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#### Summary

The availability of fossil fuels will likely decline dramatically during the first half of the twenty-first century, and the 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 beings. Agriculture will be much more at the heart of communities, but by necessity it will no longer be so dependent on fossils to fuel machinery or 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 what it means to be locally adapted to the landscapes we inhabit. In the process, 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, forages, fossil fuels, learning, livestock, people

#### Resumen

# Adaptabilidad es Sustentabilidad

La disponibilidad de combustible fósiles declinará probablemente dramáticamente durante la primera mitad del siglo veintiuno, y su déficit no será aliviado por fuentes alternativas de energía.

Esta catástrofe aparente creará oportunidades para las comunidades de beneficiarse de alimentos producidos localmente y de forma que nutre las relaciones entre el suelo, el agua, las plantas, los herbívoros y la gente para sostener su bienestar colectivo. La agricultura estará mucho más en el corazón de las comunidades, pero por necesidad no será más tan dependiente de combustibles fósiles para maquinaria o fertilizantes, herbicidas e insecticidas para cultivar y proteger plantas en monocultivos, antibióticos y antihelmínticos para mantener la salud de los herbívoros, o suplementos nutritivos y farmacéuticos para sostener humanos. Mejor dicho, del suelo y las plantas a herbívoros y gente tendremos que aprender lo que significa estar localmente adaptado a los paisajes en que vivimos. En el proceso, las plantas serán cada vez más importante como centros de nutrición y como farmacias, siendo su plétora de componentes primarios (nutrientes) y secundarios (farmacéuticos) útil en la nutrición y la salud. También habrá necesidad, como en tiempos pasados, antes de nuestra pesada dependencia de combustibles fósiles, de producir ganado en sistemas de fácil cuidado que armonicen los forrajes estacionalmente disponibles con las necesidades de producción, y que armonicen a los animales anatómica, fisiológica y comportamentalmente a los paisajes locales. Esto implicará reducir el uso de combustibles fósiles para aumentar la rentabilidad al 1) adecuar las necesidades animales a los recursos forrajeros, 2) seleccionar animales que están adaptados anatómica, fisiológica, y

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comportamentalmente a los ambientes locales, 3) refugar animales que no son capaces de reproducirse sin la intervención del hombre, y 4) crear sistemas de pastoreo que aumentarán el bienestar de los suelos, las plantas, los herbívoros y la gente.

Palabras clave: Adaptación, cambio, forrajes, combustibles fósiles, aprendizaje, ganado, gente

#### Introduction

Sustainability is first and foremost about ongoing adaptation in ever changing environments. What might that mean in the twenty-first century? Many now argue 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 (e.g., Kunstler, 2005; Rubin, 2009). 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 we currently do nationally and internationally.

Agriculture will be much more at the heart of these communities than it is nowadays, but its lifeblood will not be fossils to fuel machinery or 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 wellbeing of humans. Rather, from soils and plants to herbivores and people we will learn once again what it means to be locally adapted.

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 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 need to 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, as it requires only one third to one half the fossil fuel to produce a pound of beef from range as opposed to 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 animals

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. While 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

Grassroots efforts in agriculture now emphasize cutting costs to maximize profits, and many people are developing management philosophies and practices based upon natural processes (Howell, 2008). 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 additional forage inputs, by selecting for locally-adapted animals and by culling animals unable to reproduce without help from humans. That makes sense ecologically and economically. It also makes sense behaviorally: behavior links ecology and economy by creating a match between what animals need and what is on hand.

While 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.

Nor have we appreciated that ongoing adaptation by wild and domestic herbivores involves a continuous dialogue among genes and behavior in ever-changing social and biophysical environments. Soil, plants, animals and the continents they inhabit change constantly. Even in the short span of time since the last glaciations (roughly 20,000 years), changes in climate have drastically altered physical environments and the species of plants and animals that inhabit those environs (Pielou, 1991). Rather than adapting to these changes, 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 conception of livestock as grazers, rather than selecting among and within breeds of livestock for individuals that can use the plants that exist on landscapes. While 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 U.S., provided they have been selected anatomically, physiologically and behaviorally to survive on their own in the landscapes they inhabit (Provenza and Balph, 1990).

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We must take advantage of the marvelous variation within breeds to select for individuals able to perform efficiently on poor quality forages high in secondary compounds common in arid environments (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 able to consume the diverse arrays 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 (Provenza, 2003b). Historically, people have selected for animals of uniformly large frame sizes and body compositions, enabled in arid areas by supplemental forages, 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 (Johns, 1994).

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 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, as 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 days 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, www. PharoCattle.com).

#### At 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, and while 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).

An important form of this discourse, termed predictive adaptive responses (PAR), refers to responses that are 1) induced by the environment early in life, 2) cause changes neurologically, morphologically, physiologically and behaviorally, 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 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. To the degree that PAR 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 lifespan 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.

If, however, the fetus predicts its future reproductive environment incorrectly, either 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. 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, 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 pre-disposition to consider behaviors as fixed genetically, we have neither been aware nor 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 cause a suite of changes involving gene expression, neurological, morphological, and physiological processes that affect behavior (e.g., Schlichting and Pigliucci, 1998; Lewontin, 2000; LeDoux, 2002; Moore, 2002; Dufty *et al.*, 2002; Provenza and Villalba, 2006; Doidge, 2007).

Learning from mother begins early in life as flavors of foods mother eats are transferred to her offspring in utero and in her milk, thus preparing the developing fetus for forages it will encounter after birth. The fetal taste system is fully functional during the last trimester of gestation, and flavors in mother's diet influence food preference of her offspring (Simitzis et al., 2008). For instance, the flavors of onion and garlic are transferred in utero and in milk, which increases the likelihood young animals will eat onion and garlic when they begin to forage (Nolte et al., 1992; Nolte and Provenza, 1992a,b). 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). Lambs fed nutritious foods like wheat with their mothers for as little as 1 hour/day for 5 days eat more wheat than lambs exposed to wheat without their mothers. Even 3 years 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). Crossfostering studies show that young goats eat markedly more high-tannin browse if their mother eats high-tannin browse (Tzack et al., 2009). Young herbivores also learn motor skills needed to harvest grasses, forbs, and shrubs, all forages with different architectures (Flores et al., 1989a,b; Ortega-Reyes and Provenza, 1993a,b), they acquire preferences for foods (sheep - Nolte and Provenza, 1992a,b; Squibb et al., 1990; goats - Biquand and Biquand-Guyot, 1992), and their bodies adapt to using particular foods (Ortega Reyes et al., 1992; Distel et al., 1994, 1996). For instance, lambs exposed to saltbush in utero grow faster and handle a salt load better than lambs from mothers on pasture; they excrete salt

2009a,b,c). Livestock also eat more of poor-quality forages they have learned to eat early in life with their mothers. Goats reared from 1 to 4 months of age with their mothers on blackbrush-dominated rangeland ate over 2.5 times more blackbrush than did goats naive to blackbrush. Moreover, experienced goats consumed 30% more blackbrush than inexperienced goats when allowed to choose between the poorly nutritious blackbrush and alfalfa pellets (Distel and Provenza, 1991). Likewise, intake and animal performance differed markedly during a 3-year study when cows 5 years of age were fed straw

more rapidly, drink less water, and maintain higher

intake when eating saltbush (Chadwick et al.,

as a major part of their diet from December to May (Wiedmeier *et al.*, 2002). Half of the cows ate straw for 2 months as calves, whereas the other half had never seen straw. Throughout the study, experienced cows ate more straw, maintained better body weight and condition, produced more milk, and bred back sooner than cows not exposed to straw.

#### Linking soil, plants, herbivores and people

The health of landscapes depends on interrelationships among soils, plants, herbivores and people. Nearly 50 years 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 forgotten that our bodies come from the soil. To Voisin, it seemed that the rise of the artificial fertilizer industry has 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, soil developed naturally and rich in organic matter and nutrients provide the basis for health in plants, herbivores and people.

Importantly, people can use grazing by livestock 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 and urine and the trampling of plants (McNaughton, 1984; Bryant et al., 1991, Savory and Butterfield, 1999, Augustine et al., 2003; Gerrish, 2004; Howell, 2008). Thus, herbivores can 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, 2003a,b).

#### The Value of Plant Diversity

Natural landscapes are diverse mixes of plants that occur in patches reflecting history of use in concert with

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particular soil, precipitation and temperature regimes. 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).

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 bodies have built-in mechanisms that ensure animals satiate on foods eaten in a meal, which guarantees animals eat a variety of foods and forage in different locations (Provenza, 1995a, 1996; Bailey and Provenza, 2007). Variety enables animals to reap the benefits of ingesting various primary and secondary compounds and it also enables individuality. Bodies have the nutritional wisdom necessary to meet needs for energy, protein and various minerals (Provenza and Villalba, 2006), and to self-medicate (Villalba and Provenza, 2007). 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 years about the roles of secondary compounds in the health of plants, including functions as diverse as attracting pollinators and seed dispersers, 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 wellbeing 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 that vary in time of production, depths of rooting, and contrasting uses of water and nutrients (Provenza et al., 2007).

For people, 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 secondary metabolites (Craig, 1999; Engel, 2002). With ready access to processed foods high in sugar, carbohydrates, fat and salt, young people no longer acquire preferences for «unpalatable» foods as they lack the traditional cultural foundations to guide their selection of foods high in secondary compounds (Johns, 1994). Conversely, hunter-gatherers who have maintained their traditional diets have far less cancer, heart disease, diabetes and osteoporosis than people who forage on fast foods, and it is not because hunter-gatherers die before these ills can develop (Logan and Dixon, 1994; Johns, 1994, Engel, 2002).

Issues of diet mixing and secondary compounds are just as relevant for the nutrition and health of herbivores. While we 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 (Niezen et al., 2002; Min et al., 2004a,b). 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, 2008; Luciano et al., 2008). More generally, diverse assortments of secondary compounds in the diets of herbivores are likely to influence the flavor, color, and quality of meat, milk, and cheese for human consumption in ways that are positive, but as yet mostly unknown (Carpino et al., 2004a,b; Vasta et al., 2008a,b).

## Diet Sequencing and Complementarities among Secondary Compounds

While complementarities among secondary compounds are an important but little understood area of plant-herbivore interactions, even less is known about how the sequences of eating plants with different compounds affects foraging, though they appear to be critical. Sheep eat much more food with terpenes when they first eat food with tannins (Mote *et al.*, 2008). These findings are consistent with landscape-level studies that show ewes with a high preference for sagebrush, a shrub high in terpenes, also consume more bitterbrush, a shrub high in tannins, compared with ewes that have a lower preference for sagebrush (Seefeldt, 2005). While further studies are required to assess how sequence affects food consumption, these data indicate there is a strong effect.

Likewise, cattle steadily decrease time eating endophyte-infected tall fescue when they first graze tall fescue alone for 30 minutes followed by trefoil, alfalfa, or alfalfa-trefoil combination for 60 minutes (Lyman *et al.*, 2009). Conversely, when the sequence is reversed, cattle forage actively on trefoil, alfalfa, or trefoil-alfalfa combination and then forage actively on fescue throughout the 90-minute meal. These patterns of foraging are similar with high-alkaloid reed canarygrass (Lyman *et al.*, 2009). Sequence of ingestion thus greatly influences intake of alkaloid-containing grasses by cattle.

Our research thus suggests eating tannin- and saponin-containing forages increases intake and may reduce fescue toxicity, which highlights the potential major impact of plant diversity generally and biochemical complementarities specifically. If legumes high in tannins and saponins can offset the negative effects of the alkaloids in tall fescue, the economic impact for beef producers coping with fescue toxicosis will be enormous. More generally, other toxic plant problems worldwide may benefit from similar research and applications of biochemical diversity. While this research is promising and suggestive of the importance of the interactions between forages with different secondary compounds, we are only beginning to understand the complexities involved in diet sequencing based on a limited number of forages and compounds.

#### Conclusions

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 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. She gets her energy from the sun, she works with what she has on hand, and she provides a range of benefits (nutrition and health for plants, herbivores and people) without the costs (fertilizers, herbicides, insecticides, antibiotics and anthelmintics) of fossilfuels (Provenza et al., 2007). 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 years, not only for people in agriculture, but for societies who want clean air, abundant water and healthful foods.

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# References

- Augustine, D.J.; McNaughton, S.J. and Frank, D.A. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. Ecological Applications 13:1325-1337.
- Bailey, D.W. and Provenza, F.D. 2007. Mechanisms determining large herbivore distribution. In press in F. van Langevelde and H.T.T. Prins (eds.) Resource Ecology Spatial and Temporal Dynamics of Foraging. Wageningen University Resource Ecology Group & Frontis, Wageningen.
- Barry, T.N.; McNeill, D.M. and McNabb, W.C. 2001. Plant secondary compounds: their impact on nutritive value and upon animal production. Pages 445-452 in Proc. XIX Int. Grass. Conf., Sao Paulo, Brazil.
- Biquand, S. and Biquand-Guyot, V. 1992. The influence of peers, lineage and environment on food selection of the criollo goat (*Capra hircus*). Appl. Anim. Behav. Sci. 34:231-245.
- Bryant, J.P.; Provenza, F.D.; Pastor, J.; Reichardt, P.B.; Clausen, T.P. and DuToit, J.T. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Ann. Rev. Ecol. Syst. 22: 431-446.
- Carpino, S.; Home, J.; Melilli, C.; Licitra, G.; Barbano, D.M. and Van Soest, P.J. 2004a. Contribution of native pasture to the sensory properties of Ragusano cheese. J. Dairy Sci. 87:308-315.
- Carpino, S.; Mallia, S.; La Terra, S.; Melilli, C.; Licitra, G.; Acree, T.E.; Barbano, D.M. and Van Soest, P.J. 2004b. Composition and aroma compounds of Ragusano cheese: Native Pasture and Total Mixed Rations. J. Dairy Sci. 87:816-830.
- Chadwick M.A.; Vercoe, P.V.; Williams, I.H. and Revell, D.K. 2009a. Programming sheep production on saltbrush: adaptations of offspring from ewes that consumed high amounts of salt during pregnancy and early lactation. Anim. Prod. Sci. 49:311-317.
- Chadwick M.A.; Vercoe, P.V.; Williams, I.H. and Revell, D.K. 2009b. Dietary exposure of pregnant ewes to salt dictates how their offspring respond to salt. Physiol. Behav. 97:437:445.
- Chadwick M.A.; Vercoe, P.V.; Williams, I.H. and Revell, D.K. 2009c. Feeding pregnant ewes a high-salt diet or saltbrush suppresses their offspring's postnatal rennin activity. Animal in press.

- Craig, W.J. 1999. Health-promoting properties of common herbs. Am. J. Clin. Nutr. 70:491S-499S.
- **Crozier, A.; Clifford, M.N. and Ashihara, H.** (eds.) 2006. Plant Secondary Metabolites: Occurrence, Structure and Role in the Human Diet. Blackwell Publ. Ames, IO.
- **Davis, J.M. and Stamps, J.A.** 2004. The effect of natal experience on habitat preferences. Trends Ecol. Evol. 19:411-416.
- **Distel, R.A. and Provenza, F.D.** 1991. Experience early in life affects voluntary intake of blackbrush by goats. J. Chem. Ecol. 17:431-450.
- **Distel, R.A.; Villalba, J.J. and Laborde, H.E.** 1994. Effects of early experience on voluntary intake of low-quality roughage by sheep. J. Anim. Sci. 72:1191-1195.
- Distel, R.A.; Villalba, J.J.; Laborde, H.E. and Burgos, M.A. 1996. Persistence of the effects of early experience on consumption of low-quality roughage by sheep. J. Anim. Sci. 74:965-968.
- **Dufty, A.M. Jr.; Clobert, J. and Moller, A.P.** 2002. Hormones, developmental plasticity and adaptation. Trends Ecol. Evol. 17:190-196.
- **Demment, M.W. and VanSoest, P.J.** 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Nat. 125:641-672.
- **Doidge, N.** 2007. The Brain that Changes Itself: Stories of Personal Triumph from the Frontiers of Brain Science. Penguin Books. New York, NY.
- Engel, C. 2002. Wild Health. Houghton Mifflin Co. Boston. New York, NY.
- Flores, E.R.; Provenza, F.D. and Balph, D.F. 1989a. Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. Appl. Anim. Behav. Sci. 23:271-278.
- Flores, E.R.; Provenza, F.D. and Balph, D.F. 1989b. The effect of experience on the foraging skill of lambs: importance of plant form. Appl. Anim. Behav. Sci. 23:285-291.
- Gerrish, J. 2004. Management-Intensive Grazing: The Grassroots of Grass Farming. Green Park Press, Ridgeland, MS.
- **Gluckman, P.D.; Hanson, M.A. and Spencer, H.G.** 2005. Predictive adaptive responses and human evolution. Trends Ecol. Evol. 20:527-533.
- Green, G.C.; Elwin, R.L.; Mottershead, B.E. and Lynch, J.J. 1984. Long-term effects of early experience to supplementary feeding in sheep. Proc. Aust. Soc. Anim. Prod. 15:373-375.
- Hofmann, R.R. 1988. Anatomy of the gastrointestinal tract. Pages 14-43 in Church, D.C. (ed.) The ruminant animal. Prentice Hall, Englewood Cliffs.
- **Howell, J.** 2008. For the Love of Land: Global Case Studies of Grazing in Nature's Image. www.booksurge.com.
- Howery, L.D.; Provenza, F.D.; Banner, R.E. and Scott, C.B. 1998. Social and environmental factors influence cattle distribution on rangeland. Appl. Anim. Behav. Sci. 55:231-244.

- Johns, T. 1994. Ambivalence to the palatability factors in wild food plants. Pages 46-61 in Etkin, N.L. (ed.), Eating on the Wild Side: The Pharmacologic, Ecologic, and Social Implications of Noncultigens. The University of Arizona Press, Tucson, AZ.
- Kunstler, J.H. 2005. The Long Emergency: Surviving the End of Oil, Climate Change, and Other Converging Catastrophes of the Twenty-First Century. Grove Press. New York, NY.
- LeDoux, J. 2002. Synaptic Self: How Our Brains Become Who We Are. Viking Penguin. New York, NY.
- Logan, M.H. and Dixon, A.R. 1994. Agriculture and the acquisition of medicinal plant knowledge. Pages 25-45 in Etkin, N.L. (Ed.) Eating on the Wild Side: The Pharmacologic, Ecologic, and Social Implications of Noncultigens. The University of Arizona Press, Tucson, AZ.
- Lewontin, R. 2000. The Triple Helix: Gene, Organism, and Environment. Harvard Univ. Press, Cambridge, MA.
- Lyman, T.D.; Provenza, F.D.; Villalba, J.J. and Wiedmeier, R.D. 2009. Complementarities among tall fescue, reed canarygrass, birdsfoot trefoil, and alfalfa affect cattle foraging behavior. J. Anim. Sci. accepted.
- Lipton, B. 2005. The Biology of Belief: Unleashing the Power of Consciousness, Matter & Miracles. Mountain of Love/Elite Books. Santa Rosa, CA.
- Luciano, G.; Monahan, F.J.; Vasta, V.; Biondi, L.; Lanza, M. and Priolo, A. 2008. Dietary tannins improve lamb meat colour stability. Meat Sci. 81:120–125.
- McNaughton, S.J. 1984. Grazing lawns: Animals in herds, plant form and coevolution. Am. Nat. 124:863-886.
- Min, B.R. and Hart, S.P. 2003. Tannins for suppression of internal parasites. J. Anim. Sci. 81:E102-E109.
- Min, B.R.; Fernandez, J.M.; Barry, T.N.; McNabb, W.C. and Kemp, P.D. 2001. The effect of condensed tannins in *Lotus corniculatus* upon reproductive efficiency and wool production in ewes during autumn. Anim. Feed Sci. Tech. 92:185-202.
- Min, B.R.; Hart, S.P.; Miller, D.; Tomita, G.M.; Loetz, E. and Sahlu, T. 2004a. The effect of grazing forage containing condensed tannins on gastro-intestinal parasite infection and milk composition in Angora does. Vet. Parasit. 130:105-113.
- Min, B.R.; Pomroy, W.E.; Hart, S.P. and Sahlu, T. 2004b. The effect of short-term consumption of a forage containing condensed tannins on gastro-intestinal nematode parasite infections in grazing wether goats. Small Rum. Res. 51:279-283.
- Mirza, S.N. and Provenza, F.D. 1990. Preference of the mother affects selection and avoidance of foods by lambs differing in age. Appl. Anim. Behav. Sci. 28:255-263.
- Mirza, S.N. and Provenza, F.D. 1992. Effects of age and conditions of exposure on maternally mediated food selection in lambs. Appl. Anim. Behav. Sci. 33:35-42.

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- **Moore, D.S.** 2002. The Dependent Gene: The Fallacy of «Nature vs. Nurture.» Henry Holt and Company, New York, NY.
- Mote, T.; Villalba, J.J. and Provenza, F.D. 2008. Foraging sequence influences the ability of lambs to consume foods containing tannins and terpenes. Appl. Anim. Behav. Sci. 113:57-68.
- Niezen, J.H.; Charleston, W.A.G.; Robertson, H.A.; Shelton, D.; Waghorn, G.C. and Green, R. 2002. The effect of feeding sulla (Hedysarum coronarium) or lucerne (Medicago sativa) on lamb parasite burdens and development of immunity to gastrointestinal nematodes. Vet. Parasit. 105:229-245.
- Nolte, D.L.; Provenza, F.D.; Callan, R. and Panter, K.E. 1992. Garlic in the ovine fetal environment. Physiol. Behav. 52:1091-1093.
- Nolte, D.L. and Provenza, F.D. 1992a. Food preferences in lambs after exposure to flavors in milk. Appl. Anim. Behav. Sci. 32:381-389.
- Nolte, D.L. and Provenza, F.D. 1992b. Food preferences in lambs after exposure to flavors in solid foods. Appl. Anim. Behav. Sci. 32:337-347.
- Ortega Reyes, L.; Provenza, F.D.; Parker, C.F. and Hatfield, P.G. 1992. Drylot performance and ruminal papillae development of lambs exposed to a high concentrate diet while nursing. Small Rum. Res. 7: 101-112.
- Ortega-Reyes, L. and Provenza, F.D. 1993a. Amount of experience and age affect the development of foraging skills of goats browsing blackbrush (Coleogyne ramosissima). Appl. Anim. Behav. Sci. 36:169-183.
- **Ortega-Reyes, L. and Provenza, F.D.** 1993b. Experience with blackbrush affects ingestion of shrub live oak by goats. J. Anim. Sci. 71:380-383.
- **Pielou, E.C.** 1991. After the Ice Age: The Return of Life to Glaciated North America. The University of Chicago Press, Chicago, IL.
- Pollan, M. 2006. The Omnivores Dilemma: A Natural History of Four Meals. The Penguin Press, New York, NY.
- Priolo, A.; Bella, M.; Lanza, M.; Galofaro, V.; Biondi, L.; Barbagallo, D.; Ben Salem, H. and Pennisi, P. 2005. Carcass and meat quality of lambs fed fresh sulla (*Hedysarum coronarium* L.) with or without polyethylene glycol or concentrate. Small Rum. Res. 59:281–288.
- Priolo, A.; Vasta, V.; Fasone, V.; Lanza, C.M.; Scerra, M.; Biondi, L.; Bella, M. and Whittington, F.M. 2008. Meat odour and flavour and indloes concentration in ruminal fluid and adipose tissue of lambs fed green herbage or concentrates with or without tannins. Animal in press.
- **Provenza, F.D.** 1995a. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range Manage. 48:2-17.
- Provenza, F.D. 1995b. Tracking variable environments: There is more than one kind of memory. J. Chem. Ecol. 21:911-923.

- Provenza, F.D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. J. Anim. Sci. 74:2010-2020.
- Provenza, F.D. 2003a. Foraging Behavior: Managing to Survive in a World of Change. Utah State Univ., Logan.
- **Provenza, F.D.** 2003b. Twenty-five years of paradox in plantherbivore interactions and «sustainable» grazing management. Rangelands 25:4-15.
- Provenza, F.D. and Balph, D.F. 1990. Applicability of five diet-selection models to various foraging challenges ruminants encounters. Pages 423-459 in R.N. Hughes (Ed.), Behavioural Mechanisms of Food Selection. NATO ASI Series G: Ecological Sciences, Vol. 20. Springer-Verlag, Berlin. Heildelberg, Germany.
- Provenza, F.D. and Villalba, J.J. 2006. Foraging in domestic vertebrates: Linking the internal and external milieu. Pages 210-240 in V.L. Bels (ed.) Feeding in Domestic Vertebrates: From Structure to Function. CABI Publ., Oxfordshire, UK.
- Provenza, F.D.; Pfister, J.A. and Cheney, C.D. 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. J. Range Manage. 45:36-45.
- Provenza, F.D.; Villalba, J.J.; Dziba, L.E.; Atwood, S.B. and Banner, R.E. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. Small Rum. Res. 49:257-274.
- Provenza, F.D.; Villalba, J.J.; Haskell, J.H.; MacAdam, J.A.; Griggs, T.C. and Wiedmeier, R.D. 2007. The value to herbivores of plant physical and chemical diversity in time and space. Crop Sci. 47:382-398.
- Rosenthal, G.A. and Janzen, D.H. (eds.). 1979. Herbivores: Their Interaction with Secondary Plant Metabolites. Academic Press, New York, NY.
- Rosenthal, G.A. and Berenbaum, M.R. (eds.). 1992. Herbivores: Their Interactions with Secondary Plant Metabolites. Second Ed. Academic Press, New York, NY.
- **Rubin, J.** 2009. Why Your World is About to Get a Whole Lot Smaller. Random House, New York, NY.
- Savory, A. and Butterfield, J. 1999. Holistic Management: A New Framework for Decision-Making. Second Edition, Island Press, Covalo, Calif.
- Schlichting, C.D. and Pigliucci, M. 1998. Phenotypic Evolution: A Reaction Norm Perspective. Sinauer Publications, Sinauer, MA.
- Seefeldt, S.S. 2005. Consequences of selecting Ramboulliet ewes for Mountain Big Sagebrush (*Artemisia tridentata* ssp. vaseyana) dietary preference. Rangeland Ecol. Manage. 58:380-384.
- Simitzis, P.E.; Deligeorgis, S.G.; Bizelis, J.A. and Fegeros, K. 2008. Feeding preferences in lambs influenced by prenatal flavour exposure. Physiol. Behav. 93:529-536.
- Squibb, R.C.; Provenza, F.D. and Balph, D.F. 1990. Effect of age of exposure on consumption of a shrub by sheep. J. Anim. Sci. 68:987-997.

#### AGROCIENCIA

- Thorhallsdottir, A.G.; Provenza, F.D. and Balph, D.F. 1990. Ability of lambs to learn about novel foods while observing or participating with social models. Appl. Anim. Behav. Sci. 25:25-33.
- Tzack, A.G.; Ungar, E.D.; Landau, S.Y.; Perevolotsky, A.; Muklada, H. and Walker, J.W. 2009. Breed and maternal effects on the intake of tannin-rich browse by juvenile goats (*Capra hircus*). Appl. Anim. Behav. Sci. 119:71-77.
- Vasta, V.; Nudda, A.; Cannas, A.; Lanza, M. and Priolo, A. 2008a. Alternative feed resources and their effects on the quality of meat and milk from small ruminants. Anim. Feed Sci. Tech. 147:223–246.
- Vasta, V.; Harinder Makkar, H.P.S.; Mele, M. and Priolo, A. 2008b. Ruminal biohydrogenation as affected by tannins *in vitro*. Brit. J. Nutr. In press.
- Villalba, J.J. and Provenza, F.D. 2007. Self-medication and homeostatic endeavor in herbivores: learning about the benefits of nature's pharmacy. Animal 1:1360-1370.

- Voisin, A. 1959. Soil, Grass and Cancer. Philosophical Library, Inc. New York, NY.
- Waghorn, G. C. 1990. Beneficial effects of low concentrations of condensed tannins in forages fed to ruminants. P137 in D.E. Akin, L.G. Ljungdahl, J.R. Wilson, and P.J. Harris. (ed.) Microbial and Plant Opportunities to Improve Lignocellulose Utilization by Ruminants. Elsevier Sci. Publ., New York, NY.
- Wiedmeier, R.D.; Provenza, F.D. and Burritt, E.A. 2002. Exposure to ammoniated wheat straw as suckling calves improves performance of mature beef cows wintered on ammoniated wheat straw. J. Anim. Sci. 80: 2340-2348.
- Woodward, S.L.; Waghorn, G.C. and Laboyrie, P.G. 2004. Condensed tannins in birdsfoot trefoil (Lotus corniculatus) reduce methane emissions from dairy cows. Proceedings of the New Zealand Society of Animal Production 64:160–164.