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What does it mean to be locally adapted and who cares anyway?^{1,2}

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ABSTRACT: The availability of fossil fuels will likely decline dramatically during the first half of the twenty-first century, and the massive deficits probably will not be alleviated by alternative sources of energy. This seeming catastrophe will create opportunities for communities to benefit from foods produced locally in ways that nurture relationships among soil, water, plants, herbivores, and people to sustain their collective well being. Agriculture will be much more at the heart of communities than it is currently, but by necessity, it will no longer be so dependent on fossil fuels to power machinery or to produce fertilizers, herbicides, and insecticides to grow and protect plants in monocultures, antibiotics, and anthelmintics to maintain the health of herbivores, or nutritional supplements and pharmaceuticals to sustain humans. Rather, from soils and plants to herbivores and people, we will have to learn once again what it means to be locally adapted to the

landscapes we inhabit. In the process of relearning these skills, plants will become more important as nutrition centers and pharmacies, their vast arrays of primary (nutrients) and secondary (pharmaceuticals) compounds useful in nutrition and health. There also will be a need, as in times past before our heavy reliance on fossil fuels, to produce livestock in easy-care systems that match seasonally-available forages with production needs and that match animals anatomically, physiologically, and behaviorally to local landscapes. This will mean reducing inputs of fossil fuels to increase profitability by 1) matching animal needs to forage resources; 2) selecting for animals that are adapted anatomically, physiologically, and behaviorally to local environments; 3) culling animals unable to reproduce with minimal help from humans; and 4) creating grazing systems that enhance the well-being of soils, plants, herbivores, and people.

Key words: adaptation, change, forage, fossil fuel, learning, livestock

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INTRODUCTION

Sustainability is first and foremost about ongoing adaptation in ever changing environments. What might that mean in the twenty-first century? In a book titled *The Long Emergency*, James Kunstler (2005) argues that the availability of fossil fuels will decline considerably in the first half of the twenty-first century and that the massive deficits will not be alleviated, even

with all of the alternative sources of energy, especially given concerns about human influences on climate change. This seeming catastrophe will create opportunities as life changes from urban to rural, and the communities that emerge come to rely on foods produced locally, due to our inability to transport goods over the vast distances that we currently do nationally and internationally.

Agriculture will become much more at the heart of these communities than it is presently, but its lifeblood will not be fossil fuels to power machinery or produce fertilizers, herbicides, and insecticides to grow and protect plants in monocultures, antibiotics, and anthelmintics to maintain the health of herbivores, or nutritional supplements and pharmaceuticals to sustain the well-being of humans. Rather, from soils and plants to herbivores and people, we will learn once again what it means to be locally adapted. In this century, we will of necessity nurture relationships among soil, water, plants, herbivores, and people in ways that sustain the production, health, and well-being of ecosystems and that make farming profitable and enjoyable. Plants will be used more as nutrition centers and pharmacies, their

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vast arrays of primary (nutrients) and secondary (pharmaceuticals) compounds useful in nutrition and health. Nature provides the creatures of this earth with a full range of benefits, including the nutrition and health of plants, herbivores, or people, without many of the costs we sustain nowadays due to our heavy reliance on fossil-fuel-intensive fertilizers, herbicides, insecticides, and antibiotics.

Animals will be locally adapted to the landscapes where they will live from conception to consumption. If we continue to use ruminants as a source of food, there will be increased demand for livestock production from pastures and rangelands because it requires only one-third to one-half the fossil fuel to produce a pound of beef from range as compared with beef produced in feedlots. We will again be required to produce ruminants on forages, as nature has done for millennia. There will be a need, as in times past before our heavy reliance on fossil fuels, to produce livestock in systems that match seasonally available forages with production needs, and that match animals anatomically, physiologically, and behaviorally to landscapes. To take advantage of these benefits, we must learn to make the most efficient use of what nature provides when she provides it.

SELECTING FOR LOCALLY ADAPTED CREATURES

How might severe reductions in oil and natural gas affect trade and shipping? With regard to commerce, Kunstler (2005) argues that “The salient fact about life in the decades ahead is that it will become increasingly and intensely local and smaller in scale”. With regard to transportation, he contends “The twenty-first century will be much more about staying put than about going other places”. In this scenario, livestock will of necessity be produced from birth to death on pastures and rangelands and then sold locally.

Fossil fuels have enabled people and many of the wild and domesticated species of plants and animals that interact with us to exceed the carrying capacities of landscapes. In the process, people and the agriculture upon which we all rely have become dependent upon fossil fuels to power farm equipment (oil), synthesize nitrogen fertilizer (natural gas), and transport goods (oil) (Pollan, 2006). Low oil prices made it feasible to use high-input harvested forages and feed grains. At some point in the not-too-distant future, rising prices for oil and natural gas and demands for ethanol will increase grain prices to the point where it will no longer be feasible to finish animals on grain in feedlots. Although they were meant to do the opposite, fossil-fuel-intensive practices have increased costs and adversely affected the environment during the latter half of the twentieth century.

Cutting Costs by Mimicking Natural Processes

Many grassroots efforts in agriculture now emphasize cutting costs to maximize profits. To survive in

agriculture, people like Kit Pharo (<http://www.Pharo-Cattle.com>) are developing management philosophies and practices that harmonize with natural processes. They graze animals in ways that mimic natural grazing systems to sustain soils and plants. They retain only animals that can survive on what nature provides, without any additional forage inputs, by selecting for locally adapted cattle and by culling any animal unable to reproduce every year without help from humans. That approach makes sense ecologically and economically. It also makes sense from a behavioral standpoint: behavior links ecology and economy by creating a match between what animals need and what is on hand.

Although understanding animal adaptations to landscapes has always been an important aspect of the nutritional ecology of ruminants (Demment and Van Soest, 1985; Hofmann, 1988), until recently, land managers have not attempted to put these ideas into practice. Instead, many people involved in academia, agribusiness, and livestock production have emphasized production at the expense of profit, without linking animals ecologically to the landscapes they inhabit. Thus, animals have been selected with nutritional demands that exceeded the capacity of the forage resource to meet their needs. This problem has been exacerbated by performance testing bulls and rams in confinement on concentrate rations, which likely has selected for animals that perform well in feedlots, but are not well adapted to finishing on pastures and rangelands. Such ecological mismatches decrease animal performance, harm the productivity of plants, diminish the viability of soils, and ultimately increase costs and diminish profitability.

Nor have we appreciated that ongoing adaptation by wild and domestic herbivores must involve a continuous dialogue among genes and behavior in ever-changing social and biophysical environments. Soils, plants, animals, and the continents they inhabit change constantly. Even within the short span of 20,000 yr since the last glaciations, changes in climate have drastically altered physical environments and the species of plants and animals that inhabit those environs (Pielou, 1991). Nonetheless, we have attempted, with massive inputs of fossil fuels, to eradicate “invasive” species of plants and animals. What would we have done when the species we now consider native were “invading” after the last glaciations? Likewise, we have attempted, at great cost economically and ecologically, to change landscapes to suit domestic animals, rather than considering how animals must continually adapt to the ever-changing availability of foods and habitats. With cattle and sheep in particular, we have attempted in vain with massive mechanical and chemical inputs to convert landscapes dominated by shrubs to grass to fit our perception of livestock as grazers, rather than selecting among and within breeds of livestock for individuals that can use the plants that exist on landscapes. Although we often consider cattle to be grass eaters and

sheep to be forb eaters, they can thrive under a wide range of conditions, including shrub-dominated areas in the arid southwest United States, provided they have been selected anatomically, physiologically, and behaviorally to survive on their own in the landscapes they inhabit (Provenza and Balph, 1990).

We must take advantage of the tremendous variation within breeds to select for individuals able to perform efficiently on poor quality forages high in secondary compounds common in arid environments, as the potential certainly exists to do so (Provenza and Balph, 1990; Provenza et al., 1992, 2003). In arid areas, that means selecting for animals of smaller frame size that better match the seasonal availability and diversity of forage supplies, and selecting for animals that are able to consume the diverse array of secondary compounds found in various species of plants now “invading” landscapes. Smaller frame sizes reduce the amount of food that must be consumed, which enables animals to better mix various plant species, thereby allowing them to cope with the chemical and physical defenses abundant in plants that inhabit arid environments (Coley et al., 1985). Historically, livestock production systems have selected for animals of uniformly larger frame sizes and body compositions, as well as for meat flavor made homogeneous by finishing animals on high-grain diets. With the decline in fossil fuels, that will change as animals are produced and consumed locally, and as consumers acquire preferences for the flavors of animals produced from plants grown on local soils.

Matching animal needs to seasonally available forage supplies also means mothers will have offspring when forage quality is highest in late spring or early summer, rather than when plants are mature and dormant in the middle of winter. Wild ruminants have adapted these reproductive behaviors to ensure that they have ample nutrients during late gestation and early lactation, times when their needs are greatest. They must rely only on what nature provides each year because living on fossil fuels is not an option. In the case of cattle (and sheep), the advantages of having offspring in synchrony with nature occur because 1) feed and labor costs are reduced by 70%; 2) most (90%) calves are born in the first 30 d of the calving season, without feeding any hay; and 3) more total pounds of calves are weaned that are worth more per pound (Kit Pharo; <http://www.PharoCattle.com>).

In the book *The Last Ranch*, Sam Bingham (1996) discusses elements of change and adaptation with a livestock producer named George Whitten. George recounts the “old sheep cycle” practiced in the San Luis Valley of Colorado in the early part of the twentieth century. He points out that in 1935 they selected for ewes that produced a 75-pound lamb and they culled ewes with twins. In 1985, his sons were selecting for ewes that produced 90-pound lambs, with a 150% lamb crop. In 1935 the ewes were selected to produce on minimal forage inputs and a nomadic way of life,

whereas in 1985 they were selected for production on ever increasing inputs. George remarks that, “Our ewes were strong and as well muscled as deer, and yours wouldn’t last a day where ours went”.

George emphasizes the value of local knowledge, which once lost, is hard to regain. In the latter part of the twentieth century, people enamored with stories about the “old sheep cycle” hoped to recreate it. But as George points out, “They were crazy. Once the knowledge is gone, you can’t get it back just like that. They didn’t even have a dog that knew anything. When they went through here, you knew they were looking for trouble. And they found it”. The lack of adaptation by all involved, from dogs and sheep to people, ensured they were unable even to move the sheep from the bottom of the San Luis Valley into the surrounding mountains, let alone recreate the old cycle. Everybody involved lacked the anatomical, physiological, and behavioral knowledge to accomplish the task. In making such major changes in management, a minimum of 3 yr typically are required as soils, plants, herbivores, and people adapt to the new regimens (Provenza, 2003a). Ray Bannister, for instance, needed 3 yr to retrain a cattle herd to “mix the best with the rest” rather than “eat the best and leave the rest” on ranges in eastern Montana, and Bob Budd took 3 yr to retrain cattle to use uplands as opposed to riparian areas on Red Canyon Ranch near Lander, WY (Provenza, 2003a).

Variation Among Individuals Enables Adaptation

We emphasize means and populations in science and management, but variation is the basis for selection in natural and agricultural systems. People calculate average values for representative populations, but nature generates only individuals and variation. With regard to animals, we value the tremendous diversity of species across landscapes, but we have not fully realized the significance of the variation among individuals within a species for how we can become locally adapted to the environs we inhabit.

With regard to easy-care-lambing systems, for instance, variation in behaviors among individual ewes provides the basis for transitioning from intensive-lambing systems in jugs to easy-care systems on rangelands. The questions are: which ewes should a producer select for an easy-care system and can they be identified a priori? Based on scientific and experiential knowledge, it is probably impossible to identify a priori each ewe that possesses the combination of physiological and behavioral traits that will work best in an easy-care system. We do, however, know the traits we desire: a ewe that 1) can lamb successfully without help from humans; 2) bonds tightly to her lambs and protects them from predators, and 3) knows the best foods and habitats in which to raise her lamb. How do people like Kit Pharo (<http://www.PharoCattle.com>) and Janet McNally (<http://www.tamaracksheep.com>) select ani-

mals that can make a living without inputs from humans? Livestock producers who have changed from calving and lambing in winter to spring and who require their animals to survive and reproduce on landscapes with little or no human intervention do what natural selection does: they put them to the test; those that reproduce remain in the herd and those that do not are culled. Thus, producers enable natural selection without heavy reliance on labor or fossil fuels.

Initial conditions are vital when it comes to acquiring new behaviors. Young animals begin to experience and learn about social and biophysical environments before birth, and experiences in utero and early in life markedly influence food and habitat selection (Provenza, 2003a). As environmental conditions change, adults also must learn new behaviors, and a manager can play a key role in developing a rearing environment that encourages mothers to raise and educate their offspring with minimal intervention from humans. It is imperative that managers think carefully about matching the timing and location of calving or lambing with appropriate foods and habitats such that mothers relearn and offspring learn appropriate mothering, foraging, and habitat selection behaviors.

For cows or ewes and their owners who have been trained to calve or lamb under more intensive management systems, this may be a difficult transition. Considering the power of experience to shape behavior, changes in management will be most difficult for mature adults; young replacements, reared in the new system, adapt readily because they only know the new system. Most producers indicate major changes in management require 3 yr to complete (Provenza, 2003a). The first year is the most difficult because none of the adults (livestock or people) have any experience with the new system. The second year is better because all those involved have a year of experience with the new system and the animals that were unable to adjust to the new system have been culled. By the third year, all of the adults have 2 yr of experience with the new system and the replacement females born into the new system are becoming adult members of the herd or flock.

Home on the Range: Learning to Adapt from Mother

Since the dawn of the age of genetics, we have been taught that genes are destiny (Lipton, 2005). Even Darwin conceded, near the end of his life, that the environment was not considered suitably in evolution. In a letter to Moritz Wagner, Darwin (1888) wrote "In my opinion, the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environment". Still today, modern texts fail to address the all-encompassing influence of maternal effects on a wide assortment of traits (Wade, 1998). This bias, reinforced by quantitative genetic methods that

consider maternal effects as complicating factors in estimating heritabilities (Wade, 1998), again dates back to Darwin (1859) who emphasized that "seedlings from the same fruit, and the young of the same litter, sometimes differ considerably from each other, though both the young and the parents...have been exposed to exactly the same conditions of life; this shows how unimportant the direct effects of the conditions of life are in comparison with the laws of reproduction, and of growth, and of inheritance" (p. 10). Nowadays, news reports that regularly announce the discovery of a new gene for everything reinforce this one-dimensional view that genes function in isolation of social and biophysical environments.

Although genes certainly influence the expression of behaviors, it is just as true that behaviors influence the expression of genes. In that sense, genes learn from the environment (Lipton, 2005). There would be no need for genes to be expressed if biophysical and social landscapes were static, but the ever-changing nature of nature requires that genes converse with the environment, and much of this essential discussion occurs during development in utero and early in life.

An important form of this discourse, termed predictive adaptive responses, refers to responses that are 1) induced by the environment early in life; 2) cause permanent changes neurologically, morphologically, and physiologically, and 3) confer survival advantages when the environment of rearing matches the environment where a young animal then lives (Gluckman et al., 2005). Predictive adaptive responses do not need to confer an immediate survival advantage to the fetus or very young animal; rather, they act via developmental plasticity early in life to modify the phenotype so it matches the environment of rearing, which is expected to be inhabited later in life. This will be so if the behavior of mother is appropriate for the postweaning environment and if that environment does not change too drastically during the life of the offspring. In this process, the mother is a transgenerational link that provides stability to social systems by familiarizing offspring in utero and early in life with the locally available foods and habitats she uses. Offspring become creative forces as they explore the potential value of foods and environments not used by mother. In the process, they create a balance between constancy (mother) and creative exploration (offspring) that enables ongoing adaptation as environments change from generation to generation.

To the degree that predictive adaptive responses become fixed, there is some degree of risk of a mismatch between what has been expressed and what is actually needed to survive in an environment. Provided that environments do not change too quickly or radically relative to the life span of the individual, risk is low and gene expression helps ensure a match between a generation of organisms and the environment where they are born and reared. However, if the fetus predicts

its future reproductive environment incorrectly, due to failure of appropriate transduction of the state of the environment from mother to fetus or because the environment changes radically from that predicted, the fetus will have increased risk of poor performance and disease (Gluckman et al., 2005). This is often the case as domestic and wild animals moved from familiar to unfamiliar environments suffer more than locally adapted animals from malnutrition, ingestion of poisonous plants, and predation (Provenza and Balph, 1990; Provenza et al., 1992; Davis and Stamps, 2004). This disparity also occurs commonly when domestic animals are moved from rangelands to feedlots where the foods and social and physical environments all differ radically from what they have learned. These mismatches do not occur when animals are conceived, born, reared, and die in familiar social and biophysical haunts.

Given our predisposition to consider behaviors as fixed genetically, we have neither been aware of nor have we appreciated the significance of predictive adaptive responses in humans (Gluckman et al., 2005) or in herbivores (Provenza, 1995b; Provenza et al., 2003). Nonetheless, experiences in utero and early in life have life-long influences on diet, obesity, health, and disease in humans. Likewise, experiences with diets and habitats that vary in quality have life-long influences on performance and health of herbivores. By interacting with the genome during growth and development, social and biophysical environments influence gene expression and behavioral responses (Lewontin, 2000; McCormick et al., 2000; Dufty et al., 2002; LeDoux, 2002; Moore, 2002).

Experience early in life causes neurological, morphological, and physiological changes that influence foraging behavior (Provenza and Balph, 1990; Provenza, 1995b; Schlichting and Pigliucci, 1998; Provenza et al., 1998). In the process, young herbivores learn motor skills needed to harvest forages (Flores et al., 1989a,b; Ortega-Reyes and Provenza, 1993a,b), they acquire preferences for foods (sheep: Nolte et al., 1992b,c; Squibb et al., 1990; goats: Biquand and Biquand-Guyot, 1992), and their bodies adapt to using particular foods (Distel and Provenza, 1991; Ortega Reyes et al., 1992; Distel et al., 1994, 1996). Thus, although the body influences the structure of experience, experience is at the same time influencing the structure and function of the body. These developmental processes, which enable animals to adapt to local diets and habitats, imply that what constitutes a "high quality diet or habitat" will differ for individuals reared in different environments.

Learning from mother begins early in life as flavors of foods the mother eats are transferred to her offspring in utero and in her milk. In livestock, the flavor of plants, such as onions and garlic, is transferred this way, increasing the likelihood that young animals will eat onion and garlic when they begin to forage (Nolte et al., 1992a,b,c). As offspring begin to forage, they further learn what to eat and where to go by following mother

(Mirza and Provenza, 1990, 1992; Thorhallsdottir et al., 1990; Howery et al., 1998). Young animals learn quickly to eat foods their mother eats, and they remember those foods for life. Lambs fed nutritious foods, such as wheat, alongside their mothers for as little as 1 h/d for 5 d, eat more wheat than lambs exposed to wheat without their mothers present (Green et al., 1984). Even 3 yr later, with no additional exposure to wheat, intake of wheat is nearly 10 times higher if lambs are exposed to wheat with their mothers than if inexperienced lambs are exposed alone or not exposed at all (Green et al., 1984).

Livestock also eat more of poor-quality foods and plants high in secondary compounds when they learn to eat them early in life with their mothers. Goats reared from 1 to 4 mo of age with their mothers on blackbrush-dominated land ate over 2.5 times more blackbrush than did goats naive to blackbrush (Distel and Provenza, 1991), a poorly nutritious food high in condensed tannins (Clausen et al., 1990). Experienced goats also consumed 30% more blackbrush than inexperienced goats when allowed to choose between blackbrush and alfalfa pellets (Distel and Provenza, 1991). Likewise, food intake and animal performance differed markedly during a 3-yr study when cows 5 yr of age were fed straw as a major part of their diet from December to May (Wiedmeier et al., 2002). One-half of the cows ate straw with their mothers for only 2 mo as calves, whereas the other half had never seen straw. Throughout the 3-yr study, experienced cows ate more straw, lost less weight, maintained better body condition, produced more milk, and bred back sooner than cows not exposed to straw (Wiedmeier et al., 2002). Remarkably, with few exceptions (foraging skills: Ortega-Reyes and Provenza, 1993a; food intake: Green et al., 1984; Wiedmeier et al., 1995, 2002), these studies are conservative estimates of the degree to which experience early in life affects performance of adults as exposure and testing occurred when animals were young and still learning.

Herbivores learn to optimize intake of foods in a manner consistent with their previous experiences with the mix of foods offered (Provenza et al., 2003). When they eat only a small subset of the more palatable foods that provide adequate nutrition, animals are unlikely to learn about the possible benefits of mixing different foods, especially those high in secondary compounds. Over time, such selective foraging on pastures and rangelands will change the mix of plants available, further reducing opportunities to learn. However, herbivores encouraged to eat all plants are more likely to learn to eat mixtures of foods that mitigate toxicity, assuming appropriate choices are available. For instance, experience and the availability of nutritious alternatives both influenced food choice when the preferences of lambs with 3 mo of experience eating plants containing tannin, terpenes, and oxalates were compared with lambs naive to the foods containing these secondary compounds (Villalba et al., 2004). During the

studies, all lambs were offered 5 foods, 2 of them familiar to all of the lambs (ground alfalfa and a 50:50 mix of ground alfalfa:ground barley) and 3 of them familiar only to experienced lambs (a ground ration containing tannins, terpenes, or oxalates). Half of the lambs were offered the familiar foods ad libitum, whereas half of the lambs were offered only 200 g of each familiar food daily. Throughout the study, naive lambs ate much less of the foods with secondary compounds if they had ad libitum (66 g/d) compared with restricted (549 g/d) access to the nutritious alternatives. Experienced lambs also ate less of the foods with secondary compounds if they had ad libitum (809 g/d) as opposed to restricted (1,497 g/d) access to the nutritious alternatives. In both cases, however, lambs with experience ate markedly more than naive lambs of the foods containing the secondary compounds, whether access to the alfalfa-barley alternatives was ad libitum (809 vs. 66 g/d) or restricted (1,497 vs. 549 g/d). In a companion study, when access to familiar foods was restricted to 10, 30, 50, or 70% of ad libitum, animals ate more of the foods with secondary compounds and they gained more weight along a continuum (10% = 30% > 50% = 70%), which illustrates that animals must be encouraged to learn to eat unfamiliar foods that contain secondary compounds (Shaw et al., 2006). Critically, grazing management can influence what animals learn; continuous grazing at low stock densities encourages selective foraging, whereas management-intensive and short-duration grazing at high stock densities encourages animals to learn to mix their diets (Provenza, 2003a,b).

Young sheep and cattle also learn habitat selection behaviors from their mothers, as illustrated by cross-fostering studies with sheep (Key and MacIver, 1980) and cattle (Howery et al., 1998). Indeed, natal experiences affect habitat preferences in animal taxa from insects and fishes to birds and mammals (Davis and Stamps, 2004). In polygynous mammals, dispersal is male-based and social groups often are composed of closely related philopatric females (Greenwood, 1980; Dobson, 1982). Retention of daughters within the maternal home range and male-based dispersal form the basis of sociality in many mammalian species (Armitage, 1981). Social organization leads to culture, the knowledge and habits acquired by ancestors and passed from one generation to the next about how to survive in an environment (De Waal, 2001). A culture develops when learned practices contribute to the group's success in solving problems. Cultures evolve as individuals in groups discover new ways of behaving, as with finding new foods or habitats and better ways to use foods and habitats (Skinner, 1981).

In summary, experiences early in life, and in particular maternally mediated effects on food and habitat selection, are widespread, and their evolutionary dynamics are unusual relative to standard genetic theory (Wade, 1998). Specifically, the evolution of maternal effects involves 2 levels of selection, within and among

families; as a result of selection among families, much more genetic variance can be maintained at equilibrium with mutation than for ordinary genes. The increased heterozygosity, in turn, permits random genetic drift to quickly differentiate local populations and creates opportunities for local adaptation via individual selection. Accelerated local divergence of isolated populations due to maternal effects can quickly contribute to locally adapted individuals, social groups, and cultures, which can eventually contribute to speciation. Thus, the environment interacting with genes creates organisms, and the development of each individual is an emergent property influenced by the interplay between its genes and social and the biophysical environments where a creature is reared. Unfortunately, as Lewontin (2000) emphasizes, "Modern developmental biology is framed entirely in terms of genes and cell organelles, while environment plays only the role of a background factor. The genes in the fertilized egg are said to determine the final state of the organism, while the environment in which development takes place is simply a set of enabling conditions that allow the genes to express themselves, just as an exposed film will produce the image that is imminent in it when it is placed in a chemical developer at the appropriate temperature". If we give only lip service to the richness of how environments affect local adaptation, we don't even consider the role of chance, yet history, necessity, and chance are fundamentally interconnected in development and behavior. Lewontin (2000) provides examples of how chance influences development in plants and animals, and he makes the point as well with regard to neural networks: "A leading current theory of the development of the brain, the selective theory, is that neurons form random connections by random growth during development. Those connections that are reinforced from external inputs during neural development are stabilized, while the others decay and disappear. But the connections must be randomly formed before they can be stabilized by experience. Such a process of neural development could give rise to differences in cognitive function that were biological and anatomically innate, yet neither genetic nor environmental". Given the role of chance in development, individuals and the development social networks of which they are a part become self-organizing systems with emergent properties that cannot be predicted a priori (Provenza et al., 1998; Taleb, 2001; Laughlin, 2005).

NURTURING LOCALLY ADAPTED SOILS, PLANTS, HERBIVORES, AND PEOPLE

The health of landscapes depends on interrelationships among soils, plants, herbivores, and people. Nearly 50 yr ago, in a book titled *Soils, Grass and Cancer*, Andre Voisin (1959) highlighted these connections and warned that people, in our attempts to produce food for a burgeoning world population, have for-

gotten that our bodies come from the soil. To Voisin, it seemed that the rise of the artificial fertilizer industry had caused people to become so reliant on its products that we have forgotten our intimate relationship with the soil as nature made it, and that our adulterations of the soil from which we arise may be sealing our destiny as a species on earth. Though this quandary is little more than a century old, its progression has been geometric in the increase of diseases in plants, animals, and humans due to overuse of artificial fertilizers applied to plants grown in monoculture. Conversely, soils developed naturally and rich in organic matter and nutrients provide the basis for health in plants, herbivores, and people.

Managing for healthy relationships among soils, plants, herbivores, and people can provide invaluable services to society in the forms of clean air, water, and healthful food, while at the same time reducing costs and increasing profits, especially as the availability of fossil fuels declines and their price increases. With growing concerns about the role of fossil fuels in climate change, and increasing incentives in the form of carbon credits for sequestering CO₂, nurturing diverse mixtures of plant with abundant biomass below and above ground will be a way to increase income (Lal, 2007). These incentives, which will encourage people to manage ecosystems, rather than mine particular facets of systems for short-term gain, can buffer systems against droughts and floods, diminish ecological and economic risks by increasing choices for herbivores and people, and enhance sustainability by making best use of the sunlight, water, and nutrients that nature provides.

Soil Health and Plant Allocation to Growth or Defense

How plants allocate resources depends on the availability of water, nutrients, and sunlight. Plants can allocate carbon from photosynthesis and nutrients and water from soils to growth or to defense in the form of secondary compounds (Herms and Mattson, 1992). The degree to which they allocate to one or another over evolutionary and ecological time-spans depends on the availability of water, nutrients, and sunlight (Bryant et al., 1983; Coley et al., 1985). Soils rich in micro and macro-organisms that promote high rates of decomposition and nutrient cycling provide organic matter capable of holding vast amounts of water and nutrients (Allen, 2007; Pierret et al., 2007; Smucker et al., 2007), which stimulates plants to grow rather than defend. On the other hand, deficits of water and nutrients retard growth and lead to accumulations of excessive levels in plants of secondary compounds (Bryant et al., 1983, 1991). Too high levels of secondary compounds reduce food intake by herbivores (Provenza, 1995a,b; Provenza et al., 2003), and hinder nutrient cycling by soil organisms (Bryant et al., 1991). Indeed, extreme levels in

plants can be toxic to life in soils, herbivores, and people, especially when plants grow in monocultures. Conversely, moderate levels of secondary compounds are likely to promote health in soils, plants, herbivores, and humans (Provenza et al., 2007).

All plants contain secondary compounds that, at too high concentrations, limit how much of any particular food an herbivore can consume. Herbivores regulate intake of plants with secondary compounds in order to ingest adequate levels of nutrients and avoid toxicosis. Eating a variety of foods is the best way to accomplish this objective because different kinds of secondary compounds are processed at different rates and through different metabolic pathways, thereby providing multiple avenues for detoxification (Freeland and Janzen, 1974; Provenza, 1996). Conversely, monocultures of plants high in secondary compounds, produced through inappropriate grazing practices or genetically engineered into pasture and crop plants, can create vicious cycles that escalate to the detriment of soils, plants, herbivores, and people (Provenza et al., 2007).

As Friend Sykes (1951) wrote over 50 yr ago, "The first thing that Nature does when she has been treated with a poison is to battle against it and try to breed a resistant strain of the form of life that is being attacked. If the chemist persists in his poisonous methods, he often has to invent more and stronger poisons to deal with the resistance that Nature sets up against him. In this way a vicious cycle is created. For as a result of the conflict, pests of a hardier nature and poisons still more powerful are evolved; and who is to say that, in this protracted struggle, man himself may not ultimately be involved and overwhelmed" Diverse mixtures of plant species provide a way out of this vicious cycle by providing a variety of foods, with a diverse array of secondary compounds, to individually and collectively meet the needs of herbivores (Freeland and Janzen, 1974).

The Value of Plant Diversity

Natural landscapes are diverse mixes of plants that occur in patches reflecting history of use in concert with particular soil, precipitation, and temperature conditions. For plants, diversity is the rule for species, phenologies, growth forms, and biochemistries. Regarding the latter, plants are nutrition centers and pharmacies with vast arrays of primary (nutrients) and secondary (pharmaceuticals) compounds useful in animal nutrition and health (Craig, 1999; Engel 2002; Crozier et al., 2006). Regrettably, we have neither understood nor valued diversity in agriculture, as evident in our persistent attempts to simplify ecological systems to maximize yields of crops and pastures. Though often successful in the short term, "simplifying" ecosystems typically leads to ruinous long-term impacts, as shown in marine, forest, and rangeland systems (Gunderson et al. 1995). By maximizing the output of one component

of a system, we inevitably hasten the demise of the system. Alternatively, studies of natural systems highlight the benefits of biodiversity for reducing interannual variability in production and minimizing risk of large-scale catastrophic events, such as wildfire and outbreaks of diseases and pests (Gunderson et al., 1995). The structural and functional diversity inherent in natural systems increases productivity of plant and animal species and enhances system stability.

Although humans have dealt with nature's cornucopia in many ways, regardless of where they lived our ancestors targeted a few species, those that were abundant, palatable, and easily cultivated and harvested, for sampling and eventual use (Etkin, 1994). Of the roughly 200,000 species of wild plants on earth, only a few thousand are eaten by humans; just a few hundred of these have been domesticated; and only a dozen account for over 80% of the current annual production of all crops (Diamond, 1999). By focusing on a few species, people transformed the diverse world of plants into a manageable domain that generally met needs for nutrients, mainly energy, and limited overingestion of toxins (Johns, 1994). In so doing, however, we narrowed the genetic basis of crop production to a few plants, relatively productive in the broadest range of environments, rather than broadening the range of plants valuable in local environments. We have also discovered only a fraction of the plant mixtures useful in nutrition and health (Etkin, 1994), and we have simplified agricultural systems in ways that are having alarming consequences on the health of people and landscapes (Pollan, 2006).

Eating a diverse array of foods is fundamental for nutrition and health. Given appropriate mixtures of plants, cattle, sheep, and goats eat more and perform better when they are offered plants that contain secondary compounds (Provenza et al., 2007). Variety is so important that bodies have built-in mechanisms that ensure animals satiate on foods eaten in a meal, which guarantees that animals eat a variety of foods and forage in different locations (Provenza, 1996; Bailey and Provenza, 2007). Variety enables animals to reap the benefits of ingesting various primary and secondary compounds and also enables individuality. Bodies have the nutritional wisdom necessary to meet needs for energy, protein, and various minerals (Provenza and Villalba, 2006). Offering animals choices in confinement, on pastures, and rangelands allows each individual to meet its needs for nutrients and to regulate its intake of secondary compounds by mixing foods in ways that work for that individual (Provenza, 2003a; Provenza et al., 2003). Thus, variety not only enables individuality, it also greatly increases the likelihood of providing cells with the vast arrays of primary and secondary compounds essential for their nutrition and health.

The Roles of Secondary Compounds in Nutrition and Health

We know much about the roles of primary compounds in nutrition, but we are just beginning to appreciate

the nutritional and pharmaceutical values of nature's pharmacy, the secondary compounds. All plants produce secondary compounds, even the plants we grow in our gardens, but until recently, people thought secondary compounds were waste products of plant metabolism. Over the years, researchers came to understand the roles of nutrients such as nitrogen, phosphorus, and potassium in plant nutrition, but they had no idea why these other compounds occurred in plants. We have learned much in the past 30 yr about the roles of secondary compounds in the health of plants, including functions as diverse as attracting pollinators and dispersing seeds, helping plants recover from injury, protecting plants from ultraviolet radiation, and defending plants against diseases, pathogens, and herbivores (Rosenthal and Janzen, 1979, Rosenthal and Berenbaum, 1992).

At the same time we were learning of the value of secondary compounds, we were reducing their concentrations through selection to maximize yields of crops and pastures that were inevitably more susceptible to environmental hardships. In their stead, we resorted to fossil fuel-based fertilizers, herbicides, and insecticides to grow and protect plants in monocultures, antibiotics and anthelmintics to maintain the health of herbivores, and nutritional supplements and pharmaceuticals to sustain the well being of humans. Such systems corrupt the health of soils, plants, herbivores, and humans and gradually degrade the economic and environmental health of landscapes. Ironically, we are now attempting to genetically engineer specific compounds with similar beneficial functions back into plants. Instead, we should be asking how and why nature grows plants in diverse mixtures with remarkable arrays of secondary compounds, and reconstructing pastures and grazing lands with assorted species that together enhance soil fertility, provide benefits of secondary compounds, and vary in time of production, depths of rooting, and contrasting uses of water and nutrients (Provenza et al., 2007).

Simplifying agriculture to facilitate livestock production, coupled with a view of plant secondary compounds as toxins, has resulted in selecting for a biochemical balance in forages favoring primary compounds and nearly eliminating secondary compounds. To increase intake of single-plant diets, one must reduce secondary compounds because they limit how much of any particular food humans and livestock can consume. The outcome is energy- and protein-dense monocultures low in the secondary compounds. The alternative, which we have not pursued, is offering animals a variety of foods that differ in primary and secondary metabolites, thereby enabling them and us to obtain a much greater array of nutrition and health benefits from nature's bounty.

For people and herbivores, the biochemical composition of the meals we eat has become more uniform as the variety of foods in our diets has declined, and we no longer experience the benefits of eating an array of

plant-derived primary and secondary metabolites (Craig, 1999; Engel, 2002). That, in concert with eating the meat of animals from feedlots, means our intake of a various beneficial compounds is far lower than if we ate wild plants and herbivores reared on biochemically diverse forages (Dhiman et al., 2005; Pollan, 2006). In concert with lack of exercise, this may explain the current obesity crisis in many countries, which may get much worse unless we change our behavior. Indeed, fast-food generations may be the first to have shorter lives than their parents and grandparents due to obesity-related diseases. Certainly, many foods preferred by our ancestors are considered unpalatable by people today due to their lack of experience with secondary compounds. With ready access to processed foods high in sugar, carbohydrates, fat, and salt, young people no longer acquire preferences for unpalatable foods because they lack the traditional cultural foundations to guide their selection of foods high in secondary compounds (Johns, 1994). On the other hand, hunter-gatherers who have maintained their traditional diets have far less cancer, heart disease, diabetes, and osteoporosis than people who consume fast foods, and it is not because hunter-gatherers die before these ills can develop (Logan and Dixon, 1994). The Masai of Africa, for instance, suffer much less heart disease and cancer, even with diets very high in meat and milk, evidently because they combine animal products including up to 28 antioxidant herbs added to each meat-based soup and 12 added to milk (Johns, 1994; Engel, 2002).

Issues of diet mixing and secondary compounds are just as relevant for the nutrition and health of herbivores. They are what they eat, as we are what they eat. Cindy Engel's (2002) book titled *Wild Health, How Animals Keep Themselves Well and What We Can Learn from Them* is a fascinating discussion of the roles of secondary compounds in the health and well-being of animals. With nutrients and secondary compounds alike, everything depends on the dose. Any compound, including water, is toxic in too high doses; the right dose differentiates a toxin from a remedy, and because every individual is different, it is critical to provide animals with the opportunity to regulate their intake of primary and secondary compounds by offering them a variety of plants. Although we still have much to learn about plant mixtures and interactions among primary and secondary compounds, it is becoming increasingly clear that offering animals a variety of foods that not only meet their needs for nutrients, but that also provide a variety of secondary compounds, can enhance nutrition and health.

As case in point, tannins are increasingly recognized as compounds important in health and nutrition, though historically they were thought by agriculturalists and ecologists alike to adversely affect herbivores. Eating plants high in tannins is a way for herbivores to reduce internal parasites (Min and Hart, 2003), and tannins alleviate bloat by binding to proteins in the

rumen (Waghorn, 1990). By making the protein unavailable for digestion and absorption until it reaches the more acidic abomasum, tannins also enhance nutrition by providing high-quality protein to the small intestines (Barry et al., 2001). This high-quality-protein-bypass effect enhances immune responses and increases resistance to gastrointestinal nematodes (Niesen et al., 2002; Min et al., 2004). The resulting increase in essential and branched-chain amino acids improves reproduction efficiency in sheep (Min et al., 2001). Tannins in the diet are a natural way to reduce methane emission in ruminants (Woodward et al., 2004), which is an important issue regarding ongoing efforts to diminish the influence of livestock on global warming. Finally, tannins eaten in modest amounts by herbivores can improve the color and quality of meat for human consumption (Priolo et al., 2005). More generally, diverse assortments of SC in the diets of herbivores influence the flavor, color, and quality of meat and milk for human consumption, often in ways that are positive (Vasta et al., 2007).

Grazing to Enhance Soil and Plant Diversity and Quality

Understanding the options herbivores have when they consume foods that vary in primary and secondary compounds may help create new grazing strategies that include sequential foraging patterns to optimize intake and more evenly use all plant species. Shepherds in France stimulate animal appetites and more fully use the range of plants available by herding sheep and goats in grazing circuits (Hubert, 1993; Meuret et al., 1994). The circuit includes a moderation phase, which provides animals access to plants that are abundant but not highly preferred to calm a hungry flock; the next phase is a main course for the bulk of the meal with plants of moderate abundance and preference; then comes a booster phase of highly preferred plants for added diversity; and finally a dessert phase of palatable plants that complement previously eaten forages. Daily grazing circuits stimulate and satisfy an animal's appetite for different nutrients, they enable animals to maximize intake of nutrients and regulate intake of secondary compounds, and they ensure all plant species are utilized, which prevents directional shifts in vegetation away from diverse species to monocultures of less preferred plant species.

Diversity in the chemical composition of plants on landscapes provides the context for herbivores to learn about the consequences of eating different foods in succession. The time when herbivores eat different foods in a sequence may influence how much of different foods they can consume as food intake and preference are influenced by rates of absorption of secondary compounds and their interactions in the gastrointestinal tract. For instance, terpenes are small, fat-soluble molecules that are absorbed quickly through the rumen epi-

thelium such that they can quickly decrease food intake, whereas tannins are high-molecular-weight compounds that remain in the gut where they can interact with other chemicals. Thus, a meal of tannins followed by a meal of terpenes may lead to higher levels of intake than the reverse if tannins reduce absorption of terpenes. Sheep eat more food with terpenes and tannins when they eat a meal with foods in the sequence tannin-containing food → terpene-containing foods → alfalfa/barley than when fed alfalfa/barley → tannin-containing food → terpene-containing food (Mote et al., 2007). With the former sequence, tannins evidently are free to bind to terpenes, whereas with the latter sequence proteins in the alfalfa/barley bind to the tannins and prevent them interacting with terpenes (Jones and Mangan, 1977; Ben Salem et al., 2005). Likewise, sheep do not benefit when fed the sequence of terpene-containing food → tannin-containing food → alfalfa/barley, evidently because terpenes are absorbed so quickly through the gastrointestinal tract walls that they are not available to interact with tannins (Dziba et al., 2006).

Complementarities among secondary compounds are an important but little understood area of plant-herbivore interactions (Freeland and Janzen, 1974; Provenza et al., 2003). Even less is known about how the sequences of eating plants with different secondary compounds affects foraging, though they appear to be critical. As mentioned, sheep eat more food with terpenes when they first eat food with tannins (Mote et al., 2007). Cattle steadily decrease time eating high-alkaloid endophyte-infected tall fescue from 40 to 15% when they first graze fescue alone for 30 min followed by high-tannin birdsfoot trefoil alone for 60 min; amazingly, when the sequence is reversed they forage actively on both trefoil and fescue throughout the 90-min meal (T. D. Lyman, F. D. Provenza, and J. J. Villalba, Dept. Wildland Resources, Utah State University, unpublished data). These patterns of foraging are analogous with birdsfoot trefoil and high-alkaloid reed canarygrass. Sheep similarly decrease intake of endophyte-infected tall fescue in a meal, unless they receive intraruminal infusions of tannins before the meal, in which case they eat fescue throughout the meal; conversely, they eat trefoil readily unless they receive intraruminal infusions of tannins before the meal in which case they eat less trefoil (L. Lisonbee, J. J. Villalba, and F. D. Provenza, Dept. Wildland Resources, Utah State University, unpublished data). When sheep eat foods high in tannins or saponins along with foods high in alkaloids, the tannins and saponins bind with alkaloids, reducing their adverse effects on animal health and nutrition (Lyman et al., 2007). Collectively, these findings suggest that cattle and sheep regulate intake of plants as a function of interactions between tannins, saponins, and alkaloids and that the sequence in which they eat forages is crucial for increasing their intake of plants that differ in secondary compounds. Importantly, interactions among secondary compounds

can influence the amount of forage herbivores ingest in management-intensive grazing systems or in herding systems where animals are moved from one pasture to another.

As with the French herding circuits, in the aforementioned studies, we found that ingestion of foods with secondary compounds was greatest when highly preferred foods were fed last (Mote et al., 2007). Moreover, the ensuing food intakes and preferences for different foods that develop from learning different foraging sequences suggest that synergistic sequences increase preference for foods with secondary compounds, whereas those that are not synergistic do not (Baraza et al., 2005; Villalba et al., 2006; Mote et al., 2007). If research can elucidate how sequences of ingesting foods that differ in primary and secondary compounds affect food intake and preference, ecosystem managers will have a valuable tool to influence the health of landscapes.

Most importantly, people can use grazing circuits to generate soils rich in organic matter and nutrients and diverse in plants. Large herds of animals grazing at high stock densities for short periods of time add to soils organic matter and nutrients from feces, urine, and the trampling of plants (McNaughton, 1984; Bryant et al., 1991; Savory and Butterfield, 1999; Augustine et al., 2003; Gerrish, 2004). Thus, herbivores can help to build healthy soils and increase the palatability of plants by providing conditions conducive for plants to grow rather than defend with excessive levels of chemical defenses. High stock densities also encourage herbivores to “mix the best with the rest” rather than to “eat the best and leave the rest”, which can help to maintain plant diversity and prevent directional shifts in vegetation to landscapes dominated by one or only a few species of plants high in secondary compounds (Provenza et al., 2003; Provenza, 2003b).

Ironically, herbivores are likely to be the best judges of the health of soils and plants and the quality of their meat for humans. Through a lifetime of learned feedback from cells and organs, their bodies continually process and integrate the diverse array of biochemical interactions and signals generated by hundreds of primary and secondary compounds in the plants they eat that ultimately influence the palatability of any mixture of foods in their diets (Provenza, 1995a). Only bodies can integrate such multifaceted and dynamic signals. Chemical analyses are not up to the task, as William Albrecht (1958) wrote many years ago: “Though the cow cannot classify forage crops by variety name, or by tonnage yield per acre, she is more expert than any biochemist at assessing their nutritional value”. And what is ultimately being assessed by cells and organs are messages from soils expressed in the primary and secondary compounds in the plant mixtures selected as diets by herbivores reared in local cultures evolved in particular landscapes. That, in essence, is what it means to be locally adapted to ever-changing

landscapes in which all things are linked and evolving over time.

CHANGE PLUS CHANCE EQUALS OPPORTUNITY

What does it mean to be locally adapted to a landscape? It means reducing inputs of fossil fuels to increase profitability by 1) matching animal needs to forage resources; 2) selecting for locally adapted animals anatomically, physiologically, and behaviorally; 3) culling animals that are unable to reproduce without help from humans; and 4) creating grazing systems that enhance the well-being of soils, plants, herbivores, and people. In essence, it means getting by with what nature provides. Nature gets energy from the sun, works with what she has on hand, and provides a range of benefits (nutrition and health for plants, herbivores, and people) without the costs (fertilizers, herbicides, insecticides, antibiotics, and anthelmintics) of fossil fuels (Provenza et al., 2007).

The ongoing processes of becoming locally adapted result from interactions among history, necessity, and chance. History creates initial conditions and context, necessity provides incentives, and chance keeps the game interesting. Collectively, they create nonlinearities, those gradual processes of change that result in unending cycles of change not easily predicted or readily controlled (Kauffman, 1995, 2000; Overman, 1997; Taleb, 2001). The behaviors of systems from soils, plants, and herbivores to people emerge from complex interactions among history, necessity, and chance. As Laughlin (2005) points out, "Emergence means complex organizational structures growing out of simple rules. Emergence means stable inevitability in the way certain things are. Emergence means unpredictability, in the sense of small events causing great and qualitative changes in larger ones. Emergence means the fundamental impossibility of control. Emergence is a law of nature to which humans are subservient".

Emergence also means ongoing change and endless potential for creativity. Continual *change plus chance* equals opportunity for *creativity*. Although the undying goal of many in science and management is to predict and control change, in her very essence nature is unpredictable. Despite our best efforts, her ever emerging patterns, from climate change and hurricanes to social change and stock markets, are difficult to anticipate and predict, and even more costly and difficult to control. If nature is the ultimate tinkerer, and she loves to create, then we should be less concerned about attempting to predict and control her movements, and more intent on understanding how to dance with her. From the standpoint of management, that means we must engage in ongoing cycles of defining visions and goals → setting objectives → implementing practices → monitoring → and changing our behavior as we continually learn from and evolve with nature.

This view of management calls on science not to be a predictive oracle attempting to guide policy. Rather, science is a way to understand the processes of nature and to monitor and assess policies implemented through consensus. Playing nature's game is about flexibility in the face of change. Flexibility is about taking small steps and keeping our eyes open. Consensus helps us choose where to walk. Science helps our eyes to focus. In that sense, the challenge is to understand principles, processes, and interrelationships. The opportunity is to blend science with the local knowledge of people attempting to make their living on landscapes ever unique in time and space.

In *Leadership and the New Science*, Margaret Wheatley (1994) captures this idea perfectly when she writes about the evolution of thought in physics from the old (i.e., Newtonian) to the new (i.e., relativistic and quantum) views: "The new physics cogently explains that there is no objective reality out there waiting to reveal its secrets. There are no recipes or formula, no checklists, or advice that describes reality. There is only what we create through our engagement with others and events. Nothing really transfers. Everything is always new and different and unique to each of us. In this realm there is a new kind of freedom where it is more rewarding to explore than to reach conclusions. More satisfying to wonder than to know and more exciting to search than to stay put".

CONCLUSIONS

Who cares anyway? People who care in agriculture want to make a profit, as opposed to merely increase production, and they want to link ecology with economics to create a match between what animals need and what nature provides. That makes sense even at today's prices for fossil fuels, and it will make more sense as the availability of oil and natural gas diminishes over the next 35 to 40 yr, not only for people in agriculture, but for societies who want clean air, abundant water, and healthful foods.

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