establishes *Proposition 1*.

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Supplemental Information Appendix: Proofs of Proposition 3 and related lemmas

Proof of Lemma 3 :
Since $P_{t+1} = P_t + p_t$, it follows that for $t = 1, \ldots, W-1$,

$$
\begin{aligned}
\frac{t+1}{P_{t+1}} - \frac{t}{P_t} &= \frac{(t+1)P_t - t(P_t + p_t)}{P_{t+1}P_t} \\
&= \frac{P_t - tp_t}{P_{t+1}P_t}
\end{aligned}
\tag{SI 1}
$$

Unimodality of the distribution of winter lengths implies that $p_i < p_t$, for all $i < t \leq m$. It follows that for all $t \leq m$,

$$
P_t - tp_t = \sum_{i=1}^{t}(p_i - p_t) < 0.
\tag{SI 2}
$$

It follows from Inequality SI (2) and Equation SI (1) that "average cost" t/P_t is decreasing in t for all $t < m$.

Inequality SI (2) implies that $P_m - mp_m < 0$. For $t > m$, it is also the case that $P_t - tp_t$ is an increasing function in t. To see this we note that since $P_{t+1} = P_t + p_t$,

$$
(P_{t+1} - (t+1)p_{t+1}) - (P_t - tp_t) = (t+1)(p_t - p_{t+1}).
\tag{SI 3}
$$

Since $p_t > p_{t+1}$ for $t > m$, it follows from Equation SI (3) that $P_t - tp_t$ is increasing for $t > m$.

Since $P_W = 1$, Assumption 3 implies that $P_W - Wp_W > 0$. We have shown that $P_m - mp_m < 0$ and that $P_t - tp_t$ is increasing in t for $m < t < W$. It follows that there is a unique integer v with $m < v < W$ such that $P_t - tp_t \leq 0$ for $t \leq v$ and $P_t - tp_t > 0$ for $t > v$. Lemma 3 is then immediate from Equation SI (1).

Proof of Lemma 4: The constraints of Maximization Problem 6 require that $\bar{S}_{t+1} \leq \bar{S}_t$ for $1 \leq t \leq W - 1$. Let t be the first time period for which $\bar{S}_{t+1} < \bar{S}_t$. Consider the following perturbation $S(x)$ of $\bar{S}$. Let $S_{t+1}(x) = \bar{S}_{t+1} + x$. For $i \leq t$, let $S_i(x) = \bar{S}_i - (x/t)$, and for $i > t + 1$, let $S_i(x) = \bar{S}_i$. It is straightforward to verify that for sufficiently small $x > 0$, $S(x)$ satisfies all of the constraints of Maximization Problem 6. Therefore since $\bar{S}$ is a solution to Problem 6, it must be that

$$
\frac{d}{dx}\sum_{i=1}^{W} p_i \ln S_i(0) \leq 0.
\tag{SI 4}
$$

But

$$
\begin{aligned}
\frac{d}{dx}\sum_{i=1}^{W} p_i \ln S_i(0) &= -\frac{1}{t}\sum_{i=1}^{t} p_i + p_{t+1} \\
&= p_{t+1} - \frac{P_t}{t} \\
&= \frac{(t+1)p_{t+1} - P_{t+1}}{t}
\end{aligned}
\tag{SI 5}
$$

From Lemma 3 it follows that $(t+1)p_{t+1} - P_{t+1} \leq 0$ only if $t + 1 > v$. Therefore it must be that $\bar{S}_i = \bar{S}_1$ for all $i \leq v$.

Proof of Proposition 3:

Proof: According to Lemma 4, if $\bar{S}$ solves Maximization Problem 6, it must be that $\bar{S}_t = \bar{S}_v$ for all $t \leq v$. Then, $(\bar{S}_v, \bar{S}_{v+1}, \ldots, \bar{S}_W)$ must be a solution to the maximization problem: Maximize:

$$
P_v \ln S_v + \sum_{t=v+1}^{W} p_t \ln S_t
\tag{SI 6}
$$

subject to $vS_v + \sum_{t=v+1}^{W} S_t = Y$, $S_1 \leq 1$, and $S_v \geq S_{v+1} \geq S_{v+2} \geq \cdots \geq S_W$. In the absence of the inequality constraints, the solution to this constrained maximization problem is

$$
S_v^* = \frac{P_v}{v}Y \quad \text{and} \quad S_t^* = p_t Y \text{ for } v < t \leq W.
\tag{SI 7}
$$

According to Lemma 3, it must be that $p_{v+1} < \frac{P_{v+1}}{v+1}$. Since $P_{v+1} = P_v + p_{v+1}$, it follows that $p_{v+1} < \frac{P_v}{v}$ and hence that $S_v > S_{v+1}^*$. Since $v > m$, it must also be that $p_{t+1} < p_t$ for $t > v$ and therefore $S_{t+1}^* < S^* t$ for all $t > v$. Thus we have $S_v^* \geq S_{v+1}^* \geq S_{v+2}^* \geq \cdots \geq S_W^*$.

If $Y < \frac{v}{P_v}$, then $\frac{P_v}{v}Y < 1$ and so the condition $S_1^* = \frac{P_v}{v}Y \leq 1$ is also satisfied. Therefore $(S_v^*, S_{v+1}^*, \ldots S_W^*)$ maximizes Expression (SI (6)) subject to the entire set of constraints. It follows that if $Y \leq \frac{v}{P_v}$, the solution to Maximization Problem 6 is $\bar{S}$, where $\bar{S}_i = \frac{P_v}{v}Y$ for $i = 1, \ldots v$ and $\bar{S}_i = p_iY$ for $i = v + 1, \ldots W$. This proves assertion (i) of the proposition.

If $Y > \frac{v}{P_v}$, then $\frac{P_v}{v}Y > 1$, and the constraint $\bar{S}_1 \leq 1$ is binding, so that for all $t \leq v$, $\bar{S}_t = 1$. By assumption, $Y < W$. There since $\sum_{t=1}^{W} \bar{S}_t = Y < W$, it must be that $\bar{S}_t < 1$ for some $t \leq W$. It follows that for some $r \geq v$, $\bar{S}_r = 1$ and $S_{r+1} < 1$. Then if $\bar{S}$ maximizes Expression (SI (6)) subject to the given constraints, it must be that $(\bar{S}_{r+1}, \ldots, \bar{S}_W)$ maximizes

$$\sum_{i=r+1}^{W} p_i \ln S_i$$

subject to

$$\sum_{i=r+1}^{W} S_i = Y - r.$$

The solution to this constrained maximization problem is seen to be

$$\bar{S}_t = \frac{p_t}{1 - P_r}\left(Y - r\right)$$

for all t such that $r < t \leq W$. Since $r \geq v \geq m$, it must be that $\frac{p_t}{1-P_r}\left(Y - r\right) > \frac{p_{t+1}}{1-P_r}\left(Y - r\right)$ for all $t \geq r$. It follows that $\bar{S}$ is a solution to Maximization Problem 6 where $\bar{S}_t = 1$ for $1 \leq t \leq r$ and where $\bar{S}_t = \frac{p_t}{1-P_r}\left(Y - r\right)$ for $r < t \leq W$.