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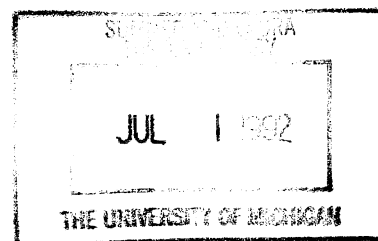
Surviving Winter: A Fitness-Based
Explanation of Hoarding and
Hibernation

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1. Introduction

Until last year, a literature on animal hoarding comprising more than 1500 articles lay scattered across various journals of behavioral ecology. Stephen Vander Wall masterfully surveys this wide-ranging literature in his encyclopedic *Food Hoarding in Animals* [1991].

Hoarding obviously enables an animal to survive when foraging for new supplies would be difficult. But as Vander Wall emphasizes, hoarding also contributes to reproductive success:

> An individual must endure periods of resource dearth in good condition if it is to breed successfully when conditions are favorable. Stored food could significantly affect reproductive success ...Potential benefits arising from use of stored food during the reproductive season include (1) promoting early breeding and increasing the number of individuals in breeding condition, (2) facilitating courtship, (3) increasing litter or clutch sizes, (4) increasing nest attentiveness, and (5) supplementing the diet of the young. [p. 27]

After the onset of winter, animals often reduce—and sometimes even suspend—their food-gathering activities. The food they consume comes to a large extent from external stockpiles or internal reserves (body fat). Vander Wall notes that hoarding facilitates hibernation:

> For many food hoarders that hibernate or regularly enter torpor, food stored in or near the hibernaculum, sometimes augmented with varying amounts of body fat, is essential to successful wintering. The animal periodically arouses, feeds from its food stores, and then becomes hypothermic again ... [p. 23]

Below, we refer to any winter-time behavior of this kind—where an animal ceases altogether to hunt for food and lives instead entirely on its external stockpile (or body fat)—as "hibernation."[1]

The literature which Vander Wall summarizes has one striking deficiency. As David Sherry observed in his glowing evaluation in *Science*, "What his [Vander Wall's] review makes clear, however, is that quantitative models of the fitness consequences of food hoarding are badly needed."

The purpose of our essay is to provide such a model. Like any work, ours owes many an intellectual debt—not only to Vander Wall and those he surveys but also to two economists, Harold Hotelling [1931] for his theory of storage and Gary Becker [1965] for his theory of time allocation.

The model we develop explains storage and hibernation as intertemporal behaviors which maximize fitness. We use the term "fitness" to mean the number of surviving offspring. Although the determinants of fitness are by no means fully understood, the evidence surveyed by Vander Wall suggests that fitness is a strictly increasing function of the food stores gathered for the offspring. Such stores not only increase the number of offspring produced but also raise the percentage which survives. The evidence also suggests that the number of surviving offspring is an increasing function of the body weight of the mother. Increases in her weight contribute to her health and result not only in more offspring but also in a larger percentage of survivors.

How an animal behaves between one litter and the next determines both its weight gain and what is stored for the offspring. Many paths of behavior are "inept" and result in unnecessarily small storage for a given maternal body weight. If

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[1]Thus, we do not distinguish between "true" hibernation and other physiological states of dormancy.

1

behavior is not inept, there remains a fundamental tradeoff between maternal body weight and food stored for the offspring: the more food an animal stores for its litter, the harder it must work throughout the year and the less food is available for its own consumption; hence, the smaller its weight gain. This tradeoff is represented in Figure 1.

[Figure 1 goes here]

Figure 1 can be used to summarize the foregoing discussion. "Inept" behavior results in points inside the frontier. Alternative behavior could result in more food for the offspring without any reduction in maternal body weight (a rightward movement toward the frontier).

Inept behavior cannot maximize fitness. As long as fitness is strictly increasing in the food provided to the offspring, the behavior which maximizes fitness will produce an outcome somewhere on the frontier.[2] Each point on the frontier can be achieved by only one time path of behaviors (storage, retrieval, foraging, consumption, energy spent in food-related activities, etc.). Such a path can be conveniently characterized as the solution to an optimization problem.

To determine which mix of body weight and bequest *maximizes* fitness requires more knowledge of the fitness function than is currently available. Even in the absence of such information, however, the hypothesis that the observed path of behaviors achieves a point *somewhere* on the frontier can—in conjunction with a few plausible assumptions—generate a rich set of predictions.

Our principal assumptions are that food-related activities require work, that work consumes energy, and that foraging is in fact—and is anticipated to be—far less productive after the onset of winter. We also assume that a portion of stored food decays, is stolen, or cannot be relocated.[3]

Given our assumptions, we show that behaviors which achieve the relevant[4] portion of the frontier of Figure 1 must have the following characteristics: food is put into storage at an increasing rate before the onset of winter and retrieved thereafter at a decreasing rate. Consumption remains constant until storage is initiated and declines monotonically thereafter. Energy expended on food-related activities remains constant until storage begins and increases until the onset of winter. Foraging and indeed overall energy expended on food-related activities drop precipitously at the onset of winter. Depending on the exogenous input parameters, there may be a "hibernation" phase during which the animal ceases to forage altogether and continues to reduce its food-related activity (which consists only of retrieval) still further. Eventually (if not immediately after the onset of winter), the animal's foraging and work effort begin to increase.

Our paper is organized as follows. In the next section, we formulate the optimization problem and present a set of conditions which must hold if a path of behaviors is optimal. Moreover, we show how these conditions can be solved recursively to *construct* the optimal path of behaviors. The proof that for any point on the frontier of Figure 1 there exists only *one* such path of behaviors is proved in Appendix 2.

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[2]Since reductions in maternal body weight would permit additional food to be stored for the offspring, either the constrained maximum occurs where fitness is strictly increasing in maternal body weight (as we assume) or the optimum occurs at the bottom right corner of Figure 1 where it is infeasible to reduce maternal body weight.

[3]Interviewed in a recent New York Times (1991) article about his book, Vander Wall indicated that, because of theft, some animals retrieve only one third of what they store! This is like putting money in the bank and not only getting zero interest but also having to give up two-thirds of the principal as a "service charge."

[4]To achieve the bottom-right portion of the frontier, the animal must never retrieve and consume accumulated stocks. Since retrieval does occur, we find this portion of the frontier of little interest.

2

The Tradeoff
Between Determinants of Fitness

Figure 1

In section 3, we describe the *qualitative* characteristics of "noninept" paths of behaviors. We emphasize that unless a path of behaviors satisfies certain arbitrage conditions, a feasible perturbation in behavior could increase the number of surviving offspring. The arbitrage conditions are then shown to imply qualitative changes over time in the endogenous variables of the model. At the end of section 3, we illustrate the predictions of the model with a spreadsheet simulation.[5] Such numerical simulations require as inputs exogenous parameters and provide as output the unique path of behaviors solving the necessary conditions of the optimization problem. Appendix 1 supplements sections 2 and 3 by deriving from the necessary conditions each behavior in a given period as a continuous function of the "co-state variable" in that period. These functions underlie our spreadsheet model. Section 4 concludes the paper.

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[5] A disk containing our spreadsheet model is available upon request. Please specify Lotus, Quattro Pro, or Excel.

2. The Model

In this section, we formulate and solve the optimization problem referred to in the introduction. To begin, we define the variables used in the model:

β = discount factor per period ($\beta\epsilon(0,1]$);

A_t = energy expended in period t in food-gathering, storage, and retrieval;

H_t = units of food gathered in period t;

R_t = units of food retrieved from storage in period t;

N_t = units of food newly-stored in period t;

C_t = units of food consumed in period t;

$\alpha_{h(t)}$ = energy required to gather one unit of food in period t;

α_r = energy required to retrieve one unit of food from storage in any period;

α_n = energy required to store one unit of food in any period;

θ = the fraction of food retrievable after being stored for one period;

S_t = food in storage at the beginning of period t;

T = number of periods in planning horizon;

t_w = the final period before the onset of winter;

$\hat{S}$ = minimal allowable stock remaining at $T + 1$.

By definition, a point on the frontier of Figure 1 maximizes the bequest to the offspring for any given maternal body-weight at the time the new litter is born. It is more convenient (and equivalent) to characterize the given point as maximizing the body weight of the mother for a given bequest to the offspring. To achieve this frontier, the consumption, foraging, storage, and work-effort decisions in each period must

$$\text{Maximize } \sum_{t=1}^{T} \beta^t \left\{ U(C_t) - F(A_t) \right\}$$

$$\text{subject to} \quad C_t = H_t + R_t - N_t \text{ , for } t = 1, ..., T$$
$$S_{t+1} \leq (S_t + N_t - R_t)\theta \text{ , for } t = 1, ..., T$$

4

$$A_t = \alpha_{h(t)}H_t + \alpha_r R_t + \alpha_n N_t \ , \ \text{for } t = 1, ..., T$$

$$S_1 \leq \overline{S}$$

$$S_{T+1} \geq \hat{S}$$

$$\text{and} \qquad A_t, N_t, C_t, H_t, R_t, S_t \geq 0 \ .$$

We assume that $U(C_t)$ and $F(A_t)$ are differentiable and, respectively, strictly concave and strictly convex in their single arguments. Economists may want to think of $U(C_t)$ as the utility of consuming C_t units of food in period t and $F(A_t)$ as the disutility of working for A_t units of time in period t. The re-interpretation suggested in the introduction is to regard $\{U(C_t) - F(A_t)\}$ as the change in body-weight in period t resulting from C_t units of consumption and A_t units of food-related energy expenditure in period t. If the term in braces is negative, interpret this weight loss as the result of drawing down internal stores of body fat. If we set $\beta = 1$, interpret T as the time when the next litter arrives, and denote as W_0 the initial body weight of the mother, then $\sum_{t=1}^{T} \beta^t \{U(C_t) - F(A_t)\} + W_0$ is her body-weight when the offspring are born.

It is convenient to substitute out of the variable C_t. Forming the Lagrangean we obtain:

$$
\begin{aligned}
L = & \sum_{t=1}^{T} \beta^t \Big\{ U(H_t + R_t - N_t) - F(A_t) + \lambda_t[\theta_t(S_t + N_t - R_t) - S_{t+1}] \\
& + \gamma_t[A_t - (\alpha_{h(t)}H_t + \alpha_r R_t + \alpha_n N_t)] \Big\} \\
& + \lambda_0 \theta(\overline{S} - S_1) + \beta^{T+1}\theta\lambda_{T+1}(S_{T+1} - \hat{S}) \ .
\end{aligned}
$$

The following Kuhn-Tucker conditions must hold if a program is optimal:
For $t = 1, 2, ..., T$,

1. $H_t \geq 0$; $\dfrac{\partial L}{\partial H_t} = \beta^t[U'(H_t + R_t - N_t) - \gamma_t\alpha_{h(t)}] \leq 0$; with complementary slackness;[6]

2. $R_t \geq 0$; $\dfrac{\partial L}{\partial R_t} = \beta^t[U'(H_t + R_t - N_t) - \lambda_t\theta - \gamma_t\alpha_r] \leq 0$; with complementary slackness;

3. $N_t \geq 0$; $\dfrac{\partial L}{\partial N_t} = \beta^t[-U'(H_t + R_t - N_t) + \lambda_t\theta - \gamma_t\alpha_n] \leq 0$; with complementary slackness;

4. $S_t \geq 0$; $\dfrac{\partial L}{\partial S_t} = \beta^t\lambda_t\theta - \beta^{t-1}\lambda_{t-1} \leq 0$; with complementary slackness;

5. $S_{T+1} \geq 0$; $\dfrac{\partial L}{\partial S_{T+1}} = \beta^{T+1}\theta\lambda_{T+1} - \beta^T\lambda_T \leq 0$; with complementary slackness;

6. $\lambda_t \geq 0$; $\dfrac{\partial L}{\partial \lambda_t} = \theta(S_t + N_t - R_t) - S_{t+1} \geq 0$; with complementary slackness;

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[6]Complementary slackness means that at least one of the two conditions in the list must equal zero. For example, in (1) either $H_t = 0$ or $\beta^t[U'(H_t + R_t - N_t) - \gamma_t\alpha_{h(t)}] = 0$ (or both).

7. $\lambda_0 \geq 0; \dfrac{\partial L}{\partial \lambda_0} = \theta(\overline{S} - S_1) \geq 0$; with complementary slackness;

8. $\dfrac{\partial L}{\partial \gamma_t} = A_t - (\alpha_{h(t)} H_t + \alpha_r R_t + \alpha_n N_t) = 0$;

9. $\lambda_{T+1} \geq 0; \dfrac{\partial L}{\partial \lambda_{T+1}} = \beta^{T+1} \theta(S_{T+1} - \hat{S}) \geq 0$; with complementary slackness;
   and

10. $A_t \geq 0, \dfrac{\partial L}{\partial A_t} = \beta^t \left(-F'(A_t) + \gamma_t\right) \leq 0$; with complementary slackness.

We make the following simplifying assumptions to which we will subsequently refer:

A1: $U'(C) > 0$

A2: $\alpha_{h(s)} = \alpha_{h(t)}$ for $s, t = 1, 2, \ldots, t_w$

A3: $\alpha_{h(s)} = \alpha_{h(t)}$ for $s, t = t_w + 1, t_w + 2, \ldots, T$

A4: $F'(0)$ is finite and $\lim\limits_{C \to 0} U'(C) = \infty$

A5: $\alpha_{h(t_w+1)} > \max(\alpha_{h(t_w)}, \alpha_r, \alpha_n)$

A6: $\alpha_{h(t_w+1)} > \dfrac{\alpha_{h(t_w)}}{\beta\theta} + \left(\alpha_r + \dfrac{\alpha_n}{\beta\theta}\right)$

A7: $\min(\alpha_r, \alpha_n, \alpha_{h(t)}) > 0$

A8: $\hat{S} > 0$

A9: $\alpha_{h(t_w)} > \alpha_r$.

Since $U(C_t) - F(A_t)$ is strictly jointly concave in C_t and A_t, the maximand $\sum\limits_{t=1}^{T} \beta^t \{U(C_t) - F(A_t)\}$ is weakly jointly concave in the full vector of decision variables. Since, in addition, the constraint set is convex any solution to the Kuhn-Tucker conditions is optimal. In Appendix 2, we show that these conditions have only one solution.

At the outset of our analysis, we verify that it is never optimal both to add to and withdraw from storage in the *same* period. For, in any program where $N_t > 0$ and $R_t > 0$ in period t, one could—without varying A_t—reduce both activities by some $\epsilon > 0$, have the same amount in storage next period, and use the energy saved to gather and consume additional food. This presumes, of course, that at least one of the two activities reduced by ϵ is requires effort ($\alpha_r > 0$ or $\alpha_n > 0$). More formally, suppose to the contrary $R_t > 0$ and $N_t > 0$. Then (2) and (3) imply

$$U'(H_t + R_t - N_t) \quad - \quad \lambda_t \theta - \gamma_t \alpha_r = 0$$
$$\text{and} \quad -U'(H_t + R_t - N_t) \quad + \quad \lambda_t \theta - \gamma_t \alpha_n = 0 .$$

Summing, we get

$$-\gamma_t(\alpha_n + \alpha_r) = 0. \tag{11}$$

But by $(A7)$, the second factor is not zero; moreover, since $(A1)$, $(A7)$ and (1) imply that the first factor $(-\gamma_t)$ is nonzero, (11) cannot hold. Hence, in an optimal program either R_t or N_t (or both) must be zero.

Next, we establish that it is never optimal to cease all food-related activity ($A_t = 0$). Suppose to the contrary that $A_t = 0$ for some t. As a result, $H_t = 0$, $R_t = 0$ and $C_t = 0$. Then (1) and (10) reduce to:

$$\frac{U'(0)}{\alpha_{h(t)}} \leq \gamma_t$$

$$F'(0) \geq \gamma_t.$$

But these inequalities are jointly inconsistent with ($A4$). Therefore, it is optimal to expend some energy on food-related activities ($A_t > 0$) in every period. Simplifying (10), we obtain:

$10'$. $A_t > 0$ and $F'(A_t) = \gamma_t$.

Since the three other decision variables (H_t, R_t and N_t) must each be either zero or strictly positive there are in principle 2^3 cases to consider. But two of these eight cases involve $R_t > 0$ and $N_t > 0$ simultaneously and, as proved above, this cannot be optimal. A third case has $H_t = 0$, $R_t = 0$ but $N_t > 0$. Since $C_t = H_t + R_t - N_t$, such a program would violate the constraint that consumption be non-negative. A fourth case has $H_t = N_t = R_t = 0$, which cannot be optimal since it implies that $A_t = 0$.

There remain 4 cases to consider:

	H_t	R_t	N_t
Case 1	0	+	0
Case 2	+	+	0
Case 3	+	0	0
Case 4	+	0	+

In Appendix 1, we show that each decision variable (A, C, H, N, R) can be written as a continuous function of the multiplier λ. These functions shift only once: at the onset of winter.

Prior to the onset of winter, optimal behavior on a given period depends on λ in that period. λ must lie in one of the disjoint regions which correspond to the cases above. If λ is in region 1, 2, 3, or 4 then case 1, 2, 3 or 4 (respectively) arises. The boundary between region i and j at date t is denoted $\lambda_{i,j}^t$. An equation defining each of these boundaries as an implicit function of the exogenous variables is presented at the end of Appendix 1.

It is shown in Appendix 1 that $\lambda_{1,2}^t < \lambda_{2,3}^t < \lambda_{3,4}^t$.

These boundaries do not change prior to the onset of winter. At the onset of winter, they jump up but retain the same order. They do not change again.

In our application, we assume the initial period occurs in the spring after the previous litter is born and that the animal initially has nothing in storage. Consequently, $\bar{S} = 0$. Moreover, we assume that the terminal requirement ($\hat{S}$) is not so oppressive that it is optimal either to store from the outset or to forego retrieval entirely.

If the stockpile is initially empty but some retrieval subsequently occurs, there must be an intermediate phase where food is placed in storage. In such cases, λ must start in region 3 or 4, must grow into the interior of region 4 prior to the onset of winter, must jump from region 4 to region 1 or 2, and then must continue to

7

increase until the end of the program.[7] Figure 2 illustrates how the boundaries of the regions (denoted R1-R4) jump at the onset of winter:
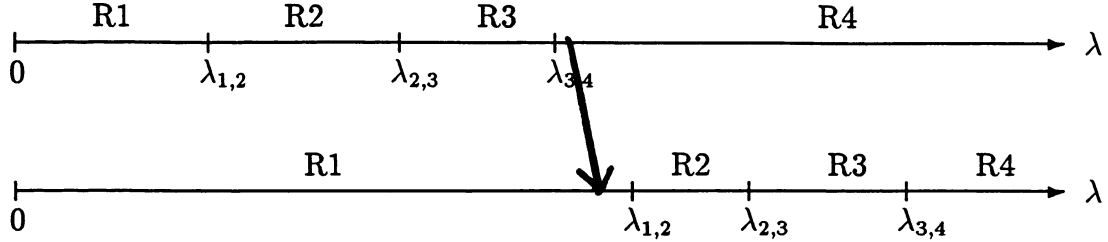

Figure 2: The 4 Regions before and after Winter Arrives

As the dashed line indicates, λ can increase by the factor $1/\beta\theta$ and nonetheless can switch from region 4 to region 1 at the onset of winter. A transition from region 4 to region 2 would occur instead if the minimal bequest $(\hat{S})$ were increased sufficiently.[8] Clearly, no hibernation (no transition to region 1) can occur if $\lambda_{3,4}^{t_w}/\beta\theta > \lambda_{1,2}^{t_w+1}$. For, in that case, if λ_{t_w} lies in region 4 before the onset of winter, λ_{t_w+1} must lie in region 2 (or higher) after the onset of winter. As is discussed in the final section of Appendix 1, our assumption A6 insures that transitions to region 1 *can* occur.[9]

To conclude this section, we describe how the Kuhn-Tucker conditions can be solved recursively. If it is not optimal to store initially, then λ_0 must be contained in region 3. For, if it were in region 1 or 2 there would be positive retrieval — violating the requirement that storage be non-negative. Similarly, if λ_0 were in region 4, there would be additions to stocks immediately—contradicting the assumption that it is not optimal to store initially.

As long as λ_t remains in region 3, no new storage or retrieval occurs. Each period, the animal finds and consumes a constant amount of food and spends a constant amount of energy on food–related activities. If $S_{t+1} = 0$, (4) implies $\lambda_{t+1} \leq \lambda_t/\beta\theta$. Hence, there is a limit to how fast the multiplier grows. If λ_t leaves region 3 before the onset of winter $(t \leq t_w)$, it must enter region 4. When this transition occurs in the optimal program is shown in Appendix 2 to be uniquely determined from the necessary conditions.

To compute the optimal program, guess at the first period when new storage occurs. Denote this as t^*. Then $S_{t^*} = 0$. Denote the boundary between region 3 and region 4 as $\lambda_{3,4}$. λ_{t^*} can be set in a small interval $(\lambda_{3,4}, \lambda_{3,4}/\beta\theta)$. Given the arbitrary choices of t^* and λ_{t^*}, the remainder of the program is uniquely determined. Given λ_{t^*}, we can compute $A_{t^*}, H_{t^*}, R_{t^*}, N_{t^*}$, and C_{t^*} using the functions derived in Appendix 1. Since $\lambda_{t^*} > 0$, S_{t^*+1} can be computed from condition (6). Since $S_{t^*+1} > 0$, λ_{t*+1} can be computed from condition (4). The entire cycle can now

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[7]We do not focus on transitions from region 4 to regions 3 or 4 although such transitions are necessary to achieve some portions of the frontier in Figure 1. In such programs, *none* of the accumulated stocks is retrieved before the litter arrives. To our knowledge, such behavior is not observed—presumably because the fitness function puts sufficient weight on maternal health. For similar reasons, we do not discuss situations where the animal *recommences* storage before the litter is born (where λ passes through the entirety of region 3 and *re-enters* region 4) although this would clearly be optimal in some circumstances.

[8]The proposed increase in $\hat{S}$ would not affect the boundaries between the regions. The boundaries are also independent of T and t_w.

[9]Our first simulation illustrates a case where hibernation is required to reach a particular point on the frontier of Figure 1.

8

be repeated given this λ_{t^*+1}...Eventually, one computes $A_T, H_T, R_T, N_T,$ and C_T. Since (6) holds at $t = T$, S_{T+1} can be determined. If $S_{T+1} < \hat{S}$, (9) is violated and the program cannot be optimal. If $S_{T+1} > \hat{S}$, $\lambda_T = 0$ or the path of behaviors can not be optimal. For, (9) requires that $\lambda_{T+1} = 0$ and (5) and (A8) require that $\lambda_T = \beta\theta\lambda_{T+1} = 0$. If $S_{T+1} = \hat{S}$, $\lambda_T \geq 0$.

If the constructed program violates any of these end-point (or "transversality") conditions, the initial guesses are incorrect and should be revised. As a practical matter, it is sensible to start λ_{t^*} at the lower end of the interval $(\lambda_{3,4})$ and to adjust t^* first. Assuming the minimal bequest $\hat{S}$ is not too oppressive, setting $t^* = 1$ will result in too much storage $(S_{T+1} > \hat{S})$. As one delays the period when region 4 is entered (t^*), S_{T+1} decreases. If possible, set t^* so that $S_{T+1} = \hat{S}$. If that is impossible, because t must be an integer, set $t*$ so that S_{T+1} is as close as possible to $\hat{S}$ but is smaller than this minimal bequest. Now increase λ_{t^*} toward the upper end of the interval $(\lambda_{3,4}/\beta\theta)$ until S_{T+1} increases to $\hat{S}$. This second step would be unnecessary in the continuous-time analog of our discrete-time model. In our application, $S_1 = 0$. In this circumstance, it will never be optimal to have $S_{T+1} > \hat{S}$. For, if stocks were bequeathed at $T + 1$ that were not present initially, they would have to be accumulated. But for them to be accumulated $\lambda_t > 0$ after $t = t^*$. If so, then (4) would imply that $\lambda_{T+1} > 0$ and this would violate the endpoint condition.

3. How Behavior Changes over Time

The model predicts how behavior changes before the onset of winter and after it arrives. These changes are summarized in Table 1 below. The purpose of this section is to explain these *qualitative* predictions intuitively.[10] At the end of the section, we also discuss how behavior jumps at the onset of winter.

Table 1
Change in Decision Variable Within a Region
as Time Elapses

Variable

Region	H	R	N	C	A
Region 1	0	↓	0	↓	↓
Region 2	↑	↓	0	↓	↑
Region 3	→	0	0	→	→
Region 4	?	0	↑	↓	↑

Key: ↑ means a positive variable strictly increases over time.

  ↓ means a positive variable strictly decreases over time.

  → means a positive variable is constant over time.

  ? means a positive variable could increase or decrease over time.

  0 means a variable remains zero over time.

We begin with a preliminary but useful observation. Whenever $H_t > 0$,

$$U'(C_t) = \alpha_{h(t)} F'(A_t). \tag{12}$$

(12) is useful because it implies that consumption and activity must change in opposite directions in successive periods. Either both variables remain fixed or $(C_{t+1} - C_t)(A_{t+1} - A_t) < 0$.

Equation (12) must hold (for $H_t > 0$) if a path of behaviors is optimal. For, suppose its left-hand side were strictly larger than the right-hand side. Then the animal could increase its activity at t by dA_t, use the additional effort to forage for more food $(dH_t = dA_t/\alpha_{h(t)})$, and consume the extra amount $(dC_t = dH_t)$. If no other changes in behavior took place, the resulting change in the maximand (scaled up by the constant β^{-t}) would be:

$$U'(C_t)dC_t - F'(A_t)dA_t = \left[\frac{U'(C_t)}{\alpha_{h(t)}} - F'(A_t) \right] dA_t. \tag{13}$$

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[10]In Appendix 1, equations are derived which define the level of each decision variable as a function of the contemporaneous co-state variable (λ). These equations underlie our spreadsheet simulation model. In addition, they imply qualitative changes in the decision variables over time and hence can be used to confirm the results in this section.

Hence, if the left-hand side of (12) were strictly larger than the right-hand side, the bracketed coefficient in (13) would be positive and a utility gain could be achieved by increasing activity ($dA_t > 0$) in period t as described above. If instead the left-hand side were strictly smaller, a utility gain could be achieved by *decreasing* activity and foraging—provided such decreases were feasible. They are feasible except in region 1 (where $H_t = 0$). In the other three regions, (12) must hold.

The foregoing argument involves perturbations within a *single* period. By considering perturbations in *successive* periods, we can explain the predicted changes in consumption and the other endogenous variables. We consider the regions in the order which is most likely to occur: region 3 followed by 4 before the onset of winter; and region 1 followed by 2 after the onset of winter.

Behavior does not change in region 3. Recall that there are neither additions to nor withdrawals from storage in that region. Hence, the only energy-consuming activity is foraging, and the entire yield from foraging is consumed: $A_t = \alpha_{h(t)} H_t$ and $C_t = H_t$. Since $H_t > 0$ in this region, (12) holds. Replacing A_t in (12), we obtain:

$$U'(C_t) = \alpha_{h(t)} F'(\alpha_{h(t)} C_t).$$

This equation uniquely defines consumption at t. Moreover, since $\alpha_{h(t)}$ is assumed (in A2 and A3) to be constant before and after the onset of winter, C_t does not change in region 3 during time intervals which exclude the onset of winter (t_{w+1}). These facts are summarized in row 3 of Table 1.

In region 4, additions to storage occur in each period. Since storage is augmented in successive periods ($N_t > 0$ and $N_{t+1} > 0$), the following arbitrage condition must hold if the path of behaviors is optimal:

$$\left\{1 + \frac{\alpha_n}{\alpha_{h(t)}}\right\} U'(C_t) = \beta\theta \left\{1 + \frac{\alpha_n}{\alpha_{h(t+1)}}\right\} U'(C_{t+1}). \tag{14}$$

For, suppose instead that the left-hand side were strictly smaller than the right-hand side. Consider now an alternative path of behaviors which is identical to the original path through period $t - 1$ and then again from period $t + 2$ until the end of the horizon but differs in periods t and $t + 1$. In period t, suppose the animal increases new storage by dN_t. If its activity at t does not change, then the energy it spends gathering food must decrease and a loss in provisions results: $dH_t = -[\alpha_n/\alpha_{h(t)}]dN_t$. Consequently, the change in consumption in period t is $dC_t = dH_t - dN_t = -\left(1 + \alpha_n/\alpha_{h(t)}\right) dN_t$.

In period $t + 1$, there is θdN_t more food in storage. If the animal changes its new storage in $t + 1$ by $dN_{t+1} = -\theta dN_t$, then stocks carried into the future will be unaffected by the perturbations in these two periods.[11]

The energy saved because of the reduced new storage at $t + 1$ can be used to increase foraging without any overall change in the energy spent on food-related activity. As a result, the change in newly acquired food would be $dH_{t+1} = -[\alpha_n/\alpha_{h(t+1)}]dN_{t+1} = [\alpha_n/\alpha_{h(t+1)}]\theta dN_t$.

Consequently, consumption increases both because of the reduction in new storage and because of the increased foraging: $dC_{t+1} = dH_{t+1} - dN_{t+1} = \left(1 + \frac{\alpha_n}{\alpha_{h(t+1)}}\right)\theta dN_t$. If no other changes in behavior take place before t or after $t + 1$, then the change in the maximand would be:

$$U'(C_t)dC_t + \beta U'(C_{t+1})dC_{t+1} =$$

$$-\left[U'(C_t)\left(1 + \frac{\alpha_n}{\alpha_{h(t)}}\right) + \beta U'(C_{t+1})\left(1 + \frac{\alpha_n}{\alpha_{h(t+1)}}\right)\theta\right] dN_t. \tag{15}$$

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[11]Since $S_{t+2} = \theta(S_{t+1} + N_{t+1}) = \theta^2(S_t + N_t) + \theta N_{t+1}, dS_{t+2} = \theta^2 dN_t + \theta dN_{t+1}$. If $dN_{t+1} = -\theta dN_t$, $dS_{t+2} = 0$.

Hence, if the left-hand side of (14) is strictly smaller than the right-hand side, the bracketed coefficient in (15) would be positive and an increase in the maximand could be achieved by increasing new storage ($dN_t > 0$) at t as outlined above; if the left-hand side were smaller, the maximand could be increased by reducing new storage at t. In region 4, each of these arbitrages is feasible.[12]

Since $\alpha_{h(t)}$ is assumed to be constant except at the onset of winter, (14) simplifies to:

$$U'(C_t) = \beta\theta U'(C_{t+1}).$$

Since $\beta\theta < 1$ and $U'(\cdot)$ is strictly decreasing, $C_{t+1} < C_t$ in region 4 for successive periods before the onset of winter or after winter has arrived.

Since foraging is positive in region 4, activity and consumption must move in opposite directions: hence, $A_{t+1} > A_t$. Moreover, the linear identity defining consumption and the linear energy-allocation constraint jointly imply:

$$N_t = \frac{A_t - \alpha_{h(t)}C_t}{\alpha_{h(t)} + \alpha_n}.$$

Since the numerator of this fraction increases over time in region 4 while the denominator is constant, $N_{t+1} > N_t$. Foraging can change in either direction in region 4. These facts are recorded in row 4 of Table 1.

In region 1, foraging is zero and retrieval from storage occurs in every period ($R_t > 0$ and $R_{t+1} > 0$). In this case, the following arbitrage condition must hold if the path of behaviors is optimal:

$$U'(C_t) - \alpha_r F'(A_t) = \beta\theta\left\{U'(C_{t+1}) - \alpha_r F'(A_{t+1})\right\}. \tag{16}$$

For, suppose that the left-hand side were strictly smaller than the right-hand side. Consider an alternative path of behaviors which is identical to the original path through period $t - 1$ and then again from period $t + 2$ until the end of the horizon but differs in periods t and $t + 1$. In period t, suppose the animal increases its retrieval by dR_t and, so as *not to alter* the amount it forages, increases its activity level by $dA_t = \alpha_r dR_t$. As a result, consumption would increase by $dC_t = dR_t$.

If at $t + 1$ retrieval changes by $dR_{t+1} = -\theta dR_t$, then the perturbations at t and $t + 1$ would not require changes in other periods for the perturbed path to be feasible. For simplicity, assume that no other changes take place. Moreover, suppose the animal reduces its activity at $t + 1$ to accommodate the reduction in

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[12]This arbitrage relationship may be derived more formally from the necessary conditions for a maximum. Since by hypothesis $N_t > 0$ and $N_{t+1} > 0$, (3) implies:

$$-U'(C_t) \quad + \quad \lambda_t\theta - \gamma_t\alpha_n = 0$$
$$-U'(C_{t+1}) \quad + \quad \lambda_{t+1}\theta - \gamma_{t+1}\alpha_n = 0 .$$

Since $N_t > 0$, $R_t = 0$, $S_{t+1} > 0$, and hence (4) implies:

$$\lambda_{t+1} = \lambda_t/\beta\theta .$$

Finally, since $N_t > 0$ and $N_{t+1} > 0$, $H_t > 0$ and $H_{t+1} > 0$ — implying from (1):

$$\gamma_t = \frac{U'(C_t)}{\alpha_{h(t)}} \quad \text{and} \quad \gamma_{t+1} = \frac{U'(C_{t+1})}{\alpha_{h(t+1)}} .$$

Substituting out of the γ's and using the relationship between the successive λ's, we obtain the arbitrage relationship. It therefore must hold whenever $N_t > 0$ and $N_{t+1} > 0$ if the program is optimal. It is left to the reader to verify that each of the other arbitrage conditions discussed intuitively in this section can be derived in a similar fashion.

12

retrieval without any alteration in foraging. Then $dA_{t+1} = \alpha_r dR_{t+1} = -\alpha_r\theta dR_t$. Consequently, the change in consumption would be: $dC_{t+1} = dR_{t+1} = -\theta dR_t$. This perturbation results in the following change in the maximand:

$$U'(C_t)dC_t - F'(A_t)dA_t + \beta\left\{U'(C_{t+1})dC_{t+1} - F'(A_{t+1})dA_{t+1}\right\} =$$
$$\left[U'(C_t) - \alpha_r F'(A_t) - \beta\theta\left(U'(C_{t+1}) - \alpha_r F'(A_{t+1})\right)\right]dR_t \qquad (17)$$

If the left-hand side of (16) were strictly smaller than the right-hand side, the bracketed coefficient in (17) would be negative and a utility gain could be achieved by reducing retrieval $(dR_t < 0)$ in period t. If it were strictly larger, a utility gain can be achieved by increasing retrieval in period t $(dR_t > 0)$. Since $A > 0$, $R > 0$, and $C > 0$ in this region, either of these arbitrages is feasible.[13] Therefore, (16) must hold if the path of behaviors is optimal.[14] Recall that $H = N = 0$ in region 1. Hence, $C = R = A/\alpha_r$. Substituting into (16), we obtain:

$$U'(C_t) - \alpha_r F'(\alpha_r C_t) = \beta\theta\left\{U'(C_{t+1}) - \alpha_r F'(\alpha_r C_{t+1})\right\}.$$

Since $\beta\theta < 1$ and $U'(C) - \alpha_r F'(\alpha_r C)$ is strictly decreasing in C, we conclude that $C_{t+1} < C_t$ in region 1. Moreover, since $C = R = A/\alpha_r$, it follows that $A_{t+1} < A_t$ and $R_{t+1} < R_t$. These facts are recorded in row 1 of Table 1.

Finally, in region 2 foraging is strictly positive $(H_t > 0)$ and retrieval occurs in successive periods $(R_t > 0, R_{t+1} > 0)$. If the path of behaviors is optimal, the following arbitrage relationship must hold:

$$\left\{1 - \frac{\alpha_r}{\alpha_{h(t)}}\right\}U'(C_t) = \beta\theta\left\{1 - \frac{\alpha_r}{\alpha_{h(t+1)}}\right\}U'(C_{t+1}). \qquad (18)$$

For, suppose that the left-hand side of (18) were strictly smaller than the right-hand side. Consider now an alternative path of behaviors which differs only in period t and $t+1$. In period t, suppose the animal changes its retrieval by dR_t. If activity is fixed, there must be an offsetting change in foraging: $dH_t = -[\alpha_r/\alpha_{h(t)}]dR_t$. Consequently, consumption in period t changes by $dC_t = dH_t + dR_t = \left(1 - \alpha_r/\alpha_{h(t)}\right)dR_t$.

Suppose retrieval at $t + 1$ offsets the change at t so that the perturbation does not affect the stockpile size at $t + 2$. This requires that $dR_{t+1} = -\theta dR_t$.

If activity is not to change, foraging must be adjusted to compensate for the change in retrieval: $dH_{t+1} = -[\alpha_r/\alpha_{h(t+1)}]dR_{t+1} = [\alpha_r/\alpha_{h(t+1)}]\theta dR_t$. The change in foraging and retrieval result in a change in consumption: $dC_{t+1} = dH_{t+1} + dR_{t+1} = \theta\left([\alpha_r/\alpha_{h(t+1)}] - 1\right)dR_t$. As a result the maximand changes by:

$$U'(C_t)dC_t + \beta U'(C_{t+1})dC_{t+1} =$$
$$\left[U'(C_t)\left(1 - \frac{\alpha_r}{\alpha_{h(t)}}\right) - \beta\theta U'(C_{t+1})\left(1 - \frac{\alpha_r}{\alpha_{h(t+1)}}\right)\right]dR_t. \qquad (19)$$

If the left-hand side of (18) is strictly smaller than the right-hand side, the bracketed coefficient in (19) would be negative and the maximand could be increased by reducing retrieval $(dR_t < 0)$ at t. Conversely, if the left-hand side of (18) is

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[13]To derive (16), use conditions (2), (4), and (10).

[14]Note that we do not vary foraging in conducting this exercise. Since $H = 0$ in this region, any arbitrage which required $dH < 0$ would be infeasible.

13

strictly larger, *increasing* retrieval at t would result in a larger maximand. Since each of these arbitrages would be feasible in region 2, (18) must hold.[15] This condition simplifies to:

$$U'(C_t) = \beta\theta U'(C_{t+1})$$

since $\alpha_{h(t)}$ does not change before the onset of winter or after winter arrives. This in turn implies that $C_{t+1} < C_t$ in region 2. Moreover, since foraging is positive in region 2, activity and consumption move in opposite directions. Hence, $A_{t+1} > A_t$. The linear identity defining consumption and the linear energy-allocation constraint jointly imply:

$$R_t = \frac{\alpha_{h(t)}C_t - A_t}{\alpha_{h(t)} - \alpha_r}.$$

Since the numerator of this fraction decreases over time in region 2 while the denominator is constant, $R_{t+1} < R_t$. If retrieval decreases and yet activity increases, the energy-budget constraint requires that foraging increase: $H_{t+1} > H_t$ in region 2. These facts are recorded in row 2 of Table 1.

To conclude this section, we consider the jumps in behavior which occur at the onset of winter. In period $t = t_w$, the animal adds to storage ($N_t > 0$). In the following period (the first period when foraging requires more energy), the animal retrieves from storage ($R_{t+1} > 0$). Since activity is positive in both periods ($A_t > 0$ and $A_{t+1} > 0$), the following arbitrage condition must hold if the path of behaviors is optimal:

$$U'(C_t) + \alpha_n F'(A_t) = \beta\theta \{U'(C_{t+1}) - \alpha_r F'(A_{t+1})\} \tag{20}$$

For, suppose the left-hand side were strictly smaller than the right-hand side. Consider now the following perturbation in behaviors at t and $t + 1$. At t, the animal stores an additional amount which would otherwise have been consumed ($dC_t = -dN_t$). This increased storage requires an additional expenditure of energy. Assume the animal does *not* alter its foraging ($dH_t = 0$), but instead increases its activity ($dA_t = \alpha_n dN_t$). In period $t + 1$, the animal retrieves and consumes what remains of the additional storage ($dC_{t+1} = dR_{t+1} = \theta dN_t$). The increased retrieval requires the additional expenditure of energy. Assume again that the animal does *not* alter its foraging ($dH_{t+1} = 0$) but instead increases its activity ($dA_{t+1} = \alpha_r dR_{t+1} = \alpha_r \theta dN_t$).

Since the stocks carried into period $t + 2$ are unchanged, restricting changes in behavior to those outlined for periods t and $t + 1$ results in a feasible perturbed path. Assume no other behaviors are altered. Then the change in the maximand would be:

$$U'(C_t)dC_t - F'(A_t)dA_t + \beta \{U'(C_{t+1})dC_{t+1} - F'(A_{t+1})dA_{t+1}\} =$$
$$[-U'(C_t) - \alpha_n F'(A_t) + \beta\theta \{U'(C_{t+1}) - \alpha_r F'(A_{t+1})\}] dN_t \tag{21}$$

If the left-hand side of (20) were strictly smaller than the right-hand side, the bracketed coefficient in (21) would be positive and a utility gain could be achieved by increasing storage ($dN_t > 0$) in period t. If it were strictly larger, a utility gain can be achieved by reducing storage in period t. Since $A_t > 0$, $N_t > 0$, $C_t > 0$, $R_{t+1} > 0$, and $C_{t+1} > 0$, either of these arbitrages is feasible. Therefore, (20) must hold if the path of behaviors is optimal.[16]

This same condition holds whether the transition is from region 4 to region 1 or from region 4 to region 2. Since $F'(\cdot) > 0$ and $\beta\theta < 1$, (20) implies that $C_{t+1} < C_t$.

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[15]To derive (18), use conditions (1), (2), and (4).

[16]To derive (20), use conditions (2), (3), (4), and (10).

14

If the transition is to region 1, it can be shown[17] that activity jumps down $(A_{t+1} < A_t)$. As for the other three endogenous variables, new storage and foraging jump down to zero and retrieval jumps up from zero.

If the transition is instead to region 2, the following arbitrage condition must hold between periods t $(= t_w)$ and $t + 1$:

$$[\alpha_{h(t)} + \alpha_n]F'(A_t) = \beta\theta[\alpha_{h(t+1)} - \alpha_r]F'(A_{t+1}). \qquad (22)$$

For, suppose the left-hand side were strictly smaller than the right-hand side and consider now the following perturbation in behaviors at t and $t + 1$. The animal increases its activity in period t and uses the increase to find and store additional food $(dA_t = \alpha_n dN_t + \alpha_{h(t)}dH_t)$. Assume consumption in period t does not change $(dC_t = dH_t - dN_t = 0)$. Consequently, $dA_t = (\alpha_n + \alpha_{h(t)})dN_t$. In period $t + 1$, assume the animal retrieves what remains of the additional storage $(dR_{t+1} = \theta dN_t)$ but cuts its foraging by the same amount so that consumption remains unchanged $(dC_{t+1} = dH_{t+1} + dR_{t+1} = 0)$. Activity must therefore change by:

$$dA_{t+1} = \alpha_{h(t+1)}dH_{t+1} + \alpha_r dR_{t+1} = (\alpha_r - \alpha_{h(t+1)})\theta dN_t.$$

Since these perturbations would not alter the stocks carried into period $t + 2$ $(dS_{t+2} = 0)$, it is feasible to restrict changes in behavior to those outlined above for periods t and $t + 1$. Assume no other behaviors are altered. Then the change in the maximand would be:

$$U'(C_t)dC_t - F'(A_t)dA_t + \beta\left\{U'(C_{t+1})dC_{t+1} - F'(A_{t+1})dA_{t+1}\right\} =$$
$$\left[-(\alpha_n + \alpha_{h(t)})F'(A_t) + \beta\theta\left(\alpha_{h(t+1)} - \alpha_r\right)F'(A_{t+1})\right]dN_t \qquad (23)$$

If the left-hand side of (22) is smaller than the right-hand side, then the bracketed coefficient in (23) would be positive and an increase in the maximand could be achieved by increasing new storage $(dN_t > 0)$ at t as outlined above; if the left-hand side were smaller, the maximand could be increased by reducing new storage at t. As long as $A_t > 0$, $H_t > 0$, $N_t > 0$, $A_{t+1} > 0$, $H_{t+1} > 0$, and $R_{t+1} > 0$, each of these arbitrages is feasible.[18] (22) must therefore hold if a path of behaviors is optimal and the transition is to region 2.

Given (A6) and $F'(\cdot) > 0$, (22) implies that activity must jump down (A_{t+1}) in transitions to region 2. Moreover, foraging must also jump down $(H_{t+1} < H_t)$. For, in region 4 (where $R_t = 0$), the linear consumption identity and the linear energy-budget constraint jointly imply:

$$H_t = \frac{A_t + \alpha_n C_t}{\alpha_{h(t)} + \alpha_n}. \qquad (24)$$

and in region 2 (where $N_{t+1} = 0$), these two equations imply:

$$H_{t+1} = \frac{A_{t+1} - \alpha_r C_{t+1}}{\alpha_{h(t+1)} - \alpha_r}. \qquad (25)$$

Since $A_{t+1} < A_t$, the numerator of (25) is smaller than the numerator of (24). Moreover, assumption (A6) is sufficient for the denominator of (25) to be larger than the denominator of (24). Therefore $H_{t+1} < H_t$.

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[17]See the concluding pages of Appendix 1
[18]To derive (22), use conditions (1), (2), (3), (4), and (10).

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It is useful to summarize the role of assumption A6 in the results we obtain. As is shown in Appendix 1, A6 is necessary if there is ever to be hibernation (a transition to region 1); but even if A6 holds, the transition can be to region 2. If the transition is to region 2, it is evident from (22) that A6 is both necessary and sufficient for activity to jump down; moreover, the comparison of (24) and (25) indicates that A6 is sufficient but not necessary for foraging to jump down.

We conclude this section with a simulation from our spreadsheet model which illustrates the qualitative properties we have been discussing. Panel (a) of Figure 2 reports hoarding behavior and panel (b) reports food-related activity over a 40 week period. Week 24 is the first period when foraging becomes more difficult because of the onset of winter. Units of food were scaled so that the animal was required to deliver at least 1 unit of food to the new litter.

[Figure 2 goes here]

Consider first panel (a). As the flat part of the graph reflects, no storage occurred until week 13. Additions to storage began on week 13 and continued at an increasing rate until week 23. This is reflected in the increasing, convex portion of the graph in panel (a). On week 24 retrieval commenced and continued at a decreasing rate through week 32. This is reflected in the decreasing, convex portion of the graph in panel (a). On week 32, retrieval stopped. Stocks declined after week 32 at a sharply reduced rate due to decay and theft. The litter received the pre-specified minimal bequest of 1 unit of food on week 40.
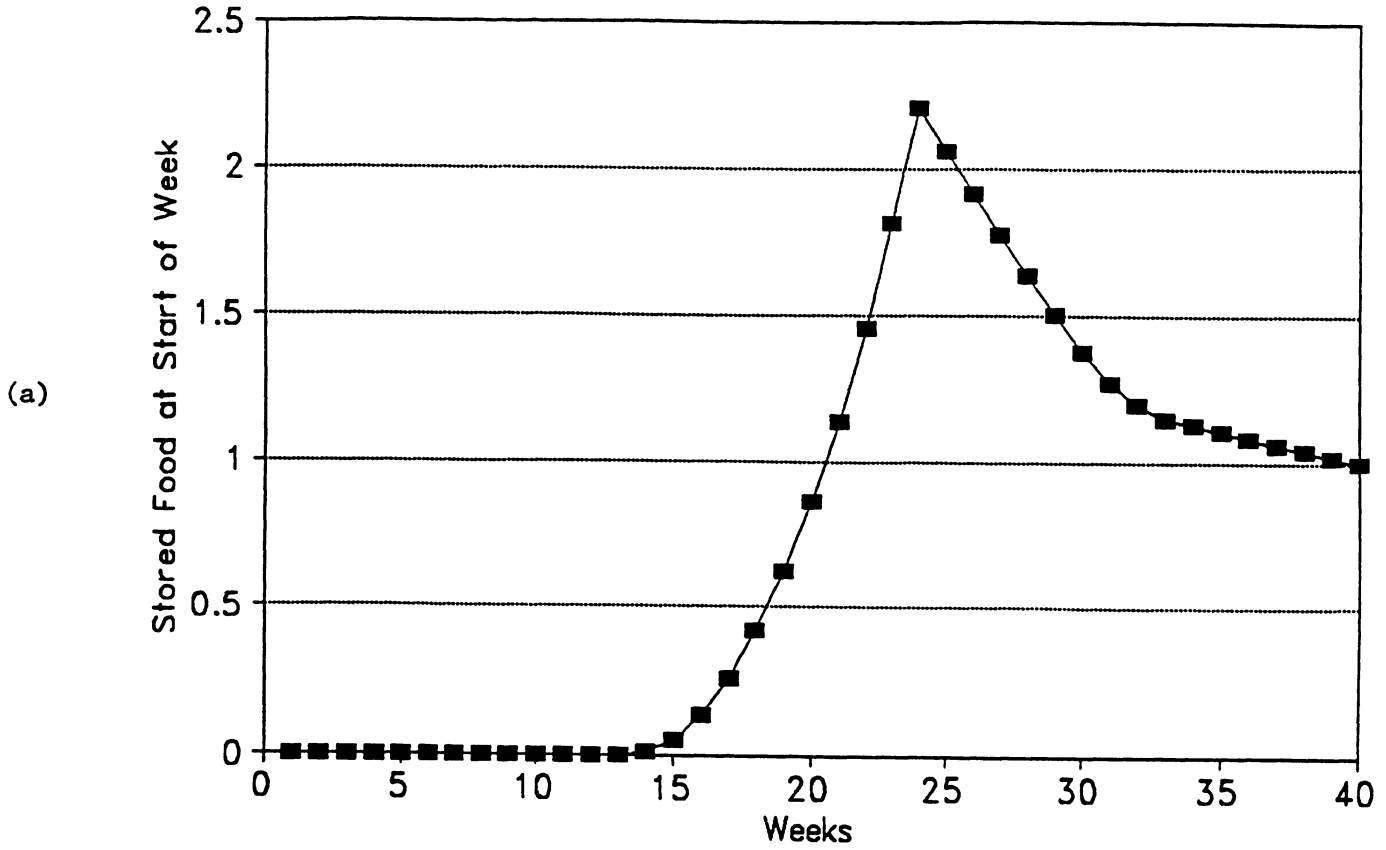
Consider next panel (b). As the flat part of the graph reflects, food-related activity remained constant until additions to storage began on week 13. On week 13, activity began to increase. Activity increased until week 23 as the rising portion of the graph in panel (b) reflects. On week 24 (the onset of winter), activity plummetted and continued to decline until week 30. Activity during this time-interval reflects retrieval only—there was no foraging. This hibernation phase is reflected in the graph in panel (b) by the discontinuous downward jump and the subsequent gradual decline in activity. On week 25, activity began to increase (coincident with the resumption of foraging) and on week 33 activity re-attained its original level.

These paths are optimal given the exogenous data specified for the simulation.[19] This simulation is included to illustrate the workings of the model. Since the input data are fictitious and do not conform to the situation confronting a particular animal, it would be inappropriate to reject the framework we have developed simply because the outputs of this particular simulation do not correspond exactly to the behavior of a particular animal.[20]

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[19]The exogenous data inputs are as follows: $\beta = 1$, $\alpha_{h(t_w)} = 5$, $\alpha_{h(t_{w+1})} = 10$, $\alpha_r = 1$, $\alpha_n = 1$, $\theta = .98$, $T = 39$, $t_w = 12$, $\hat{S} = 1$, $U(C_t) = 10 \ln C_t$, and $F(A_t) = .5A_t^2 + 10A_t$.

[20]We regret that we are unable at this point to produce a simulation using more accurate input data. If readers have a realistic set of input data, we can either run a simulation based on it or can provide them with the spreadsheet model so that they can run *their own* simulations. In response to written requests, we will provide a Lotus or Quattro Pro version for those with IBM compatible computers and an Excel version to those with MACS.

Size of Stockpile

(a)

y-axis: Stored Food at Start of Week

x-axis: Weeks

Food-Related Activity

(b)

y-axis: Energy Expended per Week
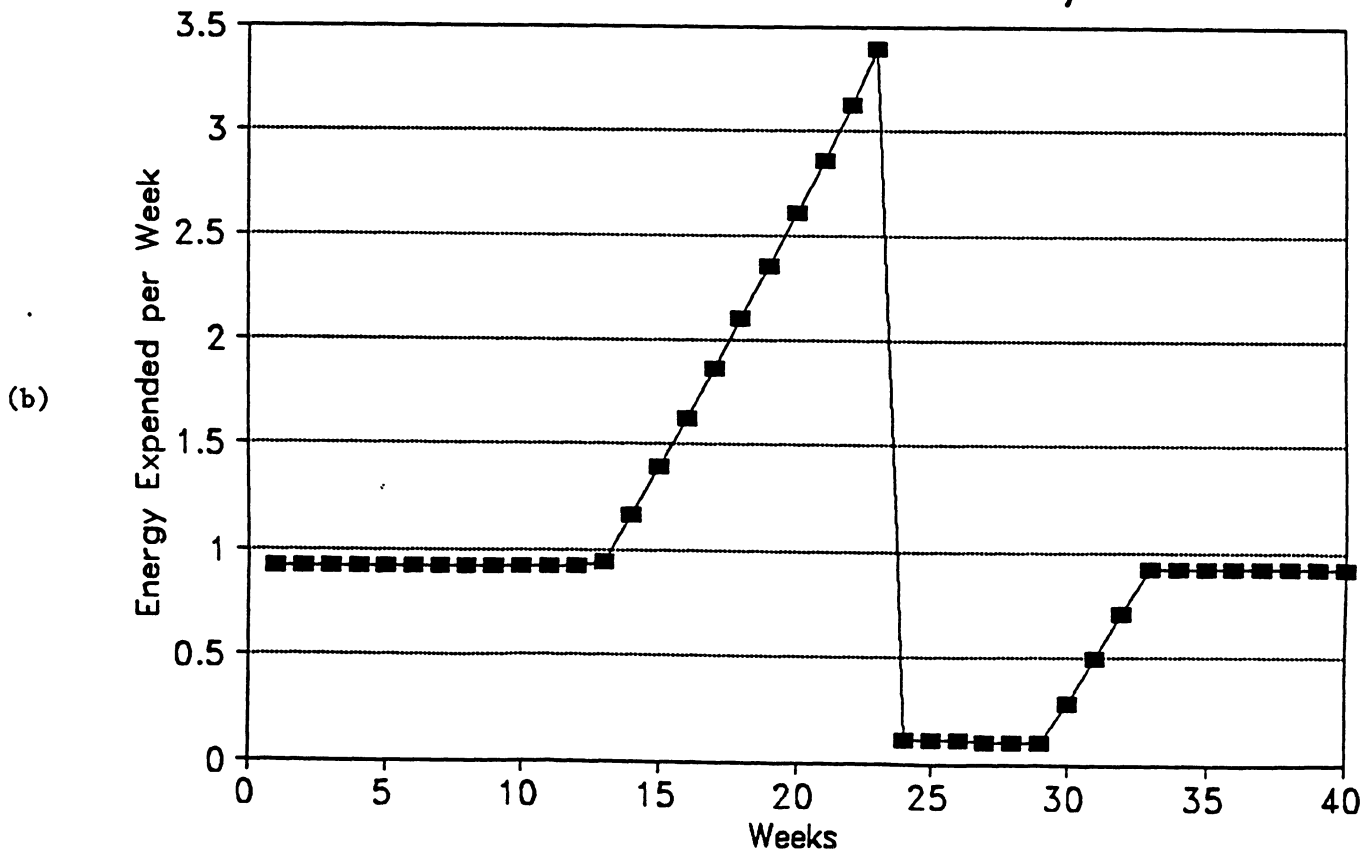
x-axis: Weeks

16A

Figure 2

4. Conclusion

To make the source of our results transparent, we have deliberately abstracted from a variety of real-world complications: various nonstationarities, differences among stored foods, uncertainty about the arrival time of winter, and so forth. However, our framework is flexible enough to accommodate any of these complications. Nonstationarities pose no problem and can be accommodated merely by adding time subscripts to the exogenous variables or functions. Distinguishing either the types or vintages of stored foods requires additional state variables (the stock of each type of stored food put into storage in a given period) but this extension should remain relatively tractable.[21] To see how uncertainty about the arrival time of winter can be incorporated into the framework, the reader should consult [Salant and Henderson, 1978] and the references therein. Introducing such complexity will, however, make the model more unwieldy. For this reason, such refinements seem to us premature. A more appropriate next step would be to implement our model empirically. This will clarify which assumptions should be modified to sharpen predictions.

For many animals, time series are reported in the literature for variables closely related to those in our model. For example, a monthly series on the hours red squirrels (*Sciurus vulgaris*) devote to food-related activitiy is reported in Tonkin [1983]. Tonkin finds that the hours spent on such activities rises monotonically over the summer and early fall, drops precipitously and continues to decline over the winter, and then recovers during the spring;[22] The litters of red squirrels are typically born in April or May. These observed patterns of *time* expenditure on food-related activities are consistent with our qualitative predictions about *energy* expenditure on such activities (see panel (b) of our Figure 2). Similar information about the food-related activity of gray squirrels (*Sciurus carolinensis*) during the year is reported in Hougart and Flyger [1981]. Information on the timing of various food-related activities for gray squirrels is reported in Thompson and Thompson [1980]. They note that storage behavior begins in August and peaks in October.[23] Food recovery begins in October and continues until May.[24]

These empirical studies typically report the *time* devoted per month to various food-related activities. In contrast, our theoretical model predicts the *energy* expended in food-related activity. Nonetheless, as a first approximation, the time required to pursue food-related activity should be roughly proportional to the energy expended in such activity. An alternative and more precise way to link our predictions to the observed data also seems possible. Recall that our model predicts the amount of food harvested, stored, and retrieved, and consumed in each period of the season. It seems to us feasible to determine empirically the time required to find, store, retrieve, or consume one unit of food during different phases of the season. This information could then be included as exogenous inputs in our model and would permit prediction of the time spent in each period on each food-related activity or the aggregate time per period spent on these activities, the series reported in the empirical studies.

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[21]As long as the maximand is independent of the state variables, the co-state variable associated with each strictly positive state variable will still rise by a fixed percentage $(1/\beta\theta)$ in each period and, given concavity, each decision variable will still be a continuous function of the co-state variables. For an example of how a large system with these characteristics can be solved, see [Salant, 1982].

[22]For a monthly series, see Table 3 of [Tonkin, 1983]. Tonkin also reports on how the body-weight of red squirrels varies over time.

[23]Thompson and Thompson distinguish among different types of food items and report a period between mid-October and mid-December when a minor amount of storage and retrieval occur at the *same* time. Such behavior cannot occur in our model as it is currently formulated; but it could occur if we were to distinguish among the stockpiles of different foods.

[24]For monthly time profiles of each activity, see Figures 3 and 4 of their paper.

17

Data on most input parameters for these animals have not yet been collected.[25] Indeed, a singular contribution of a model (ours or any other) is that it *identifies* which input variables are predicted to influence observed behaviors.

As a simplification, we have treated as given certain variables which a full-fledged theory of hoarding should explain. For example, an animal can either store food in a central location ("larder hoarding") or scatter it in a variety of locations ("scatter hoarding"). The literature surveyed by Vander Wall catalogs different strategies for preparing, transporting, placing, and concealing stored food. Assuming that more than one of these hoarding strategies is feasible for a particular animal, it is reasonable to ask why an observed strategy has evolved.

Our model is easily extended to address this question. Each hoarding strategy outlined above results in a different cache-loss parameter (θ) and requires different amounts of energy to store and retrieve $(\alpha_n$ and $\alpha_r)$. As a first approximation, it seems reasonable to assume that there are a finite number of such strategies.[26] In that case, our model can be used virtually without change to explain why one feasible hoarding strategy rather than any of the feasible alternatives is adopted in a given environment. For the observed end-of-year storage, each hoarding strategy induces a distinct optimal path of behaviors in our model and results in a distinct maximized value of the objective function. Our theory predicts that the hoarding strategy which leads to the *largest* maximized value of the objective function is the one which evolution will favor.

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[25]A notable exception is estimates of θ. Thompson and Thompson [1980] and others have conducted experiments which yield estimates of the proportion of stored food which is retrievable after various time intervals.

[26]Alternatively, one could parameterize the hoarding strategies by a continuous variable and treat it like any other decision variable in the Kuhn-Tucker problem.

Appendix 1: Optimal Time Paths Before and After the Onset of Winter

In this appendix, we show how the decision variables A_t, H_t, R_t, N_t, and C_t can be deduced as functions of λ_t for λ_t in any of four possible regions.

Region 1:
In region 1, $N_t = H_t = 0$, $A_t > 0$ and $R_t > 0$. The following conditions must hold (the numbers refer to the Kuhn-Tucker conditions in the text);

$$U'(R_t) - \lambda_t\theta - \gamma_t\alpha_r = 0 \qquad (2)$$

$$A_t - \alpha_r R_t = 0 \qquad (8)$$

$$F'(A_t) = \gamma_t \qquad (10)$$

Combining (2), (8), and (10) we obtain:

$$U'(R_t) - \lambda_t\theta - F'(\alpha_r R_t)\alpha_r = 0.$$

This uniquely defines R_t (implicitly) as a strictly decreasing function of λ_t.
In addition, (10) implies:
$$A_t = \alpha_r R_t.$$

Hence A_t is a strictly increasing function of R_t and, therefore, a strictly decreasing function of λ_t. Since $N_t = H_t = 0$, $C_t = R_t$. Hence every decision variable depends in region 1 on λ_t. As λ_t increases in region 1, R_t, A_t, and C_t strictly decrease.

Region 2:
In region 2, $N_t = 0$, $H_t > 0$, $A_t > 0$, and $R_t > 0$. The following conditions must hold:

$$U'(H_t + R_t) - \gamma_t\alpha_{h(t)} = 0 \qquad (1)$$

$$U'(H_t + R_t) - \lambda_t\theta - \gamma_t\alpha_r = 0 \qquad (2)$$

$$A_t - \alpha_{h(t)}H_t - \alpha_r R_t = 0 \qquad (8)$$

$$F'(A_t) = \gamma_t \qquad (10)$$

After subtracting (2) from (1) and simplifying, we obtain:

$$\gamma_t = \frac{\lambda_t\theta}{\alpha_{h(t)} - \alpha_r}.$$

Inverting (10), we find:

$$A_t = F'^{-1}(\gamma_t) = F'^{-1}\left(\frac{\lambda_t\theta}{\alpha_{h(t)} - \alpha_r}\right).$$

Hence A_t is a strictly increasing function of λ_t in region 2. Since $C_t = H_t + R_t$, (1) implies

$$C_t = U'^{-1}(\gamma_t\alpha_{h(t)}) = U'^{-1}\left(\frac{\lambda_t\theta\alpha_{h(t)}}{\alpha_{h(t)} - \alpha_r}\right).$$

Hence in region 2, C_t is a strictly decreasing function of λ_t.

Finally, from (8), we obtain:

$$H_t = \frac{A_t - \alpha_r C_t}{\alpha_{h(t)} - \alpha_r}$$

$$R_t = \frac{\alpha_{h(t)} C_t - A_t}{\alpha_{h(t)} - \alpha_r}.$$

Since A_t and C_t are uniquely determined by λ_t so are H_t and R_t. In region 2, as λ_t increases over time H_t strictly increases while R_t strictly decreases.

Region 3:

In region 3, $R_t = N_t = 0$, $A_t > 0$, and $H_t > 0$. The following conditions must hold:

$$U'(H_t) - \gamma_t \alpha_{h(t)} = 0 \tag{1}$$

$$A_t - \alpha_{h(t)} H_t = 0 \tag{8}$$

$$F'(A_t) = \gamma_t \tag{10}$$

Combining (1), (8), and (10) we conclude:

$$U'\left(\frac{A_t}{\alpha_{h(t)}}\right) - F'(A_t)\alpha_{h(t)} = 0.$$

Hence A_t in region 3 is independent of λ_t and is constant if $\alpha_{h(t)}$ is constant. From (8)

$$H_t = \frac{A_t}{\alpha_{h(t)}}$$

Moreover, since $C_t = H_t + R_t - N_t$, $C_t = H_t$. Note that in region 3, $N_t = R_t = 0$ and A_t, H_t, C_t remain constant provided $\alpha_{h(t)}$ is constant.

Region 4:

Throughout region 4, $H_t > 0$, $N_t > 0$, $A_t > 0$ and $R_t = 0$. The following conditions hold in region 4:

$$U'(H_t - N_t) - \gamma_t \alpha_{h(t)} = 0 \tag{1}$$

$$-U'(H_t - N_t) + \lambda_t \theta - \alpha_n \gamma_t = 0 \tag{3}$$

$$A_t - \alpha_{h(t)} H_t - \alpha_n N_t = 0 \tag{8}$$

$$F'(A_t) = \gamma_t \tag{10}$$

Adding (1) and (3), we obtain:

$$\gamma_t = \frac{\lambda_t \theta}{\alpha_{h(t)} + \alpha_n}.$$

Hence γ_t is a strictly increasing function of λ_t. Inverting (10) and substituting, we obtain:

$$A_t = F'^{-1}(\gamma_t).$$

Since A_t is a strictly increasing function of γ_t, A_t is a strictly increasing function of λ_t in region 4. Noting that $C_t = H_t - N_t$ in region 4, and inverting (1) we obtain:

$$C_t = U'^{-1}(\alpha_{h(t)}\gamma_t).$$

Hence C_t is a strictly decreasing function of γ_t and thus a strictly decreasing function of λ_t in region 4. Finally using (8) we conclude:

$$H_t = \frac{A_t + \alpha_n C_t}{\alpha_{h(t)} + \alpha_n}$$

and

$$N_t = \frac{A_t - \alpha_{h(t)} C_t}{\alpha_{h(t)} + \alpha_n}.$$

Hence N_t is a strictly increasing function of λ_t in region 4. H_t is the sum of a decreasing function and an increasing function of λ_t. As λ_t increases in region 4, A_t and N_t strictly increase, C_t strictly decreases, and H_t may either increase or decrease.

Defining the Boundaries of Each Region

In region 1, $H_t = 0$; in region 2, $H_t > 0$ and strictly increases. Equations (2), (8), and (10) hold in both regions, but equation (1) which must hold with equality when $H_t > 0$, need not hold in region 1. To determine the boundary between region 1 and 2, we find that value for λ_t, denoted $\lambda_{1,2}$, such that $H_t = 0$ in region 2. Since

$$H_t = \frac{A_t - \alpha_r C_t}{\alpha_{h(t)} - \alpha_r}$$

$$H_t = 0 \quad \Longrightarrow \quad \alpha_r C_t = A_t$$

$$\text{or} \quad \alpha_r U'^{-1}\left(\frac{\lambda_{1,2}\theta\alpha_{h(t)}}{\alpha_{h(t)} - \alpha_r}\right) = F'^{-1}\left(\frac{\lambda_{1,2}\theta}{\alpha_{h(t)} - \alpha_r}\right).$$

This equation uniquely defines $\lambda_{1,2}$. The boundary, $\lambda_{1,2}$, changes over time only if $\alpha_{h(t)}$ changes.

In region 2, $R_t > 0$ and strictly decreases; in region 3, $R_t = 0$. Equations (1), (8), and (10) hold in both regions but equation (2), which must hold with equality when $R_t > 0$, need not hold in region 3. To determine the boundary between regions 2 and 3, we find that value for λ_t, denoted $\lambda_{2,3}$, such that $R_t = 0$ in region 2. Since in region 2

$$R_t = \frac{\alpha_{h(t)} C_t - A_t}{\alpha_{h(t)} - \alpha_r}$$

$$R_t = 0 \quad \Longrightarrow \quad \alpha_{h(t)} C_t - A_t = 0$$

$$\text{or} \quad \alpha_{h(t)} U'^{-1}\left(\frac{\lambda_{2,3}\theta\alpha_{h(t)}}{\alpha_{h(t)} - \alpha_r}\right) = F'^{-1}\left(\frac{\lambda_{2,3}\theta}{\alpha_{h(t)} - \alpha_r}\right).$$

This equation uniquely determines $\lambda_{2,3}$. The boundary, $\lambda_{2,3}$, changes over time only if $\alpha_{h(t)}$ changes.

In region 3, $N_t = 0$; in region 4, $N_t > 0$. Equations (1), (8), and (10) hold in both regions but equation (3), which must hold with equality when $N_t > 0$ need

21

not hold in region 3. To determine the boundary between regions 3 and 4, we find that value for λ_t, denoted $\lambda_{3,4}$, such that $N_t = 0$ in region 4. Since in region 4

$$N_t = \frac{A_t - \alpha_{h(t)} C_t}{\alpha_{h(t)} + \alpha_n}$$

$$N_t = 0 \quad \Longrightarrow \quad A_t = \alpha_{h(t)} C_t$$

$$\text{or} \quad F'^{-1}\left(\frac{\lambda_{3,4}\theta}{\alpha_{h(t)} + \alpha_n}\right) = \alpha_{h(t)} U'^{-1}\left(\frac{\alpha_{h(t)}\lambda_{3,4}\theta}{\alpha_{h(t)} + \alpha_n}\right).$$

This equation uniquely determines $\lambda_{3,4}$. The boundary, $\lambda_{3,4}$, changes over time only if $\alpha_{h(t)}$ changes.

Next we verify that
$$\lambda_{1,2} < \lambda_{2,3} < \lambda_{3,4}.$$

Reconsider the equation defining $\lambda_{1,2}$. Geometrically it can be regarded as the intersection of a downward-sloping function of λ and an upward-sloping function of λ.

Reconsider the equation defining $\lambda_{2,3}$. Notice that it too can be regarded as defined by the intersection of an upward and a downward-sloping functions of λ. Indeed, the upward-sloping function in each case is identical:

$$F'^{-1}\left(\frac{\lambda\theta}{\alpha_{h(t)} - \alpha_r}\right).$$

However, the downward-sloping function defining $\lambda_{2,3}$ lies uniformly above the downward-sloping function defining $\lambda_{1,2}$ since

$$\alpha_{h(t)} U'^{-1}\left(\frac{\lambda\theta\alpha_{h(t)}}{\alpha_{h(t)} - \alpha_r}\right) > \alpha_r U'^{-1}\left(\frac{\lambda\theta\alpha_{h(t)}}{\alpha_{h(t)} - \alpha_r}\right).$$

This implies that $\lambda_{2,3} > \lambda_{1,2}$.

Next, reconsider the equation defining $\lambda_{3,4}$. It can be regarded as the intersection of an upward-sloping function of λ and a downward-sloping function of λ. Note that the upward-sloping function defining $\lambda_{3,4}$ is uniformly smaller than the upward-sloping function defining $\lambda_{2,3}$:
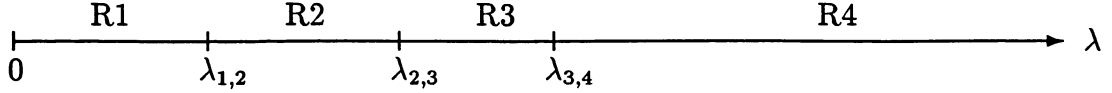
$$F'^{-1}\left(\frac{\lambda\theta}{\alpha_{h(t)} + \alpha_n}\right) < F'^{-1}\left(\frac{\lambda\theta}{\alpha_{h(t)} - \alpha_r}\right)$$

Note also that our assumptions (A2, A3, A5 and A9) jointly imply that $\alpha_{h(t)}$ uniformly exceeds α_r. Hence, the downward-sloping function defining $\lambda_{3,4}$ is uniformly larger than the downward-sloping function defining $\lambda_{2,3}$:

$$U'^{-1}\left(\frac{\alpha_{h(t)}\lambda\theta}{\alpha_{h(t)} + \alpha_n}\right) > U'^{-1}\left(\frac{\alpha_{h(t)}\lambda\theta}{\alpha_{h(t)} - \alpha_r}\right)$$

This implies that $\lambda_{3,4} > \lambda_{2,3}$.

The following diagram illustrates how the intervals fit together:

22

$$\vdash\!\!\!\!\!+\!\!\!\!\!\!-\!\!\!\!\!\!+\!\!\!\!\!\!-\!\!\!\!\!\!+\!\!\!\!\!\!-\!\!\!\!\!\!\longrightarrow \lambda$$

0 $\lambda_{1,2}$ $\lambda_{2,3}$ $\lambda_{3,4}$

These boundaries are ordered in this way regardless of the value of $\alpha_{h(t)}$.

For simplicity, consider the case where $\alpha_{h(t)}$ is constant until the onset of winter and then jumps up to a new constant level. Consider the equations defining $\lambda_{1,2}$. When $\alpha_{h(t)}$ jumps up, the upward-sloping function shifts down while the downward-sloping function shifts up. Consequently, the boundary, $\lambda_{1,2}$ jumps up. For the same reason, the boundary $\lambda_{2,3}$ must jump up. As a result λ_t can increase by $\beta\theta$ at the onset of winter and nonetheless transit from region 4 to region 1 or 2 as discussed in the text.

A Condition Sufficient for No Hibernation

To conclude this appendix, we show that if the inequality in A6 were reversed, there could be no transition to region 1 at the onset of winter.

If $\alpha_{h(t+1)} < \frac{\alpha_{h(t)}}{\beta\Theta} + (\alpha_r + \frac{\alpha_n}{\beta\Theta})$, the transition will be to region 2. By hypothesis

$$\beta\Theta < \frac{\alpha_{h(t)} + \alpha_n}{\alpha_{h(t+1)} - \alpha_r}.$$

Hence

$$\beta\Theta = \frac{\lambda_t}{\lambda_{t+1}} < \frac{\alpha_{h(t)} + \alpha_n}{\alpha_{h(t+1)} - \alpha_r}.$$

Therefore,

$$\alpha_{h(t)} U'^{-1}\left(\frac{\lambda_t \Theta \alpha_{h(t)}}{\alpha_{h(t)} + \alpha_n}\right) > \alpha_r U'^{-1}\left(\frac{\lambda_{t+1}\Theta\alpha_{h(t+1)}}{\alpha_{h(t+1)} - \alpha_r}\right).$$

Recall that since $\lambda_t > \lambda_{3,4}$

$$\alpha_{h(t)} U'^{-1}\left(\frac{\alpha_{h(t)}\lambda_t\Theta}{\alpha_{h(t)} + \alpha_n}\right) \leq F'^{-1}\left(\frac{\lambda_t\Theta}{\alpha_{h(t)} + \alpha_n}\right).$$

Hence

$$\alpha_r U'^{-1}\left(\frac{\lambda_{t+1}\Theta\alpha_{h(t+1)}}{\alpha_{h(t+1)} - \alpha_r}\right) \leq F'^{-1}\left(\frac{\lambda_t\Theta}{\alpha_{h(t)} + \alpha_n}\right).$$

But the boundary $\lambda_{1,2}^{t+1}$ implicitly solves

$$\alpha_r U'^{-1}\left(\frac{\lambda_{1,2}^{t+1}\Theta\alpha_{h(t+1)}}{\alpha_{h(t+1)} - \alpha_r}\right) = F'^{-1}\left(\frac{\lambda_{1,2}^{t+1}\Theta}{\alpha_{h(t+1)} - \alpha_r}\right).$$

Suppose $\lambda^{t+1} \leq \lambda_{1,2}^{t+1}$. Then

$$\alpha_r U'^{-1}\left(\frac{\lambda_{t+1}\Theta\alpha_{h(t+1)}}{\alpha_{h(t+1)} - \alpha_r}\right) \geq F'^{-1}\left(\frac{\lambda_t}{[\alpha_{h(t+1)} - \alpha_r]\beta}\right)$$

or

$$F'^{-1}\left(\frac{\lambda_t\Theta}{\alpha_{h(t)} + \alpha_n}\right) \geq F'^{-1}\left(\frac{\lambda_t}{[\alpha_{h(t+1)} - \alpha_r]\beta}\right).$$

23

But since $F'^{-1}(\cdot)$ is increasing and $\beta\Theta < \frac{\alpha_{h(t)}+\alpha_n}{\alpha_{h(t+1)}-\alpha_r}$, this inequality cannot hold. Therefore, $\lambda^{t+1} > \lambda_{1,2}^{t+1}$.

A necessary condition for a transition to region 1 is therefore that $\alpha_{h(t+1)} \geq \frac{\alpha_{h(t)}+\alpha_n}{\beta\Theta} + \alpha_r$. We assume that this inequality holds in A6.

Appendix 2: Uniqueness of the Solution to the Necessary Conditions

Any optimal program must satisfy the Kuhn-Tucker conditions. Moreover, since the constraint set is the intersection of convex sets, it is a convex set; and since the maximand is a weighted sum of utility functions each of which is weakly concave in the decision variables $\{A_t, C_t, H_t, N_t, R_t, S_t\}_{t=1}^{T}$, the maximand is a weakly concave function of these variables. It follows from the Kuhn-Tucker sufficiency theorem that any solution to the conditions is a global optimum. This (by itself) does not assure that the optimal program is unique. But it does assure that every solution must achieve the same (highest) feasible value for the maximand.

Next, it can be shown that every optimal program has the *same* consumption sequence and activity sequence. Consider two optimal programs. Denote the first by tildes ($\sim$) and the second by daggers ($\dagger$):

$$\{ \ \tilde{C}_t, \quad \tilde{A}_t, \quad \tilde{H}_t, \quad \tilde{N}_t, \quad \tilde{R}_t, \quad \tilde{S}_t \}_{t=1}^{T} \quad \text{and} \quad \tilde{S}_{T+1}$$

$$\text{and} \quad \{ \ C_t^{\dagger}, \quad A_t^{\dagger}, \quad H_t^{\dagger}, \quad N_t^{\dagger}, \quad R_t^{\dagger}, \quad S_t^{\dagger} \}_{t=1}^{T} \quad \text{and} \quad S_{T+1}^{\dagger} .$$

Let $\psi \in [0,1]$. Define the mixture program $\{C_t^{\psi}, A_t^{\psi}, H_t^{\psi}, N_t^{\psi}, R_t^{\psi}, S_t^{\psi}\}_{t=1}^{T}$ and S_{T+1}^{ψ} as follows:

For $t = 1, ... T$

$$
\begin{aligned}
C_t^{\psi} &= \psi \tilde{C}_t + (1 - \psi) C_t^{\dagger} \\
A_t^{\psi} &= \psi \tilde{A}_t + (1 - \psi) A_t^{\dagger} \\
H_t^{\psi} &= \psi \tilde{H}_t + (1 - \psi) H_t^{\dagger} \\
N_t^{\psi} &= \psi \tilde{N}_t + (1 - \psi) H_t^{\dagger} \\
R_t^{\psi} &= \psi \tilde{R}_t + (1 - \psi) R_t^{\dagger} \\
S_t^{\psi} &= \psi \tilde{S}_t + (1 - \psi) S_t^{\dagger} \\
\text{and} \quad S_{T+1}^{\psi} &= \psi \tilde{S}_{T+1} + (1 - \psi) S_{T+1}^{\dagger} .
\end{aligned}
$$

It is straightforward to show that since each optimal program satisfies a given linear constraint, so must the mixture program. To illustrate,

$$
\begin{aligned}
\tilde{A}_t &= \alpha_{h(t)} \tilde{H}_t + \alpha_r \tilde{R}_t + \alpha_n \tilde{N}_t \\
\text{and} \quad A_t^{\dagger} &= \alpha_{h(t)} H_t^{\dagger} + \alpha_r R_t^{\dagger} + \alpha_n N_t^{\dagger}
\end{aligned}
$$

since each optimal program satisfies the constraint. Multiplying the first inequality by $\psi \geq 0$ and the second by $(1 - \psi) \geq 0$, adding, and using the definitions of the mixture program we can verify that

$$A_t^{\psi} = \alpha_{h(t)} H_t^{\psi} + \alpha_r R_t^{\psi} + \alpha_n N_t^{\psi} .$$

Hence, the mixture program satisfies this constraint. Repeating this procedure for each constraint, we can verify that the mixture program is feasible. Suppose now that either $\{\tilde{C}_t\}_{t=1}^{T} \neq \{C_t^{\dagger}\}_{t=1}^{T}$ or $\{\tilde{A}_t\}_{t=1}^{T} \neq \{A_t^{\dagger}\}_{t=1}^{T}$. Then since the maximand,

$$\sum_{t=1}^{T} \beta^t \{U(C_t) - F(A_t)\},$$

is *strictly* jointly concave in $\{C_t\}_{t=1}^{T}$ and $\{A_t\}_{t=1}^{T}$ and since for any $\psi \in (0,1)$ the mixture program $\{C_t^{\psi}\}_{t=1}^{T}$, $\{A_t^{\psi}\}_{t=1}^{T}$ would not be identical

to either consumption and activity sequence, the mixture program must achieve a strictly higher payoff. But since the original two programs are by assumption optimal, no feasible program can dominate them. It follows that $\{\tilde{C}_t\}_{t=1}^T = \{C_t^\dagger\}_{t=1}^T$ and $\{\tilde{A}_t\}_{t=1}^T = \{A_t^\dagger\}_{t=1}^T$.

In principle, it is still possible that there might exist two or more optimal programs which generate the identical consumption and activity sequences but differ in some *other* variables $\{H_t, N_t, R_t, S_t\}_{t=1}^T$ or S_{T+1}. Indeed, if $\alpha_r = \alpha_n = 0$ (contradicting A7), there would in fact be a continuum of optimal programs with this characteristic. To verify this, add the constant K to N_t and R_t to generate a new program. *Provided* $\alpha_r = \alpha_n = 0$, N_t and R_t enter everywhere in the objective function and constraints only as the difference $(N_t - R_t)$. Since this difference would not be affected by the addition of K to each term, the new program is also feasible and would generate the same consumption sequence as the original optimal program. Hence, it is also optimal.

Given A7, however, $\alpha_r > 0$ and $\alpha_n > 0$. Then it can be verified that there exists a unique optimal program

$$\{C_t, A_t, H_t, N_t, R_t, S_t\}_{t=1}^T \text{ and } S_{T+1} \ .$$

Suppose there were two distinct optimal programs. Suppose the tilde program begins with $\tilde{S}_1 = 0$, changes at $t^* + 1$ to $\tilde{S} > 0$ and returns at t^{**} to $\tilde{S}_{t^{**}} = 0$. Until t^*, the tilde program is in region 3. It then must migrate to region 4. At t^{**} it must return to region 3. Now consider the dagger program. It too starts with $S_1^\dagger = 0$. If it has the corresponding consumption and activity in each period, then it must likewise remain in region 3 until t^*. Hence $\tilde{N}_t = N_t^\dagger = 0, \tilde{R}_t = R_t^\dagger = 0$ and $\tilde{S}_t = S_t^\dagger = 0$ until t^*.

At t^*, both programs must migrate to region 4. For, if only the tilde program migrated, then $\tilde{A}_t^* > A_{t^*}^\dagger$ and the activity sequences would be unequal. Moreover, if $\tilde{C}_t = C_t^\dagger$ and $\tilde{A}_t = A_t^\dagger$ then since both C and A are the same monotonic functions of λ (as shown in Appendix 1), $\tilde{\lambda}_t = \lambda_t^\dagger$. But as long as $S_t > 0$ the growth of λ_t is uniquely determined. Hence $\tilde{\lambda}_t = \lambda_t^\dagger$ for $t = t^*, ..., t^{**} - 1$. Since, as Appendix 1 indicates, the value of every variable at t can be determined uniquely as a function of λ_t, the two solutions must be identical in all respects until t^{**}.

At this point $\tilde{S}_{t^{**}} = S_{t^{**}}^\dagger = 0$ and both programs return to region 3. Since this was where we started, the argument can simply be repeated. To conclude, there exists a unique optimal program which satisfies the Kuhn-Tucker conditions.

References

Becker, G. (1965) "A Theory of the Allocation of Time," *Economic Journal,* **75**, 493-517.

Brody, J. (11/19/91) "A Hoarder's Life: Filling the Cache–And Finding It," *New York Times,* , C1.

Hotelling, H. (1931) "The Economics of Exhaustible Resources," *Journal of Political Economy,* **30**, 137-75.

Hougart, B. and V. Flyger (1981) "Activity Patterns of Radio-Tracked Squirrels," *Wildlife Society,* , 11-16.

Salant, S. and D. Henderson (1978) "Market Anticipations of Government Policy and the Price of Gold," *Journal of Political Economy,* **86**, 627-48.

Salant, S. (1982) "Imperfect Competition in the International Energy Market: A Computerized Nash-Cournot Model," *Operations Research,* **30**, 252-80.

Sherry, D. (1990) "Storage Ecology," *Science,* **250**, 1602-3.

Thompson, D. C. and P.S. Thompson (1980) "Food Habits and Caching Behavior of Urban Grey Squirrels," *Canadian Journal of Zoology,* **58**, 701-710.

Tonkin, J. M. (1983) "Activity Patterns of the Red Squirrel," *Mammal Review,* **13**, 99-111.

Vander Wall, S. (1991) *Food Hoarding in Animals.* Chicago: University of Chicago Press.

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