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CHAPTER 7

An Evolutionary Ecology Perspective on Diet Choice, Risk, and Plant Domestication

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Most models of plant domestication and the origins of agriculture assign causal primacy to one or more generalized, normative¹ variables (or “prime movers”; summary in Redding 1988:57–60). Examples are population, climate change affecting resource abundance or distribution, technological innovation, and energy-extraction efficiency. Typically these variables describe system-level properties and they are characterized by well-behaved mathematical averages. Population grows, climate shifts, technological proficiency improves, or energy use expands. Processes of change are removed from the daily decisions of individual ecological actors, and they are continuous and gradual. The agroecological and socioeconomic consequences cited in these models are the result of broad adaptive responses to steady changes in material conditions as the population moves from food gathering to food production.²

In this chapter we shift perspective and use evolutionary ecology models to examine the possible consequences for agricultural origins of localized decisions about resource selection. We approach the question of domestication through foraging models, beginning with a brief description of some key assumptions and concepts of that approach. We use the diet-choice model to show how resource selection decisions could bring foragers into contact with potential domesticates and how this might affect population density and subsistence risk. We turn to hunter-gatherers and show that sharing and regional exchange have evolved as highly effective responses to unpredictable day-to-day success in the food quest. We then show that the field dispersion common

to nonindustrial farmers functions to reduce risk in the same manner as does sharing among hunter-gatherers.

The heart of the argument is more speculative. We try to envision the evolutionary transformation from foragers who buffer risk primarily by sharing to farmers who mitigate it by field dispersion. To provide empirical moorings to this exercise, we review the record of agricultural origins in eastern North America in terms of our scenario. Next, we briefly compare aspects of our approach with several other recent models. Our summary highlights some strengths of microecological analysis of prehistoric economies and their transformations (Winterhalder 1993).

Domestication as an Evolutionary Question

In the usual approach to domestication a change in the key variable (e.g., population growth) poses an adaptive opportunity or challenge (e.g., food stress). One or more of the properties of agriculture known to result from domestication (e.g., greater productivity per area) are posited as a response to the opportunity or as a solution to the problem. We believe that this manner of conceptualizing the issues has three liabilities that can be mitigated using evolutionary ecology models: (a) it engages an adaptationist-functionalist form of argument that is less powerful than a more direct selectionist approach; (b) it focuses attention on the particular variable (e.g., climate) to the neglect of its adaptively salient properties (e.g., unpredictable variability); and (c) it tends to focus on highly generalized variables, deflecting attention from the actual subsistence choices faced by foragers-becoming-farmers.

Our alternative perspective (a) adopts evolutionary ecology models, (b) encompasses nonnormative properties of the environmental variables affecting subsistence adaptations, and (c) locates the key processes in the immediate and localized decisions routine to the economic lives of the actors. Because of their importance, we state each of these points as a principle, followed by brief elaboration and the references containing the fuller justification.

PRINCIPLE 1: *Selection-based explanations are more powerful than functionalist (or the closely related adaptationist) explanations.*

In most accounts the domestication of plants or animals is explained as an adaptive response to an environmental challenge (e.g., resource

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shortages caused by overpopulation or climate change). The advantages of cultivating plants or husbanding animals (e.g., increased yield) thus account for the origins of the practice. In general, the form is that of a functionalist argument: a benefit of the feature is presumed to explain its origin. Although widespread in the biological and social sciences, functionalist analyses are fraught with logical and empirical pitfalls (Elster 1983). In particular, they usually are not subject to a causal theory explaining how benefits act to produce the trait.

Many of these pitfalls can be avoided by paying careful attention to theoretical or methodological underpinnings. In Elster's (1985) terms this means using aspects of methodological individualism to illuminate system microfoundations. In evolutionary ecology it means that analyses that begin with selection³ and that attempt to deduce its consequences for behavior in specified environmental circumstances have proved more powerful than analyses that begin by trying to correlate possible functions or benefits with observed behaviors (Winterhalder and Smith 1992). Developed prehistoric agriculture may have had any number of advantages. However, the analysis that begins with the advantages attributed to mature agricultural systems may already have hopelessly obscured their possible causal effects during the process of domestication or the inception of agricultural production. In addition, the theoretical framework of evolutionary ecology places constraints on the types of benefits and beneficiaries that are plausible (Smith and Winterhalder 1992). For instance, it tells us to be skeptical of arguments that cite system stability as a benefit, large-scale aggregates (groups) of individuals as the exclusive beneficiaries, or future benefits as causal.

PRINCIPLE 2: *Analyses that include the nonnormative properties of an environmental variable are preferable to those that do not.*

Most accounts of domestication and agricultural origins rely on normative environmental analysis. The material conditions of life are set against an ecological background of shifting mean conditions. This approach has merit but underestimates the evolutionary importance of unpredictable or irregular temporal variation and spatial heterogeneity (Winterhalder 1980). It leads to an overemphasis on the source of the stress to the neglect of its properties. Description in terms of properties is especially important because it can be linked to general models of adaptive responses (e.g., Halstead and O'Shea 1989). Often the pattern of environmental variability—its frequency, duration, magnitude, spa-

tial scale, and predictability—determines the qualities of a successful coping mechanism.

PRINCIPLE 3: *The more immediate a variable to the actual conditions and options experienced by an individual organism, the more likely it will be of causal importance in evolutionary analysis.*

The broad sweep of global climate change appears as if it invokes processes of analytical scope equal to the task of explaining so widespread and profound an economic change as agricultural origins. But prehistoric individuals did not face decisions in terms of climate change. The real stuff of evolutionary profundity lies in the local factors of an organism's experience: the constraints it faces, its actions, and the consequences of those actions. Immediate details have the greatest causal efficacy in the evolutionary explanation of adaptive design. Given analyses stated in terms of (a) changing climate, (b) changing habitat structure or distribution, (c) changing abundance of resources, or (d) changing prey selection or work efficiency, we should automatically prefer the last over the first. This will be true even if ecosystem processes link (d), (c), (b), and ultimately (a). The changes that we summarize under broad concepts such as *domestication* and the *Neolithic revolution* have their origin and form in the ecologically situated choices and actions of individuals.

Slobodkin (1973) makes a like point in a short essay critical of claims that ecosystems maximize some property such as ecological efficiency or constancy (we can add homeostasis, energy utilization, complexity, etc.). Slobodkin's reasoning turns on the differences between "extensive" and "intensive" variables. Extensive variables are those measures that summarize populationwide, interspecific (community level), or long-term (multigenerational) aspects of things biological. They refer to (emergent) properties unique to sets of organisms. Extensive variables such as ecosystem efficiency or complexity rarely find a causal role in evolutionary ecology models because they are not factors directly subject to the action of selection at the level of individuals. Intensive variables by contrast are those that characterize the behavior of an individual at a particular place and time. They refer to the situated properties of the organisms making up ecological sets; they potentially are subject to the direct action of selection. Examples include prey or habitat choice, time allocation, or reproductive tactics.

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Slobodkin's injunction, "[T]he genesis of things which we believe to be the consequences of evolution . . . ought to be stateable in intensive, or local, variable terms" (Slobodkin 1973:299), is useful to us because it can guide first-order preferences among models of agricultural origins even if the empirical basis for such a choice is limited. It should immediately make us wary of any model of domestication or agricultural origins that relies on extensive variables. If empirical observations were to confirm that ecosystems (including agroecosystems) maximize efficiency, complexity, or such, we would take an interest in that fact but would attempt to explain it first as the outcome of interactions among intensive variables.

These three principles are related and reinforcing. For instance, Slobodkin's distinction between extensive and intensive variables (Principle 3) turns on the same theoretical and methodological guidance that allows us to discriminate in accepting evolutionary benefits and beneficiaries (Principle 1). An agricultural origins model that cites system-level energy maximization is suspect under both principles because it is difficult to reconcile with the workings of evolutionary processes. Likewise, to cite a shift in mean environmental conditions (Principle 2) is to state a mathematical abstraction at best weakly coercive relative to the fluctuating, patchy environment experienced by individuals.

Our commitment to an evolutionary perspective is complementary to that of Rindos (1984), who argues that domestication developed through processes of coevolution between human beings and the resources they exploited. As a consequence of harvesting certain species, hunter-gatherers became unintentional agents of dispersal, protection, pollination, and so forth. This altered selective pressures on the foragers and the plants, leading to behavioral and morphological changes, respectively. We believe that foraging theory can supply hypotheses on questions that the Rindos model neglects: What circumstances led human beings to select certain species for exploitation? What are the economic and population processes that accompany growing dependence on domesticates and cultivation?

Envisioning a Transformation

Foraging models are theoretically consistent with the principles outlined earlier (Smith and Winterhalder, eds. 1992), and they allow us

to analyze the processes that brought human beings into regular contact with species that through coevolution became domesticates. The formulation that follows joins two other preliminary applications of evolutionary ecology models to this problem (Hawkes and O'Connell 1992; Layton and Foley 1992; Layton et al. 1991; Winterhalder and Goland 1993).

The Diet Breadth Model

Central to our analysis is the issue of resource choice. The diet breadth (resource selection) model is the oldest and best known model of foraging theory (MacArthur and Pianka 1966; Schoener 1974; Stephens and Krebs 1986). It sometimes is called an "encounter-contingent" model, because it draws a conceptual distinction between searching for an acceptable food item and the pursuing and handling of different food types. Search costs are a function of resource density (encounter rates with acceptable items); pursuit and handling costs are peculiar to each resource type. The forager searches for all resources simultaneously. Upon encounter with a potential dietary item he or she must make a contingent assessment: pursue the present resource or continue searching in hopes of locating a more attractive one to pursue.⁴

In practice resources are ranked by their decreasing net efficiency for the pursuit and handling phase of foraging (figure 7.1). The top-ranked resource always is in the diet. The model determines how far down the ranked list the "optimal" forager will go. The summary rule is this: add the next item if its pursuit and handling efficiency is greater than the overall foraging efficiency of the diet without it and, conversely, stop expanding the diet and ignore the first item for which the return on pursuit and handling is less than the average return for search, pursuit, and handling of higher-ranked items.

Several additional results are of special interest. First, items of high enough rank to be in the forager's diet should always be pursued if encountered, however rare they might be. Conversely, those with a ranking that puts them outside of the diet should never be pursued, no matter how common. Second, as the abundance of highly ranked items diminishes, overall foraging efficiency declines and the diet will expand stepwise to include items of lower rank. The changing marginal rate of foraging efficiency determines whether the item at the boundary of the diet moves into or out of the optimal set. Third, any change that increases the pursuit and handling efficiency of an unharvested resource

The following example demonstrates important features of the diet breadth model (see Winterhalder et al. 1988).

The table immediately below shows the characteristics of eight hypothetical resources. The items range in size (energy value) from APREY (comparable, say, to a small ungulate) to HPREY (comparable to a tuber). In addition to energy value, each resource type is described by its average pursuit and handling time, the forager's energy expenditure rate during pursuit and handling, and its density (a component of encounter rates).

Resource Characteristics

Resource Type	Energy Value (kcal)	Pursuit/Handle Time (min)	Pursuit/Handle Cost (kcal/min)	Resource Density (#/sq km)
APREY	60000	1864	6	0.8
BPREY	24000	836	6	2.6
CPREY	13800	235	6	8.0
DPREY	3600	95	6	6.4
EPREY	2800	174	6	12.0
FPREY	1500	67	6	40.0
GPREY	240	26	6	300.0
HPREY	90	7	6	500.0

Three further variables jointly determine how quickly and efficiently the forager can locate potential resources. The forager's search velocity and width affect his or her rate of encounter with resources of varying densities; the caloric cost of the searching has been set at 4 kcal/min, roughly the energy expenditure of a walking human.

Forager Characteristics

Forager's velocity of movement:	0.500 (km/hr)
Forager's search width:	35.0 (m)
Forager's search cost:	4.000 (kcal/min)

Figure 7.1. The diet breadth model.

Figure 7.1. *Continued*

Analysis 1 (below) shows how the diet breadth model treats this data. Resource types (column 1) are ranked (column 2) by their decreasing net return rates for pursuit and handling. Because rank is a net measure per unit time, it need not correlate directly with size of the resource type. Column 3 shows the overall foraging efficiency that would result from a diet breadth that begins with only the first item (CPREY, a diet breadth, or db, = 1) and successively adds additional resources through HPREY (db = 8).

At db = 1, the forager's efficiency is 965.3 kcal/hr. Although CPREY returns more than 3100 kcal/hr when located, it is rare, and searching for it exclusively is quite costly. Overall foraging efficiency can be increased to 1062.8 kcal/hr by adding DPREY to the diet. Though this is a less profitable item, the forager more than compensates by reduced search costs as more resource encounters produce acceptable items. The same is true of APREY and BPREY, but addition of the fifth item, FPREY, results in a decline in foraging efficiency from 1209.9 kcal/hr to 1160 kcal/hr. Expansion to items of yet lower rank causes further declines in overall foraging efficiency.

Analysis 1

Name	Rank (kcal/hr)	Full Density Foraging Efficiency (kcal/hr)	60% Density Foraging Efficiency (kcal/hr)
CPREY	3163.4	965.3*	602.5*
DPREY	1913.7	1062.8*	691.2*
APREY	1571.3	1165.1*	827.4*
BPREY	1362.5	1209.9*	925.9*
FPREY	983.3	1160.4	941.6*
EPREY	605.5	1079.6	882.4
HPREY	411.4	948.6	775.1
GPREY	193.8	719.1	579.3

The peak foraging efficiency at db = 4 establishes an optimal diet of species C, D, A, and B (all marked with an asterisk [*]). Even if encountered, FPREY (or any item of yet lower rank) returns less energy for the time spent pursuing and handling it than the forager can expect from exploiting only the top four resources. The cost of picking up these suboptimal items is seen in the declining foraging efficiency for a db > 4.

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Figure 7.1. *Continued*

Column 4 shows how changing resource encounter rates can affect the optimal diet. In this instance, the densities of resource types A through D have been reduced by 40% (to 0.48, 1.56, 4.80, and 3.48/sq km, respectively). This increases search costs and lowers overall foraging efficiency so that FPREY enters the optimal diet. Its pursuit and handling efficiency (983.3 kcal/hr) is now greater than the foraging efficiency for a diet breadth of only four items (925.9 kcal/hr).

A suboptimal resource item can also move into the optimal diet through an increase in rank. In Analysis 2 (below) the pursuit and handling time of FPREY has been reduced by 20% (to 53.6 minutes). No other variables have been changed. FPREY's pursuit and handling efficiency increases from 983.3 kcal/hr to 1319.1 kcal/hr, enough to move it into the optimal diet. Note that overall foraging efficiencies are the same for diet breadths up to 4 items, but a new peak foraging efficiency (1229.9 kcal/hr) is established with FPREY in the diet at $db = 5$.

Analysis 2

Name	Rank (kcal/hr)	Full Density Foraging Efficiency (kcal/hr)
CPREY	3163.4	965.3*
DPREY	1913.7	1062.8*
APREY	1571.3	1165.1*
BPREY	1362.5	1209.9*
FPREY	1319.1	1229.9*
EPREY	605.5	1135.5
HPREY	411.4	989.1
GPREY	193.8	742.1

above the marginal foraging efficiency will move that item into the optimal set (see figure 7.1).

Diet Selection and Domestication

We begin our scenario by positing a resource (one, for simplicity, a plant we label TD, for transitional domesticate) that has a pursuit and

handling efficiency that is somewhat too low to make it an element in the optimal diet. We presume a decrease, for any of a variety of reasons, in the abundance of more highly ranked species. This lowers the marginal efficiency of foraging sufficiently that resource TD enters the diet and becomes subject to coevolutionary pressures such as described by Rindos (1984). Following foraging theory, these pressures can be separated for analytical purposes into those that affect ranking and those that affect density. The former profitability changes might correspond to ease of harvesting or processing (e.g., size of a cereal grain); density changes might reflect growth conditions (e.g., inadvertent human effects such as clearing or soil enrichment). Although it can be ambiguous in practice, we will show that this analytical distinction between density and pursuit and handling profitability is an important one.

Figure 7.2 allows us to examine the possible outcomes of this coevolutionary relationship. We begin with the case in which TD is low in density. Its ranking (profitability) slowly increases with coevolution. When it first enters the diet (*cell 3*; low rank, low density) it has a limited impact on the subsistence economy. However profitable it may be, it is infrequently encountered and harvested. It makes up a small portion of the foods consumed. Its use has little effect on the exploitation of more highly ranked items. In fact, little about the foraging situation will change as TD coevolves to a position of low density and high rank. Neither the list of other species exploited (diet selection), nor the degree of their exploitation, nor the density of the foragers should change significantly. Thus, even if it is a species subject to some degree of human management, a low-density resource might be absorbed into a forager's diet without causing any striking changes in the existing hunter-gatherer economy. This situation corresponds to incidental domestication in Rindos's terms (1984:138-66). We will observe below that some premaize indigenous domesticates in eastern North America may have followed just this pattern.

Imagine, however, that the TD is very abundant (*cell 1*; low rank, high density). By foraging logic it will be ignored despite its density until a decline in overall foraging efficiency (or elevation of its rank) brings it within the optimal diet. Once in the diet, however, its economic impact will be relatively great. Although of limited profitability, its high yield will initiate forager population growth (see Winterhalder and Goland 1993). With a relatively dense human population sustained by a prolific if marginally profitable TD, high-ranking resources (those

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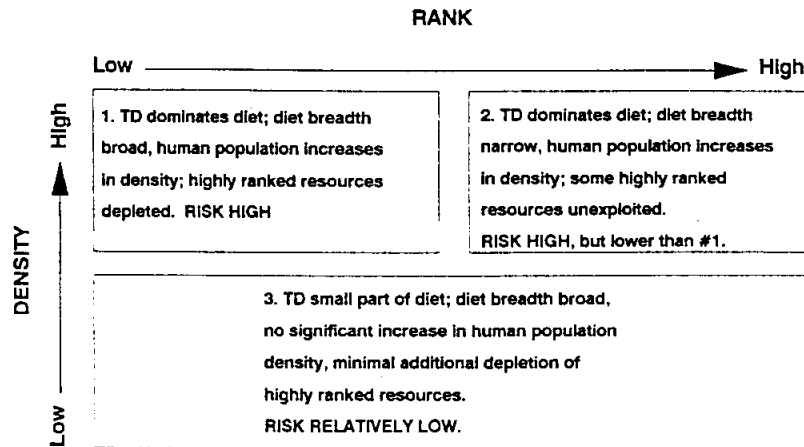


Figure 7.2. Model of plant domestication.

within the optimal diet) are likely to be overexploited and depleted. They are always worth capturing or harvesting when encountered. If some of these resource populations are locally extinguished the diet breadth may narrow. However, even if there is no local extinction, high-ranked items will become rare in the diet as their populations shrink. The foraging-becoming-agricultural population of cell 1 may find its subsistence regime dominated by the TD.⁵ If the TD fluctuates stochastically in yield, the human population's risk will increase just as the option of compensating through the harvest (and perhaps sharing) of foraged foods is disappearing.

Cell 1 makes it evident that a minor change in the marginal efficiency of foraging can have quite significant economic ramifications, if the expanding diet happens to pick up an item of relatively high yield. Again referring to the Rindos (1984:138-66) terminology, this situation of relatively sudden dependence on a domesticate sets the stage for "specialized domestication."

In the last instance (*cell 2*; high rank, high density), we again posit that the profitability of the TD increases through coevolutionary processes. As in the case of cell 1, the diet will become dominated by the TD. However, the number of resources harvested will diminish as previously exploited foods are excluded from the optimal diet by the abundant and highly ranked TD. Risk will be high—the growing human

population is increasingly dependent on the TD—but not so high as in cell 1. The items once harvested but now excluded from the diet constitute relatively profitable fallback foods. However, even at unexploited levels of population density, their yield might not long sustain a human group that has grown dense on the potential of a high-density TD in its most prolific years.

The overexploitation and depletion of foraged resources predicted in cells 1 and 2 may help to explain why domestication has strong elements of irreversibility (see also Layton et al. 1991:261) and why food production would spread once initiated in a locality. We note that it also is possible that rank and abundance both begin low and increase together, the coevolutionary direction moving from cell 3 to cell 2. In this intermediate scenario the impacts of a high-yield TD will develop much more gradually.

Evolutionary Ecology and Risk

The plant and animal resources of both foragers and farmers are subject to drought, flood, frost, epidemic, and other irregular calamities. In either system an adequate local food supply can be precarious. Episodes of scarcity are recurrent. Both foragers and farmers require adaptations that mitigate the effects of unpredictable subsistence shortfalls, and it is likely that these adaptations have quite dissimilar manifestations and consequences in the two economic modes. We suggest that there is much to be learned by considering how the structural parameters of risk and the effectiveness of alternate risk-buffering strategies change in the transition from food gathering to food production.

Because short-term yields are probabilistic, each subsistence choice can be characterized by an average reward and a variance. Risk reduction models demonstrate how foragers or farmers can select the mean/variance combination that maximizes the probability of survival by avoiding critical energy shortfalls. One of the clearest formulations of this approach is the *Z*-score model (Stephens 1990; Stephens and Charnov 1982). This model is based on a normal distribution, described in terms of an average harvest rate or income (m), the variability of income (s , measured in standard deviations), and a minimum requirement or critical threshold (R). The probability of falling below the minimum requirement is Z (the standard normal deviate), where $Z = (R - m)/s$. Risk is minimized as the value of Z decreases (figure 7.3).

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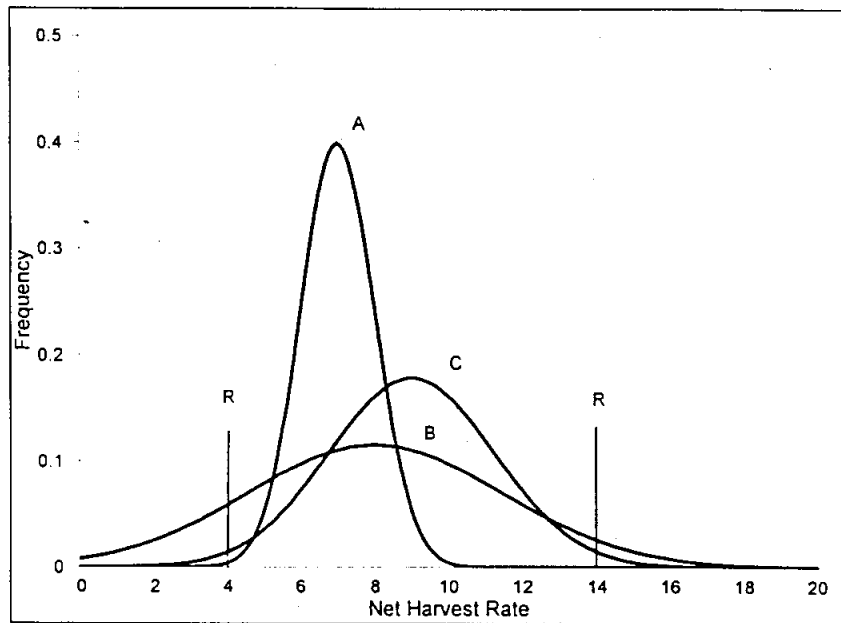


Figure 7.3. The Z-score model. Shown is the frequency distribution of net harvest rates for three resource options, with means and standard deviations as follows: (A) 7 and 1; (B) 8 and 3.5; and (C) 9 and 2.2. If $R = 4$, then the low-variance option (A) minimizes the chance of dropping below that value even though it also has the lowest average net harvest rate. If $R = 14$, then the high-variance option (B) offers the best (but not good) odds of success, even though it has a lower average return than option (C).

The model shows that the appropriate choice for enhancing probability of survival is dependent on the forager's minimum income requirement (R) and on the statistical properties (mean, m , and standard deviation, s) of the resource choices. When short-term requirements are greater than expected mean reward ($R > m$), the forager might do better to pursue more variant (high s or "less predictable") resource options, since they provide the greatest likelihood of fulfilling extraordinary requirements. Conversely, if needs are lower than expected rewards ($R < m$), as is more likely to be the case, probability of survival may be increased by selecting the less variant resource option (low s), even though it may on average yield less energy than another choice. As we describe below, the Z-score model summarizes the relevant considerations for both foraging and agricultural societies (Winterhalder 1990).

Foragers, Sharing, and Exchange

Hunter-gatherers face fluctuations in the encounter and successful capture of game on a day-to-day basis. To a lesser extent the same kind of irregular variation will affect the availability and yield of plant foods. In terms of the Z-score model, we expect a forager to select the set of resources that, by a combination of high average return rate (m) and low variance (s), minimizes the chances of falling below a critical threshold (R). However, simulation modeling (Winterhalder 1986) has shown that foragers may be able to reduce only modestly their risk of food shortfalls by this means. Even the optimal selection of resources to minimize risk may not efficaciously avoid it. For instance, in the common situation in which $m > R$, adjustments to reduce variance (thus the probability of a deleterious shortfall) typically also sacrifice average foraging efficiency. Thus even as the offending left tail of the food acquisition distribution (figure 7.3) gets pulled away from dangerously low levels, the whole curve shifts toward lesser return rates.

Intraband sharing, or the regular pooling of food captured by individuals foraging separately, is a highly effective means of overcoming this constraint (Winterhalder 1986). It requires only that the success rates of those contributing to the pool are unsynchronized (that is, not strongly positively correlated). Sharing groups with as few as six to eight productive foragers gain the greater part of the marginal benefits that result from this tactic. Given the ubiquity of environmental fluctuations in the lives of foragers, it is quite reasonable to view risk minimization as an explanation for the sharing routinely observed in this mode of production (Kaplan and Hill 1985).

If resources fail simultaneously over the whole range of a foraging band, then the remedy available through pooling and spatial asynchrony must be sought at a regional scale. Smith (1991) has explored the conditions that make exchange among bands located in different regions an effective means of risk reduction. Most often this entails the temporary movement of foragers from areas of shortfall to those of greater abundance. These residential shifts depend on a system of land tenure that Smith terms *reciprocal access*, and although the costs and benefits can be subtle, in general such arrangements appear to be quite efficacious.

Other risk-buffering tactics available to foragers appear to be less effective. Carryover averaging (short-term storage) by a single forager is mathematically equivalent to intraband sharing among a group of

foragers. However, it would take an individual practicing this tactic six to eight foraging intervals, some of them unsuccessful and hungry, to gain the same benefit achieved daily within a sharing group of six to eight individuals. In addition, carryover averaging entails processing costs and storage losses that do not affect intraband sharing. The ecological conditions under which long-term storage will be an effective counter to periodic scarcity are also fairly restricted for hunter-gatherers (Goland 1991). Periods of resource scarcity and high yield must alternate with regularity over long periods if storage is to become an important and routinized aspect of hunter-gatherer economies. In good years quite high yields must be attained, both to provision the population at a level that will permit extended residence at the storage locale and to provide the surplus for processing, storage, and storage losses. Because of such constraints, storage is infrequent among ethnographically documented hunter-gatherers.

Of the five options (resource selection, intraband sharing, regional movement, short-term carryover averaging, and long-term storage), sharing and regional movement appear to be the most effective for foragers. Empirical findings confirm that both act as effective risk-buffering strategies. Kaplan and Hill (1985), for instance, found that food sharing among Aché foragers occurs when (1) individuals experience fluctuations in yield, sometimes acquiring foods of higher energetic value than can be immediately utilized by an individual or family, and (2) returns of foraging among individuals are not highly (positively) correlated. Aché foragers most frequently share meat and honey, precisely the resources that are unpredictably and infrequently encountered and that provide more calories than can be consumed by an individual at one time. As a consequence of sharing, all Aché group members eat a diet that is more predictable than any of them would be able to capture on their own. Smith (1991) describes ethnographic cases of risk-buffering through reciprocal access. Prehistoric foragers presumably adopted similar mechanisms.

Food Producers and Field Dispersion

The same Z-score model that illuminates the situation of foragers has a direct analog among food producers: pooling of resources from spatially dispersed plots that are likely to have unsynchronized yields.

Field dispersion characterizes nonindustrial agriculture in much of the world. Agricultural economists and economic historians usually

have depreciated this arrangement as wasteful and inefficient. They point to the costs of moving labor and materials among small, scattered parcels. The economic historian Donald McCloskey (1975, 1976) has explored instead the potential risk-reduction benefits of field dispersion. He uses the example of the open-field system found in the Medieval Midlands of England. Each year families planted wheat or barley in up to a dozen dispersed plots within the common fields of the manor. Other household fields were left in fallow. McCloskey demonstrates that given the localized vagaries of weather and pathogens, along with other spatially heterogeneous or "patchy" qualities of the agricultural landscape, a harvest that pooled yields from dispersed locations provided a more secure living. He calculates that compared with results from a single consolidated field, scattering doubled the probability of surviving twenty years without a subsistence calamity; it tripled that probability for a thirty-year interval. McCloskey's analysis shows that the greatest gains in risk reduction can be achieved by pooling the yields of about eight fields. His "safety first" model is a direct analog of the Z-score approach.

In the contemporary, high-altitude Andean communities of Cuyo Cuyo that we have studied (Goland 1992a, 1992b), families each year plant as many as two dozen scattered agricultural plots. These are dispersed across a topographically rugged landscape in which many of the agroecological factors affecting production (precipitation, edaphic conditions, pest infestations, etc.) are patchy and unpredictable. Yields from individual potato fields vary widely. If families were to rely on a single large plot rather than multiple smaller ones, the coefficient of variation of their production (standard deviation/mean $\times$ 100) would be about 75. As their holdings are broken into dispersed fields the coefficient of variation drops steadily. For three fields it averages 43; for six fields, 21. This is a striking benefit. We also have measured the costs of field dispersion that arise from added travel and transport. They reduce net productivity by 7%,⁶ a noteworthy loss for a community on the margin of adequate production, but not an unduly large one.

With both the benefits and costs considered, frequency of disaster (which we define as failure to attain a critical threshold of calories) shows dramatic reduction as a household's fields are scattered. Of nineteen families studied, twelve reduced their probability of disaster to 0% by cultivating multiple fields. Under a hypothetical scenario of consolidated production these same families had probabilities of cata-

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strophic shortfalls between 12.5% and 57.1% in the year sampled. Each of these families has minimum requirements (disaster thresholds) lower than the average potato yield for their fields. They illustrate the first half of the rule of thumb generalized from the Z-score model: if you can expect more than your requirement, choose the small variance subsistence option or, in this case, plant more scattered fields.⁷

A field that produces well one year may yield poorly the next. Cuyo Cuyo families cannot predict in advance of planting (even well into the agricultural season) how each of their fields will produce nor do they have the flexibility to disperse quickly or consolidate their landholdings. Given these constraints, an effective solution to subsistence risk is a scattered field system. Despite the added 7% cost, in a situation of marginal production and high risk like that experienced by Andean peasants, field dispersion dramatically reduces the odds of household production calamities.

The risks facing an agricultural household were presumably no less in prehistory than for contemporary farmers living in marginal environments. Nor, despite being situated in high mountain terrain, does the Peruvian case appear exceptional when compared with the degree of interannual subsistence variance and (intraannual) asynchrony documented for the Midlands of England. This raises the possibility of strong selective pressures for field dispersion or a comparable risk-reducing mechanism during the nascent stages of agricultural production.

Subsistence Risk During Domestication

We can now ask about risk as the various changes depicted in figure 7.2 take place. In the low-density cell (cell 3) incorporation of the TD into the diet causes no changes that would impede the risk-reducing effectiveness of sharing, exchange, or temporary, regional migration. Diet breadth remains broad and human population density presumably is low and relatively stable. The mean and variance of foraging efficiencies should change only modestly; exploitation pressure on harvested resource species does not jump dramatically. We propose that low-density TDs will function economically more or less like the undomesticated resource items in the repertoire of the hunter-gatherer.

However, in the high-density cases (cells 1 and 2) we must consider several new elements: human population density increases and humans grow increasingly dependent on one or a few species and thus more

susceptible to their stochastic fluctuations. In addition, alternative food sources are either depleted by overexploitation (cell 1) or, even if unharvested (cell 2), perhaps less able to mitigate a food crisis afflicting a high-density human population. The type of pooling practiced by foragers will have diminished effectiveness, producing selection for alternatives.

The changes that will occur are constrained by two structural elements that also will be shifting in this transition. One is temporal and the other spatial. First, although there can be strongly seasonal elements to the food quest of foragers, typically their production interval is measured in days. From start to conclusion in success or failure, several complete production episodes (hunting trips, gathering expeditions) can take place before hunger would begin to debilitate the forager. The temporal scale of consumption roughly matches that of the production cycle. However, as annual crops begin to dominate the diet of temperate-zone agriculturalists, the production interval lengthens to a year. Months pass between planting and harvest; only near or at harvest is the success or failure of the productive effort fully evident. Months more may pass before another planting can be initiated. The temporal scale of production for food producers in a seasonal environment is much greater than that of consumption.

This difference in production interval has at least two consequences for the present argument. First, long-term temporal averaging will not be as effective for food producers simply because they cannot survive through several failed production intervals (whereas foragers, with their short production interval, might survive). Larger processing costs and greater storage losses that accompany the longer period (months or years versus days) needed for temporal averaging among agriculturalists further reduce the attractiveness of this option. Second, any pooling strategy is vulnerable to the impact of cheaters, the laggards who slack off on their own efforts but who receive a full share of the combined effort. Hunter-gatherer groups certainly face this problem, but for foragers the relatively short duration of the production interval allows for quick assessment, sanction, and correction before imbalances grow too large. Detection of a free rider will be significantly more difficult for farmers, who might inadvertently subsidize a shirking neighbor for years before being able to detect his or her deficiencies. Likewise, correction through social control may be more difficult when the production interval is measured in years.

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The second structural element that differs in the two cases is the spatial dispersion opportunities. The one or two active foragers of a hunter-gatherer domestic unit are constrained in their ability to take advantage of unpredictable and spatially uncorrelated resource opportunities. This is because the foraging mode of production is both immediate and active, requiring the presence "on the spot" of the hunter-gatherer. The forager realizes the resource possibilities of a location only by being there at the right time. Effective spatial averaging requires intraband pooling. Farmers do not face this constraint. By dispersing fields a lone farmer can gain all of the advantages of spatial pooling from multiple environmental sites. Production at a particular locality does not require the individual's presence, except for periodic attentions of plant cultivation as the growing season progresses, and these can be staggered. In short, an individual forager cannot be hunting and gathering in six places at once; the farmer, however, can plant, manage, and harvest fields that are in six dispersed locations. Foragers are constrained to pool on an intraband basis; farmers have the option of adopting an interhousehold (perhaps at the village or kin level) or an intrahousehold approach.

Despite this option, we propose that populations increasingly dependent on a few high-yield domesticates will face selection pressures to move risk management within the household. Temporal averaging (beyond routine, seasonal storage) is costly because it implies a large surplus above annual needs, high processing costs, and potential losses in food that must be stored for several years. The free-rider problem is exacerbated by the long production interval and denser population, which thereby reduces the attractiveness of interhousehold pooling. We hypothesize that in the circumstances of early agricultural production the costs of intrahousehold field dispersion (say, 7% to 10% of net production) were less than the free-rider costs attached to continued interhousehold pooling. We envision the transition accompanying the origins of agriculture to be one in which interhousehold sharing eventually was supplanted by intrahousehold field scattering (supplemented initially or eventually by regional trade). We propose that community controls and social relations among early farming households were aimed primarily at organizing dispersed production opportunities rather than interhousehold distribution. We again draw on our Andean research to provide an example.

Field scattering in the Andes is associated with sectorial following

systems (Orlove and Godoy 1986). Households manage the production process through community-level coordination of planting schedules and rotations. Agreement on the initiation of planting dates ensures that animals will be removed from the zones slated for cropping, thereby reducing the probability that they will damage crops. Coordination of crop rotations also reduces the threat of pest and disease infestations and soil depletion. Community-level controls associated with the sectorial system regulate rights in the control, use, and transfer of property in land. They protect isolated fields, which are vulnerable to theft and other depredations. We propose that early agricultural communities are under strong selection pressures to develop similar coordination mechanisms, especially if households claim and invest in multiple, dispersed fields.

Social relations among households are key in the allocation of labor in agricultural communities. We earlier noted that fields do not require continuous presence, supervision, or input. Nonetheless, production is constrained by peak periods of labor demand (planting, harvesting) at key points in the agricultural cycle. In the Andes, shortages of workers within the household are met by interhousehold labor exchanges that draw on mutual assistance (*ayni*). These relations provide the fabric for community functioning and reproduction. In contrast to the case for hunter-gatherers, social relations in these agricultural communities are built on seasonal reciprocities of labor rather than on continuous reciprocities of food.

We predict that field scattering built around sectorial rotation systems or their equivalent would have characterized early agricultural communities, with these or like implications for social structure and interhousehold political life. The regional exchange mechanisms emphasized by archaeologists (see Rindos 1989) may have augmented these mechanisms or may have appeared somewhat later, coincident with the development of regional sociopolitical organization. Yet later, centralized political administration (e.g., the Inca State) may have complemented or supplanted these household-level means of insurance. The specific hypothesis that we have proposed is set within a more general and somewhat separable claim, to the effect that changing patterns and sources of subsistence risk may have been more important to socioecological adaptation during the origins of agriculture than were changing production efficiencies.

Discussion

In the following discussion we set our proposal in the context of plant domestication and agricultural origins in eastern North America, compare it briefly with three other recent models of plant domestication, and comment critically on the widespread use of energy efficiency to frame questions about agricultural origins.

Plant Domestication in Eastern North America

Although opinion has shifted several times during the past century, since the mid to late 1980s the consensus has held that eastern North America was an independent center of plant domestication. The earliest possible domesticates include bottle gourd (*Lagenaria siceraria*) and gourd/squash (*Cucurbita pepo*). The former has been identified in archaeological contexts as early as 7300 B.P. (Doran et al. 1990); its status as a domesticate at this early date has not yet been clearly determined. A stronger case can be made for domesticated *Cucurbita pepo*. Fragments of *Cucurbita* have been recovered from archaeological contexts as early as 7000 B.P. (Smith 1992b). Some researchers (e.g., Asch and Asch 1985b) believe that these early occurrences represent an introduced tropical cultigen; others (e.g., Decker 1988; Fritz 1990 and this volume; Smith et al. 1992; Watson 1985) feel that these represent a native wild gourd, independently domesticated after 3000 B.P. in the eastern United States. Support for the great antiquity of this taxon north of Mexico is provided by the occurrence of *Cucurbita pepo* seeds from preoccupation levels associated with Pleistocene megafauna at the Page-Ladson site in northern Florida (Newsom et al. 1993). The domesticated status of three other species is more secure. These are the oily-seeded sumpweed (*Iva annua*: see Asch and Asch 1978, 1985b; Ford 1985; Yarnell 1972, 1978, 1986) and sunflower (*Helianthus annuus*: see Ford 1985; Yarnell 1978, 1986) and the starchy-seeded chenopod (*Chenopodium berlandieri*: see Fritz and Smith 1988; Smith 1984, 1985a, 1987a; Smith and Cowan 1987). The evidence for domestication of sumpweed and sunflower rests on increased achene size (Asch and Asch 1985b; Smith 1989; Yarnell 1978). Domesticated *Chenopodium* is recognized by reduction in the thickness of the seed coat and associated morphological changes (Fritz and Smith 1988; Smith 1984, 1985a, 1989; Smith and Cowan 1987). These plants were regularly harvested in small quantities in their

wild form perhaps as early as 8000–7000 B.P. By 4000–3000 B.P. they had been brought into cultivation and had undergone morphological changes indicative of domestication. Throughout this long period of use and cultivation they appear to have made only a modest contribution to the diet (Gremillion 1993c, 1994; Smith 1989).

Several other native plants were also regular components of the prehistoric diet, but it is less certain that they were domesticates. They are identified as possible crops because they are recovered from archaeological contexts well beyond their natural geographic ranges or in quantities great enough to suggest harvest of managed stands. Cases have been made on archaeological, ecological, and/or geographical grounds for prehistoric cultivation of maygrass (*Phalaris caroliniana*) (Cowan 1978a), giant ragweed (*Ambrosia trifida*) (Fritz 1990), little barley (*Hordeum pusillum*) (Watson 1989), and erect knotweed (*Polygonum erectum*) (Asch and Asch 1985b; Fritz 1990). As yet, however, no clear-cut morphological indicators of domestication have been identified for these plants.

Several recent hypotheses about plant domestication in eastern North America (e.g., Smith 1987b, 1992c; Watson 1989) have incorporated elements of Anderson's (1952) "dump heap" theory. Smith (1987b, 1989) subsumes this idea within a coevolutionary framework like that proposed by Rindos (1984), with climate change as the initial trigger. He argues that Hypsithermal warming (from 8000 to 4000 B.P.) led to changes in stream flow and alluvial deposition patterns that resulted in the formation of more productive aquatic habitats in the midcontinental area. Because of this enrichment of river valley resources, floodplain locales were visited more frequently and occupied for longer times than during earlier periods. The net effect of these two trends was to foster the development of anthropogenic habitats (which Smith terms *domestilocalities*).

Smith believes that plant cultivation and domestication occurred in these contexts. In this process, the significant properties of the *domestilocalities* included increased sunlight, enhanced soil fertility, continual soil disturbance, and the constant introduction of seeds. Weedy colonizers invading *domestilocalities* were subjected to selection pressures that produced two changes: seed production was increased and seed dormancy decreased. Both improve a plant's competitiveness in the disturbed habitat (see also King 1987). Neither of these changes re-

quires human intervention but each makes a plant more attractive because they enhance its economic potential.

According to Smith, once people began to utilize a plant they became agents of intervention in its life cycle. At first inadvertently, for example, through creation of disturbed habitats and dispersal of seeds, human beings encouraged the growth of plants with economic potential. Eventually interventions became intentional, leading to husbanding activities such as weeding. This reduced interspecies competition and may have increased the stand of the quasicultigen plant. Planting seed was the next significant step. Harvesting by human beings of planted areas and replanting of harvested seeds automatically selected for increased seed retention and more compact, terminalized seed heads, along with uniform seed maturation, which led to greater harvest yields. Seed bed competition selected for reduced dormancy, more rapid growth, and increased seed size. Smith believes this accounts for the morphological changes observed on specimens of sumpweed, chenopod, and sunflower dating from the period 4000–3000 B.P.

In the last half of the third millennium B.P., economies based on significant food production emerged in the Midcontinent. Though not all were utilized in every region, the main plant foods were the domesticates gourd/squash, chenopod, sunflower, and sumpweed; crops such as knotweed, maygrass, giant ragweed, amaranth, and little barley were also economically important in many localities. But despite their long period of cultivation and use, the native domesticates never dominated the diet (Ford 1981; Watson 1989). Throughout the Archaic and subsequent Woodland periods, up to about A.D. 1000 (late Late Woodland), the inhabitants of the Midcontinent essentially maintained a foraging economy, relying on wild foods, especially nuts, and terrestrial or aquatic fauna. Thus native crops did not become significant food sources until long after their domestication. Smith (1989) suggests that these garden crops provided an important storable resource for the critical late winter–early spring period when alternate food supplies were low.

There are scattered identifications of maize in the archaeological record beginning in the Middle Woodland period. The earliest occurrences are dated to 2017 ± 50 and 2077 ± 70 B.P. at the Holding site in the American Bottom of Illinois (Riley et al. 1994), 1775 ± 100 B.P. at the Icehouse Bottom site in Tennessee (Chapman and Crites 1987), and

1730 $\pm$ 85 and 1720 $\pm$ 105 B.P. at the Edwin Harness site in Ohio (Ford 1987). Although maize is present in archaeobotanical assemblages infrequently and in small quantities for roughly 600 years (Smith 1989; Yarnell 1993; Keegan and Butler 1987), in collections dating to about 800 B.P. its archaeological visibility begins to increase dramatically. By A.D. 1150 maize-centered field agriculture emerged across much of the Eastern Woodlands, sometimes accompanied by beans and squash, though the importance of these two crops was variable throughout the region (Smith 1992c; Watson 1989). Skeletal studies of dietary patterns parallel the archaeobotanical record of maize (Fritz 1990; Smith 1989; Wagner 1986). For example, in west central Illinois carbon isotope data indicate that maize was present for several centuries before it became a substantial component of the diet (Buikstra et al. 1987). Thus maize may have been an experimental or minor garden crop during the initial 400- to 600-year period of its use, but after ca. 1000 B.P. (depending on the region) maize production was intensified, field agriculture became more extensive, and maize came to dominate the food production system (Fritz 1990; Smith 1992c).

Considering this evidence on prehistoric domestication in light of our model will shed light on the interrelationships of resource density, rank, diet breadth, and risk. We leave aside consideration of early squash and bottle gourd, since these may have been used as containers rather than as dietary staples (however, see Cowan, this volume). The evidence demonstrates that sumpweed, sunflower, and chenopod exhibited morphological indications of domestication by 4000–3000 B.P. We propose that after they initially entered the diet they were exposed to the co-evolutionary forces responsible for these changes. We see two possible and nonexclusive pathways to this result. First, following Smith, changes in stream flows and landscape development during the Hypsithermal induced longer-term occupation of localities. Localized depletion of the resources surrounding the occupation sites would result. This depletion, which would require foragers either to travel farther to collect the same quantity of food or to collect foods of lesser caloric value locally, decreased overall foraging efficiency. Diet expanded as foragers incorporated lower-rank resources previously ignored, including the earliest native domesticates. A second scenario posits that the same alteration, increased duration of occupation at bottomland sites, created more disturbed habitats in which the candidate cultigens could invade and thrive, as Smith's "floodplain weed" theory postulates. If their

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growth were favored in these areas, then by virtue of their more proximate location and/or more dense growth, their profitability might rise enough so that they would enter the optimal diet,⁸ initiating the process of domestication under coevolutionary pressures.

By either of these mechanisms, a change in settlement pattern might alter the diet to include early domesticates. However, our model suggests other alternatives (figure 7.4) not requiring alterations of scheduling around the postulated domestilocalities. For instance, a simple reduction in the number of high-ranked resources, whether because of climate, overexploitation, or other causes, would be sufficient to bring foragers into contact with potential domesticates.

With reference to figure 7.2, we posit that the initial native domesticates were low-density resources that remained in the lower cell throughout the long period of their prehistoric use. Even if exploited and grown for several thousand years as domesticates, we expect their impact on diet and economic activities to be limited. The prehistoric record indicates that inhabitants of the Midcontinent maintained a broad-spectrum economy that included hunting and gathering while also cultivating and domesticating plant foods that made a relatively modest contribution to subsistence. We would also expect relatively little change in population density during this long period, a prediction more difficult to assess with empirical evidence. Prehistoric population trends are difficult to identify and quantify and even when recognized are often specific to extremely localized regions.

In contrast, maize was an introduction that eventually achieved the qualities of a highly ranked and potentially dense resource (the upper half of figure 7.2). It came to dominate the diet as human populations increased in density. The prehistoric record indicates that the proportion of the diet composed of maize increased relatively rapidly, beginning about A.D. 800. This would represent a quick shift from cell 3 to cell 1 or 2. Changes in the technology of food production or characteristics of the maize variety itself could be responsible for this development.

Depending on its rank, we can also make specific predictions about the impact that expanding maize dependence had on the exploitation of other food resources: If maize was a low-ranking resource, then diet breadth should remain broad, but other nondomesticated resources of higher rank should show evidence of overexploitation, depletion, and reduced absolute contributions to the diet (cell 1). If maize was (or eventually became) a high-ranking resource, then diet breadth should

Possible Causes of Increased Foraging Efficiency

1. Increase in the density of high-ranked food items (those in the diet), thus the forager's encounter rate, due to habitat improvement, game population cycles, release from over-exploitation, etc.
2. Reduced search costs, perhaps due to decreased energy expenditure in movement.
3. Changes in resource distribution (e.g., resources become more spatially aggregated).
4. Increase of pursuit and handling efficiencies of items in the diet (see below).

Possible Causes of Increased Rank of a Food Item (i.e., increased efficiency in pursuit and handling)

1. Improved transportation in pursuit (e.g., snowshoes, horses, mechanized transport).
2. Improved technology of harvest (e.g., traps, firearms for mobile prey, sickles for plants).
3. Increased capacity for transporting produce (e.g., improved or lighter-weight containers, baskets, pack animals).
4. Improved methods of food processing
 - a. More efficient tools for cutting, cracking, grinding, etc. (e.g., mortar and pestle for removing glumes).
 - b. Better fuels (e.g., hotter burning firewood species).
 - c. Improved technology in heat transfer in cooking (e.g., pottery rather than stone boiling, thin-walled pottery).
5. More effective storage methods (e.g., those that reduce storage loss) or storage facilities that are more efficiently constructed.
6. Morphological changes to the resource increasing its profitability (e.g., tougher rachis so grains hold together at maturity; reduction in toughness of glumes reduces threshing labor, larger fruits).

Figure 7.4. Possible causes of increased foraging efficiency.

narrow as items of lower rank are dropped (and their populations recover from exploitation).

The evidence to test these predictions is inconclusive at present. For example, Fort Ancient populations in the Ohio River drainage appear to have relied heavily on maize to the exclusion of most of the native cultigens (Wagner 1987). In contrast, most archaeobotanical assemblages from other maize-dominated sites demonstrate continued if re-

duced reliance on indigenous crops and wild species of plants and animals (Smith 1992c). Rindos (1989:31-32) notes that introduction of the new maize crop did not exclude cultivation of the starchy and oily seeds. In our terms, this suggests that maize entered the diet as a resource of low rank (cell 1) relative to the seeds, which by then had presumably moved toward the right in cell 3.

Our model leads us to believe that a population's exposure to risk will be significantly altered in the course of the coevolutionary processes of plant domestication. Risk will increase if a single high-density resource dominates the diet (cells 1 and 2). Maize-dominated agriculture may be a prime example (Rindos 1989). Risk will be especially high under conditions described in cell 1, in which a dominant high-density/low-ranked resource is accompanied by broad diet breadth, population increase, and depletion of highly ranked resources. Early farming peoples such as Mississippian populations may have faced greater risk at the same time that they had fewer strategies for buffering shortfalls, on account of population increases, reliance on fewer crops, and a diminished array of wild fallback resources because of environmental deterioration resulting from overexploitation and land clearing (Armstrong et al. 1991; Ford 1977; Rindos 1989; see also Scarry and Steponaitis, this volume).

O'Shea (1989) analyzes the ethnohistoric record for contrasts between risk-buffering mechanisms of the Plains-dwelling Pawnee and the Huron of the Upper Great Lakes. He focuses on the use of wild resources to buffer shortfalls in agricultural production. To be an effective buffer, a nondomesticated must (1) occur in dense patches so that it can be intensively exploited, (2) be storable, (3) exhibit interannual fluctuations in availability that are independent of those affecting agricultural production, and (4) have a pattern of intraannual availability that does not compete with agricultural pursuits and a periodicity capable of buffering seasonal agricultural shortages.

Pawnee subsistence, based on maize agriculture, was vulnerable to droughts and grasshopper infestations. Buffering strategies included the use of scattered fields, interannual storage, and diversification (the regular planting of maize varieties and the use of fallback wild foods in times of emergency). The Pawnee also emphasized social obligations for sharing within the village and for intercommunity exchange. According to O'Shea, the most important risk-buffering strategy was the large mammal hunt, principally of bison. Communal hunts were sched-

uled at times when agricultural labor was not needed, and they regularly provided a storable resource for the winter and early spring months of scarcity. During years when the harvest was poor, the hunts were intensified and could provide an enormous quantity of meat to be dried and stored.

Like the Pawnee, the Huron also depended principally on maize agriculture. Large village fields of corn were supplemented by other domestic crops and wild foods. The principal threats to agricultural production were frosts and drought. Buffering strategies included storage, a diverse subsistence base of crops along with wild plant and animal foods, and exchange between Huron villages and between the Huron and other tribes, but apparently did not include field dispersion. Despite these means, the threat of starvation was real: in the years between 1628 and 1650 severe crop failure was reported once every four or five years. Periodic hunger was a result in part of the lack of appropriate wild resources. The only fallback wild food available to the Huron that fulfills the requirements outlined by O'Shea (1989) was anadromous fish. In normal years the smoked fish from the autumn fishing could see the population through to the spring. In poor agricultural years this resource was insufficient to make up the agricultural shortfall. The amount available for direct consumption or use in exchange was limited by the requirements for processing and transport. Villages were not located near fishing grounds, and the small task groups sent to exploit the fish runs were unable to process and bring back large quantities.

These two examples highlight several important aspects of risk buffering in the midcontinental region. First, field scattering played a role in risk management where clearing was relatively easy (the Plains) and was not used where clearing exacted heavy labor costs and where high-quality soils were patchily distributed (the forested Great Lakes). Second, the Pawnee amplified the benefits of field scattering by pooling resources among production units. By contrast, the Huron planted in large village fields and so the harvests of individual production units would have been essentially identical and intravillage sharing of agricultural products would add little as a measure of security. Third, the ability of a wild resource to buffer agricultural risk depends on the degree to which it can be intensively harvested, processed, and stored. Although, according to O'Shea, the pattern of availability for anadromous fish is independent of the factors responsible for interannual and intraannual variability in agricultural harvests, the Huron's ability to

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utilize this resource to buffer agricultural shortfalls was limited by their capacity to harvest and store it in sufficient quantities.

Finally, the buffering capacity of wild resources depends in part on their potential yield relative to the human population. By late prehistoric times in the Great Lakes region the deer population had been significantly depleted and was thus unable to serve as a fallback resource. In contrast, the success of risk buffering among the Pawnee can be attributed at least in part to low human density relative to the (bison) resource base. As population increases, whether because of dietary improvement (as postulated in our model) or because of other factors (population aggregation for defensive purposes, as in the Huron case), the ability of wild resources to buffer the population from agricultural shortfalls can be diminished. Moreover, low population density in the Plains allowed communities to maintain autonomous territories that included hunting grounds. This territoriality, absent in the Great Lakes, allowed Plains villages to shift adaptive postures easily in order to emphasize hunting rather than agriculture. Low population density is thus also correlated with greater flexibility in responding to production crises.

O'Shea's ethnohistoric reconstruction indicates the importance of risk buffering in the agricultural economy of two early historic-period agricultural groups. The risk of agricultural production is apparent at earlier periods as well, though the evidence is less direct. Throughout the world a sharp decrease in the health of early farmers relative to that of hunter-gatherer forebears is fairly well established;⁹ an increase in the frequency of episodic nutritional stress is less securely documented, but evidence is suggestive (Armélagos 1990; Cassidy 1984; Cohen and Armélagos 1984; Cook 1984; Goodman and Armélagos 1985; Goodman et al. 1984; Larsen 1984; Perzigian et al. 1984). For example, studies of dental enamel pathologic conditions (linear enamel hypoplasias and enamel microdefects) indicate more frequent and/or more severe episodes of stress in early farming populations compared with the hunter-gatherers who preceded them. We suggest that this apparent jump in sporadic food crises corresponds to the period in which high-density domesticates had significantly elevated subsistence risk (cells 1 and 2 in figure 7.2) but before effective risk-management practices had developed. We would expect such a lag because of the sociopolitical complexity of shifting to intrahousehold field dispersion or some other means of risk management.

Related Studies

From the extensive general literature on agricultural origins, we have selected three recent models for brief discussion. We focus on a few salient points of each model in order to sharpen comparison with our own approach.

Flannery and Reynolds (Flannery, ed. 1986:435-507) have designed a complex, semirealistic computer simulation that attempts to replicate the resource collection (scheduling) choices faced by a small microband of transitional foragers at Guilá Naquitz, a prehistoric cave site in the Valley of Oaxaca, Mexico. The model incorporates quantified data on prehistoric resources, their nutritional properties, and their spatial distribution. It allows resources to fluctuate through irregular sequences of wet, normal, and dry years. Members of the hypothetical microband periodically compare their resource-acquisition success (protein-calorie yield relative to effort) with that attained in earlier time units and adjust both the foraging tactics used (the resource-collecting schedule) and their more general rules for appraising success and choosing tactics (decision-making policies). The simulation begins with a randomly selected schedule; as it runs it traces the growing effectiveness of resource-harvesting decisions until a stable plateau is reached. At this point, the simulated band members harvest plant resources in relative proportions nearly the same as those actually documented from the excavated cave deposits.

The Flannery-Reynolds (hereafter FR) model emphasizes the information (knowledge) gained by foragers through trial-and-error learning. Although its authors disavow the term *optimization*, the FR simulation mimics a process of foraging optimization just like that which might be guided by selection: "The group is not instructed to 'optimize' or to 'maximize' any particular variable. They are merely told to make small changes in their foraging strategy each time step, to remember how well each strategy did, and to improve through time by repeating more successful strategies and disdaining less successful ones" (Flannery 1986:501). The second sentence of this citation describes a model that in fact does instruct the microband to optimize its foraging efficiency in precisely the constrained sense used by evolutionary ecology models.¹⁰ There is one operational difference: the FR model replicates a process of optimization whereas an optimal foraging analysis usually assumes that the process will occur and attempts instead to pre-

dict the outcome. This difference aside, our observation that the FR model incorporates an optimization premise is of more than semantic importance because it removes a false distinction that would impede fruitful comparison of the two approaches.

Experiments with the FR simulation show that the rate of improvement in preagricultural scheduling strategies is greatest when variability is present (unpredictable sequences of wet and dry years). By contrast, in their model of incipient agriculture, gradual changes in average climate (slowly increasing humidity or aridity) or population density did not speed the rate at which cultivars were adopted into the plant utilization schedule. In effect, the empirical success of the FR model appears to depend on its incorporating stochastic environmental fluctuations. This independently confirms the importance of Principle 2. Redding (1988:71; discussed below) makes a similar point: "fluctuations have the potential for being a very important factor in the evolution of human subsistence."

Full comparison of the assumptions, formulation, and predictions of the FR approach and evolutionary ecology must await another opportunity and fuller development of the latter. Though the FR simulation is quite unlike anything developed so far by foraging theorists, the premises and form of this simulation are concordant with the principles cited earlier.

A second recent model of domestication and agricultural origins is that of Redding (1988). Redding states premises much like those of evolutionary ecology: he proposes a focus on the selective pressures affecting subsistence choices, is skeptical of group-based functionalist explanations, and gives unpredictable interannual fluctuations in food supplies a key role in his model. He views the transition from foraging to food production as an evolutionary one of shifting subsistence tactics and strategies.

Redding's model mixes population growth and unpredictable resource abundance. He proposes that risk avoidance becomes important as foragers first approach the carrying capacity of their environment because resource fluctuations matter more under conditions of general scarcity. Redding postulates that foragers pass through a sequence of responses. Migration to a more favorable zone is the least expensive and thus the first buffering tactic to be used. Its success elevates the effective carrying capacity of the environment. However, with growth the population again comes under selective pressure of resource fluctuations. Di-

versification is adopted next. Population growth resumes and the cycle repeats with storage being the third response of choice and food production being the final risk-avoidance tactic adopted. In effect, food production is the last-introduced and most costly of a sequential set of risk-mitigating tactics; it is initiated to supplement gathering when all other options for coping with periods of shortfall have been exhausted. Redding states, "Without population pressure and unpredictable, severe depressions in the subsistence base, individuals that invest labor in planting a wild resource or caring for captured animals would be wasting their time; there would be no selective advantage to planting and herding" (Redding 1988:80). For Redding, plant cultivation is the answer to the short-term risks of foraging.

While the Redding study shares premises with evolutionary ecology, in making them operational it appears rather more like the older functionalist-adaptationist models. It is a refinement of the population-as-prime-mover argument: problems of hunter-gatherer population pressure are solved with agriculture. However, in Redding's view, the problem is not one of increasingly severe chronic food shortages. Rather it is one of resource fluctuations that grow in severity as the population approaches carrying capacity. Of possible solutions, agriculture is the last taken up in a sequence of four options that first involve migration, diversification, and storage.

Two further observations will highlight differences between Redding's approach and our own. First, Redding assumes that migration, diversification, storage and finally agriculture are interchangeable means of risk buffering as concerns their properties and that they differ only in their (increasing) costs. We would argue (see above and Halstead and O'Shea 1989) that each of these techniques is suited to different spatiotemporal patterns of resource fluctuations. There is no reason to expect a group in a particular environment to find all of them effective (if differentially costly) or to adopt them in the sequence given. Second, for Redding plant cultivation is the solution to subsistence risk. In our approach the shift to cultivation changes the ecological and economic nature of risk but does not eliminate it. Plant cultivation has its own risks and uncertainties: perhaps exceptional ones early in its evolution. We are skeptical that an activity with unpredictable success over a long production interval can be an effective solution to the short-term fluctuations of foraging success. We prefer to view risk as a condition of

enduring causal importance but differing consequences throughout the transition from food gathering to food production.

The third model we mention is that of Layton et al. (1991; see follow-up comments in Hawkes and O'Connell 1992; Layton and Foley 1992; Winterhalder and Goland 1993). Layton et al. (1991) examine how different social and natural environments produce economies based on foraging, herding, and cultivation or some flexible combination of these subsistence practices. Their discussion brings together an eclectic mixture of environmental and sociopolitical elements that includes optimal foraging theory. They state, "If the cost of relying on high-ranking foods becomes too great, it should be worthwhile for foragers to add lower-ranking foods to their diet" (Layton et al. 1991:255). In their view, various consequences then may follow: the low-ranked resources may become subjected to cultivation in order to increase their yield, the distribution and predictability of the resource base may change such that territoriality becomes a more favorable option, or the human population may increase (Layton et al. 1991:257-60). The last hypothesis is a prediction that also occurs in our model.¹¹

In a reply, Hawkes and O'Connell (1992) show that with closer attention to foraging theory one can question, sharpen, or extend on technical grounds several of the conclusions of Layton et al. (1991). Most of the points made by Hawkes and O'Connell are well taken, but we believe that they are mistaken (and that Layton et al. were correct in their original paper) on the issue of population. Hawkes and O'Connell (1992:64) say this: "Increases in diet breadth result from reduced foraging return rates and so lead to declines in population growth rates . . . sharper growth should be associated not with broader diets but with subsequent increases in handling efficiency associated with practices which result in domestication." We agree that declining foraging rates lead to increased diet breadth, but we believe that they also are consistent with enhanced forager population growth and increased density. The marginal reduction in foraging efficiency that brings such a resource into the diet is less important for population growth than the absolute magnitude of its sustainable yield and hence the population growth it will support (Winterhalder and Goland 1993).

Thus population growth may be associated with broader diets (even at lower foraging efficiencies) as Layton et al. (1991) predict. This effect will be augmented if there also are increases in handling efficiency as

a consequence of coevolution and domestication. This observation allows us to refine a prediction of the diet breadth model that states that so long as highly ranked resources are sufficiently abundant, low-ranked items outside of the optimal diet will be ignored whatever their density. We add that they will also be ignored whatever their sustainable yield (which is a function both of density and intrinsic rate of increase, r). Thus they will be ignored whatever their potential consequences for forager population size. Put another way, from the perspective of foraging theory diet breadth and associated foraging efficiencies are intensive variables subject to (optimizing) selection. In contrast, the ultimate population-level consequences of incorporating a particular resource into the diet are extensive variables subject to the qualifications of Principle 3 (above).

Comparative Production Efficiencies of Foraging and Farming

We conclude with a comment on an issue that more than any other has framed and, we believe, has caused mischief in analyses of agricultural origins: the relative production efficiencies of foraging and farming.

Early models of domestication and agricultural origins assumed that food production was inherently more efficient than food gathering. Comparative evidence suggested that agriculture had such advantages of efficiency that it was an adaptation "waiting to happen," poised for the right combination of human preparedness and environmental circumstance. From this perspective one asked, Why did it take so long? However, with the dramatic revision of anthropological perceptions of hunter-gatherers in the early 1970s the comparative evidence was inverted. Foragers became the "original affluent society" (Sahlins 1972). Suddenly, the energy efficiency and limited effort of foraging looked quite good relative to the low productivity and high labor requirements of primitive agriculture. The new question became, Why would agriculture happen at all? Indeed, prime movers became critical to hypotheses on agricultural origins as anthropologists sought external variables capable of pushing socioeconomic development against the impedance of declining per capita energy efficiency. Why besides externally imposed necessity would foragers give up a secure and comfortable means of production for the uncertainty and drudgery of agriculture?

From an evolutionary ecology perspective either way of framing the question misleads the analysis. Whichever way the comparison falls,

the juxtaposition of before and after production efficiencies to set the causal question places extensive variables at the heart of an evolutionary analysis. This violates Principle 3. The long temporal separation of the economies that define the before/after ratio makes it unlikely that it has causal evolutionary significance. No generation of foragers evolving to food producers faced choices in terms of the relative efficiencies attributed to the two distinct production systems. Energy production and efficiency may have mattered greatly, but they are properly set in terms of intensive variables (e.g., foraging efficiency), and these were generation-by-generation matters of selection among options with marginal differences.

Summary and Discussion

Our speculations to this point have been framed implicitly in the context of seasonal, temperate-zone agriculture, and with reference to "immediate return" (Woodburn 1982) hunter-gatherer societies. Other ecological situations (which differentially affect production interval, dispersion opportunity, and other variables identified here as important) presumably will produce variant outcomes. For instance, heavy use of traps or weirs allows a forager to disperse simultaneous production opportunities over space and thus to act more like a cultivator in adopting intrahousehold risk management. Sharing should be of less importance in such a society. Or, inasmuch as it is aseasonal, with the potential of a continuous harvest, tropical horticulture mimics the short duration of a forager's production interval. Despite heavy reliance on plant domesticates in the diet we might expect these horticultural systems to appear more like foraging societies than temperate-zone food producers. "Delayed return" (Woodburn 1982) hunter-gatherer societies that rely heavily on "seasonal" produce (e.g., salmon runs on the Pacific Northwest coast or acorns in central California) might have socioecologic structures more like those of temperate-zone farmers because of a long production interval. To the extent that evidence for ethnographic diversity can be related to this kind of ecological variability, it will help to test evolutionary ecology approaches to domestication and agricultural origins.

With respect to the processes that we propose accompany the prehistoric origins of agriculture, these summary points are worth emphasis:

1. The profitability (ranking) of a resource should be analyzed separately from its yield (density and intrinsic rate of increase) because these two variables have quite different ecological consequences. The differing evolutionary impacts of seed crops and maize in eastern North America may be an instance of this distinction.
2. The incorporation of low-rank but high-yield species into the diet forms the basis for population growth and creates a situation in which resources of higher rank will be heavily exploited and possibly depleted. Conversely, high-rank, high-density resources will exclude previously consumed items from the diet, allowing them to recover to preexploitation population levels.
3. Evolutionary ecology models show that local or regional pooling from spatially unsynchronized food sources is an effective means of reducing subsistence risk for both foragers and farmers.
4. Subsistence risk is likely to increase as high-yield domesticates enter the diet of foragers-becoming-farmers. An increasingly dense human population either overexploits alternative foods (if the TD is at low rank in the diet), thus decreasing effective dietary diversity, or (if the TD is at high rank) may grow to such an extent that previously foraged foods can provide only a modest buffer should the domesticate food or foods fail.
5. Growing dependence on plant cultivation changes both the subsistence production interval and dispersion opportunities in a manner that favors a shift from interhousehold (sharing) to intra-household (field dispersion) as a primary means of avoiding risk. Regional exchange remains a secondary risk-buffering mechanism.
6. Early agricultural households may be under strong selection pressure to develop community-level means of regulating rights in dispersed parcels of land. We speculate that they will develop mechanisms similar to those of the sectorial rotation systems seen in existing, nonindustrial agricultural systems.
7. We expect a lag in the development of risk-management strategies appropriate to increased reliance on high-yield, cultivated resources. The prehistoric record of increased paleopathologic conditions caused by nutritional insults during the transition to food production is consistent with this expectation.
8. The evolutionary ecology approach we advocate for explaining domestication focuses on selection-based models, nonnormative

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properties of environmental variables, and the types of resource decisions actually faced by individual foragers. We propose that a microecological approach based on intensive variables is preferable to prime-mover analyses based on extensive variables, normatively described.

9. We have used literature summaries from the Great Plains and eastern North America to suggest how current archaeological evidence on processes of domestication and risk management might be interpreted using foraging theory. Although very preliminary, we hope that this material demonstrates the potential of an evolutionary ecology framework, for these and other regions of the world.

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Notes

1. By *normative* we refer to central tendency variables such as averages.
2. If environmental fluctuations are invoked, typically they are the regular ones of seasonality as they affect the scheduling of resource procurement (Flannery 1971) or transhumant migrations (Lynch 1973). Flannery and Reynolds (Flannery, ed. 1986) and Redding (1988) provide exceptions.
3. We use the term *selection* broadly and with some deliberate ambiguity. For this analysis it is unnecessary to choose between natural selection acting on genetic dispositions, cultural selection arising from adaptive biases in cultural inheritance, or the rational decisions of individuals (see Blurton Jones 1990; Durham 1992). Whatever the mechanism or combination, differential inheritance of the more advantageous option or options will produce cumulative, evolutionary change.
4. We refer here to the fine-grained, encounter-contingent model for prey selection, not the patch-choice model.
5. Although the diet breadth (defined as the number of resource types) will not narrow, the effective breadth (measured by both the number of types and the relative evenness of their representation in the diet) will drop.
6. This measurement is very close to McCloskey's estimate of 10%.

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7. Three other families were at 100% probability of disaster for all possible numbers of fields. These are families with unusually high minimum requirements (because of factors such as shortage of potato land, large family size, or disastrously poor yields from other crops). No single field—or combination of fields—yielded well enough that it could have met their needs. Another three families actually experienced increasing probability of disaster with greater numbers of fields planted. These families provide an illustration of the second half of the rule of thumb: since their critical threshold is greater than the average yield, they might have done better to plant fewer fields (the high variance option). For these farmers, however, the choice is somewhat hypothetical. It would require that they know far in advance that their average yield would be less than their minimum needs. Lacking this prescience, these families bet as they had to on a reasonably good year, adopted risk-minimizing tactics accordingly, and then had the fate to experience increasing probability of disaster with increasing numbers of fields. The last family experienced 0% probability of disaster for all numbers of fields. This was the family with the smallest requirement, because of ample potato land and good yields among its other crops.

8. A denser stand of a grain crop may become more profitable because of increased efficiency in handling costs. This is quite unlike any benefit that would be gained, for example, in hunting, where the handling costs of a large ungulate will remain the same whether it is solitary or among a large herd at the time it is harvested. Following the diet breadth model, once the plant resource enters the diet, it will always be pursued once encountered. If such resources become physically associated with human settlements (by virtue of their establishment in disturbed habitats) then they will obviously be frequently encountered.

9. The decrease in health is not necessarily a direct result of changed dietary and nutritional circumstances. Diminished health may have resulted from population aggregation, which favors the spread of infectious diseases. Synergy between nutritional health and infectious disease may also have been important.

10. This citation is a mild instance of optimophobia, an affliction that causes one to be highly critical of optimality analysis even while practicing it in informal, implicit, or unrecognized forms (such as functionalist or adaptation approaches). It is an affliction more common among anthropologists than among economists.

11. The magnitude of the population increase will depend on the density of the resource.