Behavior-based management of ecosystems

Provenza F.D., Papachristou T.G.

in

Papachristou T.G. (ed.), Parissi Z.M. (ed.), Ben Salem H. (ed.), Morand-Fehr P. (ed.).
Nutritional and foraging ecology of sheep and goats

Zaragoza : CIHEAM / FAO / NAGREF
Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 85

2009
pages 13-28

Behavior-based management of ecosystems

F.D. Provenza* and T.G. Papachristou**

*Department of Wildland Resources, Utah State University, Logan, Utah 84322-5230 (USA)
**Forest Research Institute, National Agricultural Research Foundation, 57006 Vassilika, Thessaloniki (Greece)

Abstract. Once understood, behavioral principles and processes can be translated into practices that provide an array of solutions to the challenges people face in managing to maintain livelihoods and the integrity of landscapes. Unlike the infrastructure of a ranch such as corrals, fences, and water development, behavioral solutions cost little to implement and they are not fossil-fuel intensive. They are also easily transferred from one situation to the next. Unfortunately, scientists and managers often ignore the power of behavior to transform systems, despite compelling evidence. The environment, continually interacting with the genome during the growth and development of an organism, creates behavioral responses that in social animals are transferred across generations. Given time, that forms the basis for what it means to be locally adapted to a landscape. Though experiences during development in utero and early in life are especially critical, genome-environment interactions continue throughout life. Thus, the issue is not whether if soils, plants, herbivores, and people are adapting to ongoing changes in biophysical and social environments; they all do so continually. For those willing to understand how these ongoing interactions influence behavior, the potential is unlimited. In the case of grazing, behavioral solutions are increasingly attractive given growing social, economic and ecological concerns with wildfires, herbicides, and mechanical means of rejuvenating landscapes. Behavior-based management offers opportunities, for example, to use understanding of: (i) the relationship between palatability and plant biochemistry to rejuvenate landscapes to benefit wild and domestic animals; (ii) the importance of variety in the diet and daily grazing sequences of livestock to enhance wildlife benefits to land owners, managers, and users; and (iii) the value of biochemical complementarities for developing plant mixes for pastures that provide a full range of benefits – nutrition and health for plants, herbivores, and people – without the unsustainable fossil fuel costs associated with fertilizers, herbicides, insecticides, antibiotics and anthelmintics.

Keywords. Grazing management – Rangelands – Plant-herbivore interactions – Landscape biodiversity.

Gestion des écosystèmes basée sur le comportement animal

Résumé. *La compréhension des principes et processus comportementaux permet leur transfert à l'échelle pratique qui apporte une gamme de solutions pour les personnes faisant face aux défis liés à la gestion afin de maintenir les moyens d'existence et l'intégrité des paysages. Contrairement à l'infrastructure d'un ranch telle que les corrals, les clôtures, et le développement hydrique, les solutions basées sur le comportement sont moins coûteuses à la mise en œuvre. Leur transfert d'une situation à une autre est aussi facile. Néanmoins, les scientifiques et les gestionnaires ignorent souvent la capacité du comportement à transformer les systèmes, en dépit d'une évidence convaincante. L'environnement inter-réagit de façon continue avec le génome durant la croissance et le développement de l'organisme. Il est aussi à l'origine de la création des réponses comportementales qui sont transférées au niveau de la société animale à travers les générations. Bien que les expériences pendant le développement in utero et au début de la vie soient particulièrement critiques, les interactions génome environnement se poursuivent pendant la vie de l'animal. Par conséquent, le problème pourrait être évité si les systèmes, sols, plantes, herbivores, et l'homme, étaient adaptables aux prochains changements des environnements sociaux et biophysiques. Pour ceux qui souhaitent comprendre comment les environnements inter-réagissent avec le génome pour influencer le comportement, le potentiel est pratiquement illimité. En effet, dans le cas du pâturage, les solutions comportementales sont de plus en plus attractives compte tenu des soucis sociaux, économiques et écologiques relatifs aux incendies, aux herbicides et aux moyens mécaniques de rajeunissement des paysages. La gestion basée sur le comportement offre des opportunités relatives, par exemple, à la compréhension : (i) des relations entre la palatabilité et la biochimie végétale pour rajeunir les paysages au profit des animaux sauvages et domestiques ; (ii) de l'importance de la composition de la ration et des séquences journalières de pacage des animaux pour améliorer les bienfaits de la faune pour les propriétaires des parcours, les gestionnaires, et les usagers ; et (iii) de la valeur des complémentarités biochimiques pour le développement de mélanges de plantes pour les pâturages qui apportent une gamme élargie d'avantages ; nutrition et santé pour les plantes, les herbivores, et l'homme sans* *dépenses non durables pour les fertilisants, les herbicides, les insecticides, les antibiotiques et les produits anthelminthiques.*

Mots-clés. *Gestion du pacage – Parcours – Interactions plante herbivore – Biodiversité paysagère.*

I – Introduction

There is evidence that behavioral principles and processes can be translated into practices that provide an array of solutions to the problems people face in managing to improve the integrity of the land and to make a living from the land (Provenza, 2003a). Unlike the infrastructure of a ranch or a public grazing land, such as corrals, fences, and water development, behavioral solutions cost very little to implement, they are not fossil-fuel intensive, and they are easily transferred from one situation to the next. In the case of grazing, for instance, behavioral solutions are increasingly attractive given growing economic and environmental concerns with fire, herbicides, and mechanical means of rejuvenating landscapes. Scientists and managers often ignore the power of behavior to transform systems, despite compelling evidence. We know the environment continually interacting with the genome during the growth and development of an organism creates behavioral responses. Though experiences during development in utero and early in life are especially critical, genome-environment interactions continue throughout life and they constitute what it means for all organisms to be locally adapted to landscapes. Thus, the issue isn't if creatures are adapting to ongoing changes in biophysical environments, they do so every day of their lives. The only question is whether or not people want to be a part of that process. For those willing to understand how environments interact with the genome to influence behavior, the potential is virtually unlimited. The challenge is to understand and apply the principles to all facets of one's life. In that sense, rather than developing and transferring "technology" packages, we aim to change, fundamentally, the way people understand and use behavior to manage ecosystems. We want people to realize the power of behavior to transform systems ecologically, economically, and socially.

To do so, we are engaged in research and outreach activities that: (i) improve the economic viability and ecological integrity of range-based enterprises on privately and federally managed landscapes; (ii) use natural plant communities as models to develop bio-diverse pastures that provide the full range of benefits – nutrition and health for plants, herbivores, and people – without the unsustainable costs of monocultures associated with fertilizers, herbicides, insecticides, antibiotics and anthelmintics; (iii) first enhance and then maintain the biodiversity of landscapes dominated by weeds; (iv) optimize wildlife benefits to land owners, managers, and users; (v) use contact with nature – gardens as ecosystems and lambs as models – to encourage healthy lifestyles in children in middle-schools and young women with eating disorders; (vi) improve the ability of people to adapt within and manage complex adaptive social, ecological, and economic systems; and (vii) bring innovative researchers and managers from around the world together to share their growing understanding of behavioral principles and processes and their integration with indigenous knowledge and practices.

For the past 30 years, considerable information has appeared in the literature on how learning influences food and habitat selection in the ruminants (see Provenza, 1995, 1996, 2003a). Recently, there is an attempt to actively engage land managers, as described above (see www.behave.net), that is leading to an integration of scientific understanding with local knowledge to create applications for the research. As discussed in what follows, behavior-based grazing management offers opportunities to use understanding of: (i) the relationship between palatability and plant biochemistry to rejuvenate landscapes to benefit wild and domestic animals; (ii) the importance of experiences early in life in creating locally adapted animals; and (iii) the value of biochemical complementarities for developing plant mixes for pastures that provide a full range of benefits – nutrition and health for plants, herbivores and people – without the unsustainable costs of fertilizers, herbicides, insecticides, antibiotics and anthelmintics.

II – A functional explanation for palatability

Palatability is considered to be a matter of taste, and all popular definitions focus on either a food's flavor or its physical and chemical characteristics. Yet, if palatability is merely a matter of taste, why do goats eat woodrat houses? Why do goats, sheep and cattle supplemented with polyethylene glycol increase their intake of unpalatable plants high in tannins? Why can sheep and cattle be trained to avoid eating grapes and poisonous plants? Why can they be trained to rejuvenate landscapes?

1. Flavor-feedback interactions

Palatability is more than a matter of taste. Palatability is a functional relationship between a food's flavor and its postingestive consequences from cells and organs in response to primary and secondary compounds in foods. Flavor is the combination of odor, taste, and texture (Provenza and Villalba, 2006). Postingestive effects are feedback from the cells and organs. Feedback is positive (increases palatability) if the food meets nutritional needs. Feedback is negative (decreases palatability) if the food is inadequate or excessive relative to nutritional needs or if the food is toxic. Thus, flavor-feedback interactions are influenced by the nutrient and toxin content of the food and the nutritional needs of the animal. The senses of smell, taste, and sight enable animals to select among foods and provide pleasant or unpleasant feelings associated with eating. Thus, postingestive feedback influences an animal's liking or disliking for a food and that depends on how well a food meets the needs of the body.

Feedback within the body is critical for health and well-being. Bodies are made up of cells, organs, and organ systems all with nutritional needs. They interact with one another through feedback from nerves, neurotransmitters, and hormones. In the case of flavor-feedback interactions, nerves for taste converge with nerves from the body at the base of the brain. These nerves interact as they send information throughout the central nervous system. Feedback from the body to the palate is how groups of cells and organs influence which foods and how much of those foods are eaten (Provenza, 1995).

Changes in palatability through flavor-feedback interactions occur automatically. Animals don't need to think about or remember the feedback event, just as none of us need to consider which enzymes to release to digest the foods we eat. Even when animals are anesthetized or tranquilized, postingestive feedback still changes palatability (Provenza *et al.*, 1994a). When sheep eat a nutritious food and then receive a toxin dose during deep anesthesia, they become averse to the food because the negative feedback of the toxin occurs even when the animals are deeply asleep. Thus, feedback operates automatically, and often in the absence of rationality, to change palatability. For example, people acquire food aversions even when they know their illness was not caused by the food. A person often acquires strong aversions to foods eaten just before becoming nauseated even if the person knows that the flu or seasickness – not the food – was responsible for the nausea.

2. Goats and woodrat houses

The shrub blackbrush (*Coleogyne ramosissima*) is deficient in energy and protein. Several years ago during a winter-grazing study, Provenza *et al.* (1983) placed small groups of goats on six blackbrush pastures. As the study progressed, goats became increasingly averse to blackbrush. In one pasture they began to eat the bark-covered and vegetation structured houses of woodrats (*Neotoma lepida*). Goats acquired a preference for woodrat houses because the houses contained urine-soaked (nitrogen-rich) densely-packed vegetation that helped goats overcome their N deficiency. By the end of the study, goats that ate woodrat houses lost 12% of body weight, whereas goats that had not discovered woodrat houses as a source of macronutrients lost 20%. Animals deficient in nutrients seek out new foods, and animals are likely to form a preference for a food, no matter how odd, if postingestive feedback from the food corrects a nutritional deficit or imbalance.

3. Polyethylene glycol

Depending on their structure and concentration, tannins can reduce the digestibility of protein and energy in foods, and some tannins are toxic (Clausen *et al.*, 1990; Makkar, 2003). Polyethylene glycol binds with tannins, preventing their adverse effects. Animals fed small amounts of polyethylene glycol eat much more of foods high in tannins because the tannins no longer produce negative effects. Thus, the aversive post-ingestive effects of tannins, not their flavor, renders plants high in tannins unpalatable, and the positive post-ingestive effects of nutrients in the food that makes high-tannin foods palatable. That's why polyethylene glycol can be used to train animals to eat unpalatable weeds, such as *Sericea lespedeza*, that are high in tannins (Mantz, 2008).

4. Training livestock to eat or avoid foods

Livestock including sheep, cattle and horses have been trained to eat or avoid particular foods. Kathy Voth has developed a program of training livestock to eat various species of weeds by spraying them with molasses, which provides positive postingestive feedback (see www.livestockforlandscapes.com). Conversely, compounds such as LiCl that condition food aversions (Provenza *et al.*, 1994b), have been used to train sheep to avoid eating grape vines in vineyards (see www.sciencentral.com, life sciences – Eco Mowers posted 09/11/07), cattle to avoid eating poisonous plants such as larkspur (Ralphs, 1997), and horses to avoid eating poisonous plants such as locoweed (Pfister *et al.*, 2002, 2007). Important considerations in the training process have been outlined by Ralphs and Provenza (1999), and they include food novelty, compound dosage, and social influences.

5. Rejuvenating landscapes

A critical application of behavior-based management is on grazed landscapes, especially in light of ever increasing costs of fossil fuels relied upon heavily in conventional range improvement programs (Provenza, 2008). For example, sagebrush-steppe is one of the largest ecosystems in North America. Herbicides and mechanical removal of sagebrush (*Artemisia tridentata*) is expensive and can adversely impact environments. Fire often is useful, but where sagebrush is dense, intense fire storms may render areas sterile and subject to invasion by annual grasses such as cheatgrass (*Bromus tectorum*) (West, 1999). In contrast, grazing is a more economical way to enhance diversity of landscapes by creating mosaics of grasses and forbs within sagebrush stands, thereby changing the small-scale distribution pattern, density, and age-class structure of sagebrush-steppe communities (Woodland, 2008). Grazing may also minimize re-invasion of sagebrush into areas previously treated mechanically, with herbicides, or with fire. This behavior-based management is extremely important for Mediterranean shrublands, such as *matorral*, *maquis*, *garrigue* and *phrygana*, which are managed as grazing lands (Papachristou *et al.*, 2005).

Sheep and goats supplemented with energy and protein eat double the amount of sagebrush as unsupplemented animals, evidently because macronutrients enhance detoxification processes (Banner *et al.*, 2000; Villalba *et al.*, 2002). Thus, intake of sagebrush may be increased, and the impacts of sagebrush on livestock mitigated, if large numbers of supplemented animals graze sagebrush for short periods as demonstrated in a field study on how supplemental macronutrients influence consumption of sagebrush by sheep (Dziba *et al.*, 2007), and subsequently confirmed in another field study (Woodland, 2008). In the initial study, stock densities were too low and we provided too little supplement, and hence use of sagebrush was low. When we increased stock densities and provided more supplement, sheep were much better able to consume sagebrush. Increased efficiency of detoxification likely enabled supplemented sheep to eat more sagebrush by providing nutrients required for elimination of sagebrush terpenes and their metabolites. We postulate that faster rates of elimination allow animals to ingest more sagebrush because they are able to maintain terpene concentrations in the central circulation below the critical levels that limit intake. Although these satiation thresholds vary among herbivore species and individuals within species, our results indicate that without supplements the limit toxins set may have considerable negative effects on intake of sagebrush and other chemically defended plant species. These findings are now being put into practice by sheep and cattle producers in the western US.

The role of supplemental nutrients on intake of chemically defended plants by herbivores is critical to enhancing rangeland biodiversity. Nutrient supplies to the soil, provided by livestock in the form of urine and feces derived from supplements and sagebrush, likely enhance the production and nutritional quality of herbaceous plants, thereby increasing the amount and variety of forage and improving the nutritional value of sagebrush steppe ecosystems for domestic and wild herbivores (Provenza, 2008; Woodland, 2008). This applied grazing management could be extended to Mediterranean Kermes oak (*Quercus coccifera*) shrublands where the management objective is to maintain a balance between kermes oak and other woody and herbaceous species (see Papachristou *et al.*, 2005).

III – Social learning and culture

Palatability is the interrelationship between flavor and feedback from primary and secondary compounds. But if that's all there is to palatability, then why do dairy cows reared in confinement perform poorly on pasture and livestock reared on pastures and rangelands perform poorly in drylots or feedlots? In both cases, animals have nutritious food available free choice, but food intake is low, performance is poor, and animals are more likely to suffer diseases. Likewise, why do cows of uniform age and breeding differ markedly in performance when ingesting ammoniated straw?

1. Livestock culture

Pasture and rangeland researchers and managers typically consider foraging only in terms of how the physical and chemical characteristics of plants influence an animal's ability to achieve high rates of intake. The social environment is rarely considered when studying diet and habitat selection. This is an unfortunate oversight as a young animal's interactions with mother and peers have a lifelong influence on what it eats and where it goes. When it comes to managing landscape with a variety of foods and terrain, it is critically important to understand how social factors influence the foods eaten by creatures and the locations where they forage, both of which affect animal performance and carrying capacity.

The impact of social learning on adaptation helps account for why herbivores of the same species can occur in very different environments and survive on radically different foods (Provenza, 2003a). A young herbivore learns what kind of creature it will be through social interactions. A calf reared in shrub-dominated deserts of southern Utah is different from a calf reared on grass in the bayous of Louisiana. A bison reared on shrub-dominated ranges in Alaska is different from a bison reared on grasslands in Montana. We typically consider cattle, elk, and bison to be grazers and goats, deer, antelope, and sheep to be forb eaters and browsers. However, "grazers" can live nicely on diets of shrubs, and "browsers" can survive primarily on grass if they learn to do so.

Socializing with mother helps young animals learn about every facet of the environment from the location of water and cover to the wide array of hazards such as predators to the kinds and locations of nutritious and toxic foods. Learning from mother about foods begins early in life as flavors of foods mother eats are transferred to her offspring in utero and in her milk. For instance, in livestock the flavor of plants like onions and garlic is transferred this way, which increases the likelihood that young animals will eat onion and garlic when they begin to forage.

As offspring begin to forage, they further learn what to eat and where to go by following mother. Young animals learn quickly to eat foods mother eats, and they remember those foods for years. Research shows that lambs fed nutritious foods like wheat with their mothers for 1 hour per 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 lambs are exposed alone (Green *et al.*, 1984). Lambs exposed with their mothers to various foods – grains like barley, forbs like alfalfa (*Medicago sativa*), and shrubs like serviceberry (*Amelanchier arborea*) – eat considerably more of these foods than lambs exposed without their mothers. Mother also reduces her offspring's risk of eating toxic foods. If a mother avoids harmful foods and selects nutritious alternatives, the lamb acquires preferences for foods its mother eats and avoids foods its mother avoids. Lambs given a choice of palatable shrubs such as mountain mahogany or serviceberry – one of which their mother was trained to avoid – prefer the shrub they ate with mother. Through her actions, mother models appropriate foraging behaviors for her offspring, who learn what to eat and where to forage.

2. Feeding animals in confinement and on pastures

In many parts of the world, livestock are reared on rangelands and then moved to feedlots for fattening. For animals reared on rangelands, riparian areas and uplands are habitat, grasses, forbs, and shrubs are food, and water comes in streams and ponds. When these animals are moved to feedlots, total-mixed rations aren't food and feedlot pens aren't habitat. One way to improve performance, and reduce illness, is to expose young animals with their mothers to foods they will later encounter when moved to feedlots. This can enhance intake and performance as shown with sheep (Ortega-Reyes *et al.*, 1992).

The same is true for beef cattle. To reduce the cost of ranch operation, researchers have explored ways to feed low-cost foods such as straw to livestock during winter. During a 3-year study, 32 cows – 5 to 8 years of age – were fed ammoniated straw from December to May. Some cows performed poorly, while others maintained themselves. Researchers were baffled until they examined the dietary histories of the animals. Half of the cows were exposed to ammoniated straw with their mothers during their first 3 months of life, while the other half had never seen straw. Throughout the study, the experienced cows had higher body weight and condition, produced more milk, and bred back sooner than cows with no exposure to straw, even though they had not seen straw for 5 years (Wiedmeier *et al.*, 2002).

To reduce the high cost of feeding lactating dairy cows in confinement, many producers are using intensively managed pastures as a source of lower-cost, high-quality forage (Emmick, 2007). Unfortunately, for a dairy cow raised in confinement, the barn is habitat, ingredients from a total-mixed ration are food, and water comes in a trough. Mature dairy cattle reared in confinement on processed foods are at a disadvantage when put on pastures and expected to harvest forages they have never seen. Although they may be quite hungry, they lack the knowledge and the skills to eat pasture. Little wonder they stand at the gate and bellow to be fed – grass isn't food and the pasture isn't home. The fear and stress of new foods and environments cause huge decreases in intake and milk production. To ease these losses, dairy cows should be exposed to green chop in the barn before grazing the first time. The time cows spend on pasture should be increased gradually to reduce stress and losses in production. Exposing calves to pastures where they will be expected to forage later in life will help them be more productive as adults by increasing their preferences for pasture species and enabling them to acquire needed foraging skills. Likewise, before leaving home, cattle on their way to the feedlot should be exposed to the foods they will be expected to eat in the feedlot (Provenza, 2003a).

3. Managing livestock on rangelands

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 (Provenza, 2003b). Over time, such selective foraging on pastures and rangelands will change the mix of plants on offer, 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 months' experience mixing 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 five foods, two of them familiar to all of the lambs (ground alfalfa and a 50:50 mix of ground alfalfa:ground barley) and three of them familiar only to experienced lambs (a ground ration containing either tannins, terpenes, or oxalates). Half of the lambs were offered the familiar foods *ad libitum*, while 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) as opposed to 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 (1497 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 (1497 *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 animals must be encouraged to learn to eat unfamiliar foods that contain secondary compounds by restricting the amount of familiar foods provided (Shaw *et al.*, 2006). The results of this study have been manifest each time we have trained both sheep and cattle to eat sagebrush. Typically, 2 to 3 weeks are required for the animals to make the transition. During that time they must be supplemented enough so they are able to cope with the terpenes in sagebrush, and not acquire an aversion to the plant, but not so much they avoid eating sagebrush all together. In essence, one must play a "cat and mouse" game during the familiarization and adaptation period that requires ongoing monitoring and adjustment of the amount of supplement offered.

Grazing management influences 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, as illustrated by Ray Banister who manages 7200 acres of hardscrabble land in eastern Montana (Provenza, 2003a). His management style evolved over 40 years from reliance on rotational grazing that involved relatively short periods of grazing and rest to boom-bust management that consists of intensive periods of grazing followed by a 2-year period of rest. Ray's boom-bust grazing management stresses soils, plants and herbivores with intensive grazing pressure, and then allows them to recover. Ray believes that stress, and recovery from stress, strengthen systems. Occasional disturbance, followed by rest, creates and maintains a diversity of micro and macro habitats. It is hard to find any part of the ranch that lacks abundant plant cover. Heavy use of all plant species reduces undesirable plants. Abundant plant cover in the uplands and riparian areas mitigates soil erosion, which leads to clean water and great habitat for fish, waterfowl, and terrestrial species of wildlife.

The change to boom-bust grazing challenged the cattle on his ranch as they were no longer allowed to eat only the most palatable plants as they had under rotational grazing. Instead, they were forced to eat all of the plants. Under the new management procedures, Ray monitors the least palatable plant species – shrubs like sagebrush and snowberry (*Symphoricarpos albus*) and various weeds – as indicators of when to move the cattle to a new pasture. Cattle are allowed to move only after their use of the unpalatable species reaches high levels. In so doing, Ray reduces the competitive advantage unpalatable plants have over more palatable species. Heavily grazed plants are at a disadvantage when competing with ungrazed plants for moisture and nutrients. It took Ray's cows 3 years to adapt to the boom-bust style of management. During that time, the weaning weights of calves plunged from robust animals well over 227 kg to scrawny individuals that weighed closer to 159 kg, and then rebounded back to over 227 kg.

Under boom-bust management, cattle begin to eat formerly unpalatable species like snowberry and sagebrush as soon as they enter a new pasture. The cows evidently have learned how to mix their diets in ways that better enable them to eat both the palatable and the unpalatable species. Once the older cows made the transition to a new way of behaving, the young calves were able to learn from their mothers how to thrive under boom-bust management. The calves that Ray keeps as replacements never have to make the harsh transition. They were trained by their mothers that all plants are food at Ray's place. Such learned patterns of foraging behavior are transferred culturally from one generation to the next.

Finally, the same is true for habitat selection. In the western US, many people have come to accept that cattle degrade riparian ecosystems, and that nothing can rectify the situation except to remove cattle from waterways with fencing or remove them from rangelands altogether. This view suggests that animals are somehow programmed genetically to live in specific habitats, and that cattle are bottom-dwelling swamp creatures. The belief is naive, especially when it comes to understanding the origins of animal behavior and the ability of people to change the behavior of livestock and humans. Cattle can be trained to prefer uplands over riparian areas. Experiences early in life teach livestock to prefer habitats like uplands and riparian areas. No gene codes for living in riparian areas. A rider on horseback can train cows and calves to use uplands, and discourage their use of riparian areas, by persistently and consistently moving them to desired locations. Managers also can cull individuals that prefer riparian areas and retain animals and their offspring that prefer upland sites.

Bob Budd, an innovator who formerly managed Red Canyon Ranch near Lander, WY, for The Nature Conservancy, and his co-workers used these techniques to increase cattle use of uplands and improved riparian areas (Provenza, 2003a). Bob argues that the costs of riding are offset by the benefits from additional forage in uplands, improved herd care and health, better riparian areas, and enhanced diversity of plants and wildlife. Riding is less costly than fencing and more effective in the long run. Fencing addresses only the symptoms of animal-distribution problems. By relying on fences, managers reinforce undesirable behaviors. Riparian areas are often over-utilized, even in fenced pastures that contain both uplands and riparian areas. Riding, on the other hand, allows managers to use behavioral principles to train adults and their offspring to use upland forages and habitats, a long-term solution to the problem. Intimate knowledge of where different individuals and subgroups of animals live can be used to enhance dispersion across a landscape by culling animals that use sensitive areas and retaining animals that use different areas. Within any group, some individuals will never conform to management needs concerning food or habitat selection criteria while others will conform well. A rider also can identify cows and calves that consistently use riparian areas so that undesirable individuals can be culled.

IV – Keeping it interesting: The importance of variety

Palatability is the interrelationship between flavor and feedback, as they are influenced by an animal's past experiences with food. But if that's all there is to palatability, then why do animals perform better when offered choices of different foods and why is the grass always greener on the other side of the fence? For example, why do sheep and cattle perform better when offered individual ingredients from a total mixed ration than when fed a total mixed ration formulated to meet their needs? Why do sheep prefer to eat clover in the morning and grass in the afternoon, even though clover is more digestible and higher in protein than grass? More generally, what is the value of variety in the diet?

1. Every body is different

With the advent of statistics in the 20th century, great emphasis has been placed on assessing the response of the "average" animal to a treatment. While the discipline of statistics has advanced our ability to conduct experiments, it also has made variation among individuals an enemy to counteract rather than a friend to embrace. Scientific studies and management practices emphasize means and populations rather than individuals and variation, while nature and evolutionary processes do the opposite. For example, research and management strategies in nutrition determine needs and formulate diets for the "average" member of the herd, not for individuals. Yet, marked variation is common even among closely related animals in needs for nutrients and abilities to cope with secondary compounds common in plants.

Differences among individuals in food intake and preference depend on how animals are built morphologically, and how they function physiologically, and on their past experiences. When we unduly constrain individuals by mixing food to meet the needs of the "average" animal, by planting monocultures of forages on pastures, or by restricting the ability of animals to fully use pastures and rangelands, we may only meet the nutritional needs of a subset of individuals in a herd – and abuse landscapes in the process. Individuals can better meet their needs for nutrients and regulate their intake of toxins when offered a variety of foods that differ in nutrients and toxins than when constrained to a single food, even if the food is nutritionally balanced. Variety allows the uniqueness of the individual to be manifest.

2. The spice of life in confinement, on pastures and rangelands

Whether confined or foraging on pastures or rangelands, variety is the spice of life for herbivores. Like us, they satiate on foods and foraging locations and thrive on variety (Provenza, 1996; Bailey and Provenza, 2008). That causes them to use different foods and foraging locations. Sheep and cattle prefer foods in different flavors in the same way eating maple-flavored oatmeal for breakfast every day causes people to prefer oatmeal in a different flavor. When sheep and cattle eat a food in one flavor, such as maple- or coconut-flavored grain or straw, they prefer food with the alternate flavor on the following day (Early and Provenza, 1998; Scott and Provenza, 1998; Atwood *et al.*, 2001a,b, 2006).

The satiety hypothesis attributes changes in palatability to transient food aversions due to flavors interacting with primary and secondary compounds along concentration gradients (Provenza, 1995, 1996). Aversions typically are mild and below the level of conscious awareness. However, they become pronounced when foods contain too high levels of primary or secondary compounds or imbalances of these compounds. Aversions also arise when foods are deficient in nutrients or when amounts of nutrients required for detoxification are inadequate. Aversions occur even when a food is nutritionally adequate because satiety and surfeit are on a continuum. Thus, cyclic patterns of intake of different foods are due to eating any food too often or in too large an amount, and the less adequate a food is relative to an animal's needs, the greater and more persistent the aversion. The satiety hypothesis has implications for how animals are fed in confinement as well as on pastures and rangelands (Manteca *et al.*, 2007).

For example, food intake and performance of steers fed barley, corn, alfalfa, and corn silage were compared with steers fed a chopped and mixed ration of those ingredients**.** Averaged throughout the trial, animals offered the mixed-ration ate slightly more food than animals given a choice but they did not gain at a faster rate. Gain per unit food consumed was similar for both groups. However, daily food costs were less for animals offered a choice than for those fed the mixed-ration ($1.36 per day *vs* $1.58 per day) because animals offered a choice ate less, and they ate less grain. Cost/kg gain was less for the choice group than for the mixed-ration group ($1.50/kg *vs* $1.85/kg). Collectively, these findings suggest that: (i) animals can more efficiently meet their *individual* needs for macronutrients when offered a choice among dietary ingredients than when constrained to a single diet, even if it is nutritionally balanced; (ii) transient food aversions compound the inefficiency of a single mixed diet by depressing intake even among animals suited to that nutritional profile; and (iii) alternative feeding practices may allow producers to efficiently capitalize on the agency of animals, thus reducing illness and improving performance.

Variety is also important for animals foraging on pastures. Sheep satiate on clover in the morning and switch to grass in the afternoon (Newman *et al.*, 1992; Parsons *et al.*, 1994). In the morning, hungry sheep initially prefer clover because it is highly digestible compared with grass. As they continue to eat clover, however, they acquire a mild aversion to clover, likely due to the combined effects of nutrients like soluble carbohydrates and proteins, from the effects of toxic cyanide compounds, and from eating the same flavor. The mild aversion causes them to switch to grass in the afternoon. During the afternoon and evening, the sheep recuperate from eating clover, and the aversion subsides. By morning, they are ready for more clover. The combination of clover and grass likely enables sheep to eat more each day than if only one species was available. Sowing clover and grass in spatially separated strips can further enhance intake and performance compared to clover-grass mixtures (Chapman *et al.*, 2007). When grass and clover are planted in distinct strips, as opposed to conventional intermixtures, dry matter intake of sheep increases by 25% (265 g/sheep/day) and milk production of dairy cows increases by 11% (2.4 kg/cow/day). The choice allows each animal to balance the mix of grass and clover, and the strip evidently minimizes time spent searching for the desired amounts of the different forages. Planting forages in strips overcomes many difficulties inherent in establishing and maintaining mixed pastures. It also mimics what happens naturally as different plant species aggregate in response to environment.

Finally, herders in France use understanding of plant diversity to stimulate food intake and more fully use the range of plants available by herding in grazing circuits under extensive conditions on rangelands (Meuret *et al.*, 1994). Daily grazing circuits are designed to stimulate and satisfy an animal's appetite for different nutrients, and they enable animals to maximize intake of nutrients and regulate intake of different secondary compounds. The circuits include a moderation phase, which provides sheep and goats 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 abundant and palatable plants that complement previously eaten forages.

Grazing management based on grazing circuits designed to stimulate and satisfy an animal's appetite for different nutrients, enable animals to maximize intake of nutrients and regulate intake of different toxins. The circuits also ensure all plants in a landscape get used, not just a subset of plants. Papachristou *et al.* (2007) provide evidence for the biochemical basis of grazing circuits, since they indicated that sheep ate more foods containing secondary compounds, and more nutritious food, when food with secondary compounds were offered in the morning as opposed to the afternoon. Moreover, lambs learned the benefits of mixing food with tannins, terpenes, and oxalates and continued to do so even when they subsequently had *ad libitum* access to nutritious foods. These findings have implications for managing animals on landscapes generally and for using domestic animals to control noxious weeds specifically. An integrated understanding of how plant biochemical diversity influences foraging by large mammalian herbivores at the landscape-level and what bearing this has on plant community dynamics will have profound implications for enhancing biodiversity of landscapes. Knowledge of foraging behavior can markedly influence and enhance ecological relationships among people, herbivores, plants and landscapes, and in the process, improve the quality of life for land and livestock managers as well as the integrity of the environment. Ultimately, there are likely to be thresholds of knowledge – for people and herbivores – and plant biochemical diversity above which diversity is likely to beget diversity and below which a lack of diversity leads inexorably to less diversity (Provenza, 2003b).

3. Value of variety of secondary compounds in nutrition and health

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. 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 re-constructing pastures and grazing lands with assorted species that together enhance the fertility of soils, the health and nutrition of plants and herbivores and the health of humans (Provenza *et al.*, 2007; Provenza, 2008).

Ecologists and agronomists alike have come to view secondary compounds as "plant defences" that negatively affect herbivores. This view ignores the fact that the effect of every compound depends on the dose – at too high doses, nutrients are toxic, whereas at appropriate doses, plant secondary compounds may have health benefits (Engel, 2002; Provenza, 2003b; Provenza and Villalba, 2006; Athanasiadou *et al.*, 2009) and protect dietary proteins against ruminal degradation, thus increase the flow of intestinal proteins (Ben Salem *et al.*, 2005; Waghorn, 2008). We are just beginning to realize the benefits of plant secondary compounds in human health and in the health of wild and domestic herbivores (see for example Provenza, 2003a; Makkar *et al.*, 2007; Provenza, 2008).

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 the health and nutrition of 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.*, 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 secondary compounds 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).

Complementarities among secondary compounds are an important but little understood area of plant-herbivore interactions (Freeland and Janzen, 1974; Provenza *et al.*, 2003). Animals may be able to ingest more nutrients, or nutrients not encountered in "safe" plants, by ingesting a variety of plants with plant secondary compounds. In principle, herbivores can eat more of a combination of foods with different kinds of plant secondary compounds as different plant secondary compounds have different effects in the body and they are detoxified by different mechanisms (Freeland *et al.*, 1985).

Even less is known about how the sequences of eating plants with different secondary compounds affects foraging, though they appear to be very important for increasing intake. Sheep eat more food with terpenes when they first eat food with tannins (Mote *et al.*, 2007). Cattle steadily decrease time eating high-alkaloid varieties of tall fescue (*Festuca arundinacea*) from 40% to 15% when they first graze tall fescue alone for 30 minutes followed by high-tannin varieties of birdsfoot trefoil (*Lotus corniculatus*) for 60 minutes; remarkably, when the sequence is reversed they forage actively on both trefoil and fescue throughout the 90-minute meal (Lyman *et al.*, 2008a). These patterns of foraging are analogous with birdsfoot trefoil and high-alkaloid reed canarygrass (*Phalaris arundinacea*) (Lyman *et al.*, 2008a). Sheep similarly decrease intake of tall fescue in a meal, unless they receive intraruminal infusions of tannins prior to the meal, in which case they eat tall fescue throughout the meal; conversely, they eat trefoil readily unless they receive intraruminal infusions of tannins prior to the meal in which case they eat less trefoil (Lisonbee, Villalba and Provenza, 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.*, 2008b).

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 as 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 forage on 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. 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.

4. Managing herbivores and landscapes

Generalist herbivores typically encounter several plant species during a meal and the frequency of food encounter influences diet selection. The dynamics of the diet selection process is also influenced by the sequence in which herbivores ingest the foods they encounter (Papachristou *et al.*, 2007). The sequence of food ingestion within and between feeding bouts will be influenced by food patchiness. In turn, the way herbivores learn about foraging sequences in patchy environments may impact habitat partitioning in plant communities. Herbivore density is also likely to influence how herbivores learn about consuming foods in specific sequences (Provenza, 2003b). Many herbivores forage in herds of high densities, and the close proximity to other animals may limit selectivity (Augustine *et al.*, 2003) and influence the temporal resolution of meal patterns.

Selective foraging influences plant assemblages (Augustine and McNaughton, 1998; Augustine *et al.*, 2003), and certain associations among palatable and unpalatable plants may encourage herbivory, provided animals learn the nutritional and toxicological relationships among the plants. Experienced animals eat substantial amounts of foods with secondary compounds even though nutritious alternatives were available *ad libitum*. Thus, animals who learn to mix diets may achieve more uniform use of different species, which may enable palatable and less tolerant species to maintain their abundance, and may prevent unpalatable, chemically defended species from increasing in abundance. Conversely, when herbivores eat only a subset of plants, because of experiences or prevailing management regimens, chemically defended species may increase in abundance (Provenza, 2003b).

In some communities, an increase in dominance by unpalatable species can increase species richness if palatable species gain "associational protection" by growing close to unpalatable neighbours (Atsatt and O'Dowd, 1976), with the costs of competition offset by the benefits of less herbivory (Hay, 1986). However, a multidimensional view, which considers biochemical interactions among foods and changes in herbivore behaviour due to experience, suggests unpalatable plants may not always protect palatable neighbours. Certain associations between palatable and unpalatable plants or among unpalatable plants may encourage herbivory, provided animals experience the benefits of nutritional and/or toxicological relationships among plants in those communities.

Herbivore density and plant chemistry can influence what animals learn about foods. Low to moderate herbivore densities encourage selective foraging, which may prevent learning about complementarities among less palatable foods (Provenza, 2003b). This effect may be exacerbated when the preferred plants in the community are accompanied by a variety of unpalatable species that advertise their toxicity by strong odour and taste (Eisner and Grant, 1980; Provenza *et al.*, 2000). In contrast, high herbivore densities may encourage animals to learn complementary relationships among foods. Many herbivores forage in herds of high densities, which may limit selectivity and encourage diet mixing (Augustine and McNaughton, 1998; Augustine *et al.*, 2003; Provenza, 2003b). Besides the short-term effect of preventing chemically defended species from increasing in dominance, animals that eat unpalatable plants and learn food complementarities will likely continue such behaviour even when high-quality alternatives are available. Importantly, once mixing patterns are learned, they are likely to be transmitted trans-generationally from mothers to offspring (Mirza and Provenza, 1990).

V – Conclusions

Scientists and managers often ignore the power of behavior to transform systems, despite compelling evidence for it. For those willing to understand how environment interacts with the genome to influence behavior, the potential is virtually unlimited. Once mastered, understanding of behavioral principles and processes become a part of the "infrastructure" of the person, so they can be transferred readily among situations and locales. Such knowledge can be used: (i) to improve economic viability and ecological integrity of confinement-, pasture-, and range-based enterprises; (ii) to enhance and maintain biodiversity of rangelands; (iii) to restore pastures and rangelands dominated by weeds; (iv) to alleviate livestock abuse of riparian areas; (v) to anticipate the influence of behavior on systems; and (vi) to improve our ability to manage complex adaptive systems. By understanding and applying behavioral principles to our lives and those of the creatures we manage, we can transform systems ecologically, culturally, and economically. But understanding isn't enough. We must also learn to behave with compassion toward others who have different beliefs and values. To do so challenges us all to embrace one another as we collaborate to change the world.

References

Athanasiadou S., Kyriazakis I., Giannenas I. and Papachristou T., 2009. Nutritional consequences on the outcome of parasitic challenges on small ruminants. *Options Méditerranéennes, Series A*. This volume.

Atsatt P.R. and O'Dowd D.J., 1976. Plant defense guilds. In: *Science*, 193. p. 24-29.

Atwood S.B., Provenza F.D., Wiedmeier R.D. and Banner R.E., 2001a. Changes in preferences of gestating heifers fed untreated or ammoniated straw in different flavors. In: *J. Anim. Sci.*, 79. p. 3027-3033.

Atwood S.B., Provenza F.D., Wiedmeier R.D. and Banner R.E., 2001b. Influence of free-choice versus mixed-ration diets on food intake and performance of fattening calves. In: *J. Anim. Sci.*, 79. p. 3034-3040.

Atwood S.B., Provenza F.D., Villalba J.J. and Wiedmeier R.D., 2006. Intake of lambs offered *ad libitum* access to one of three iso-caloric and iso-nitrogenous mixed rations or a choice of all three foods. In: *Livestock Sci.*, 101. p. 142-149.

Augustine D.J. and McNaughton S.J., 1998. Ungulate effects on the functional species composition of plant communities; Herbivore selectivity and plant tolerance. In: *J. Wildl. Manage.*, 62. p. 1165-1183.

Augustine D.J., McNaughton S.J. and Frank D.A., 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. In: *Ecological Applications*, 13. p. 1325-1337.

Bailey D.W. and Provenza F.D., 2008. Mechanisms determining large-herbivore distribution. In: Prins H.T.T. and van Langevelde F. (eds). *Resource Ecology: Spatial and Temporal Dynamics of Foraging*. Dordrecht, Netherlands: Springer. p. 7-28.

Banner R.E., Rogosic J., Burritt E.A. and Provenza F.D., 2000. Supplemental barley and activated charcoal increase intake of sagebrush by lambs. In: *J. Range Manage*., 53. p. 415-420.

Barry T.N., McNeill D.M. and McNabb W.C., 2001. Plant secondary compounds: Their impact on nutritive value and upon animal production. In: *Proc. XIX Int. Grassland Congress*, Sâo Pedro, Sâo Pablo, (Brazil), 11-21 February 2001. p. 445-452.

Ben Salem H., Makkar H.P.S., Nefzaoui A., Hassayoun L. and Abidi S., 2005. Benefit from the association of small amounts of tannin-rich shrub foliage (*Acacia cyanophylla* Lindl.) with soya bean meal given as supplements to Barbarine sheep fed on oaten hay. In: *Anim. Feed Sci. Technol.*, 122. p. 173-186.

Chapman D.F., Parsons A.J., Cosgrove G.P., Barker D.J., Marotti D.M., Venning K.J., Rutter S.M., Hill J. and Thompson A.N., 2007. Impacts of spatial patterns in pasture on animal grazing behavior, intake, and performance. In: *Crop Sci.*, 47. p. 399-415.

Clausen T.P., Provenza F.D., Burritt E.A., Bryant J.P. and Reichardt P.B., 1990. Ecological implications of condensed tannin structure: A case study. In: *J. Chem. Ecol.*, 16. p. 2381-2392.

Craig W.J., 1999. Health-promoting properties of common herbs. In: *Am. J. Clin. Nutr.*, 70. p. 491S-499S.

Dhiman T.R., Nam S.H. and Ure A.L., 2005. Factors affecting conjugated linoleic acid content in milk and meat. In: *Crit. Rev. Food Sci. Nutr.*, 45. p. 463-482.

Dziba L.E., Provenza F.D., Villalba J.J. and Atwood S.B., 2007. Supplemental energy and protein increase use of sagebrush by sheep. In: *Small Rum. Res.*, 69. p. 203-207.

Early D. and Provenza F.D., 1998. Food flavor and nutritional characteristics alter dynamics of food preference in lambs. In: *J. Anim. Sci.*, 76. p. 728-734.

Eisner T. and Grant R.P., 1980. Toxicity, odor aversion, and "olfactory aposematism". In: *Science*, 213. p. 476.

Emmick D.L., 2007. Foraging behavior of dairy cattle on pastures. PhD Thesis: Utah State University (Logan, UT, USA).

Engel C., 2002. *Wild Health*. New York, NY, USA: Houghton Mifflin Co.

Freeland W.J. and Janzen D.H., 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. In: *Am. Nat.*, 108. p. 269-289.

Freeland W.J., Calcott P.H. and Anderson L.R., 1985. Tannins and saponin: Interaction in herbivore diets. In: *Biochem. Syst. Ecol.*, 13. p. 189-193.

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. In: *Proc. Aust. Soc. Anim. Prod.*, 15. p. 373-375.

Hay M.E., 1986. Associational plant defenses and the maintenance of species diversity: Turning competitors into accomplices. In: *Am. Nat.*, 128. p. 617-641.

Johns T., 1994. Ambivalence to the palatability factors in wild food plants. In: Etkin N.L. (ed.). *Eating on the Wild Side: The Pharmacologic, Ecologic, and Social Implications of Noncultigens*. Tucson, AZ, USA: The University of Arizona Press. p. 46-61.

Logan M.H. and Dixon A.R., 1994. Agriculture and the acquisition of medicinal plant knowledge. In: Etkin N.L. (ed.). *Eating on the Wild Side: The Pharmacologic, Ecologic, and Social Implications of Noncultigens*. Tucson, AZ, USA: The University of Arizona Press. p.25-45.

Lyman T.D., Provenza F.D., Villalba J.J. and Wiedmeier R.D., 2008a. Foraging behavior of cattle grazing tall fescue, reed canarygrass, birdsfoot trefoil and alfalfa in different sequences. In: *Agronomy J.* (submitted).

Lyman T.D., Provenza F.D. and Villalba J.J., 2008b. Sheep foraging behavior in response to interactions among alkaloids, tannins and saponins. In: *J. Sci. Food Agric.*, 88. p. 824-831.

Makkar H.P.S., 2003. Effects and fate of tannins in ruminant animals, adaptation to tannins, and strategies to overcome detrimental effects of feeding tannin-rich feeds. In: *Small Rum. Res.*, 49. p. 241-256.

Makkar H.P.S., Francis G. and Becker K., 2007. Bioactivity of phytochemicals in some lesser-known plants and their effects and potential applications in livestock and aquaculture production systems. In: *Animal*, 9. p. 1371-1391.

Manteca X., Villalba J.J., Provenza F.D., Atwood S.B. and Dziba L.E., 2007. The influence of food choice on animal well-being. In: *J. Vet. Behav.* (in press).

Mantz G.K., 2008. Using polyethylene glycol to enhance the intake of *Sericea lespedeza* by cattle. PhD Thesis: Utah State University (Logan, UT, USA).

Meuret M., Viauz C. and Chadoeuf J., 1994. Land heterogeneity stimulates intake during grazing trips. In: *Ann. Zootech.*, 43. p. 296.
Min B.R. and Hart S.P., 2003. Tannins for suppression of internal parasites. In: *J. Anim. Sci.*, 81. p. 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. In: *Anim. Feed Sci. Tech.*, 92. p. 185-202.
Min B.R., Pomroy W.E., Hart S.P. and Sahlu T., 2004. The effect of short-term consumption of a forage containing condensed tannins on gastro-intestinal nematode parasite infections in grazing wether goats. In: *Small Rum. Res.*, 51. p. 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. In: *Appl. Anim. Behav. Sci.*, 28. p. 255-263.
Mote T.E., Villalba J.J. and Provenza F.D., 2007. Sequence of food presentation influences intake of foods containing tannins and terpenes. In: *Appl. Anim. Behav. Sci.*, 113(1). p. 57.68.
Newman, J.A., Parsons, A.J. and Harvey, A., 1992. Not all sheep prefer clover: diet selection revisited. In: *J. Agric. Sci. Camb.*, 119. p. 275-283.
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. In: *Vet. Parasit.*, 105. p. 229-245.
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. In: *Small Rum. Res.*, 7. p. 101-112.
Papachristou T.G., Dziba L.E. and Provenza F.D., 2005. Foraging ecology of goats and sheep on wooded rangelands. In: *Small Rum. Res.*, 59. p. 141-156.
Papachristou T.G., Dziba L.E., Villalba J.J. and Provenza F.D., 2007. Patterns of diet mixing by sheep offered foods varying in nutrients and plant secondary compounds. In: *Appl. Anim. Behav. Sci.*, 108. p. 68-80.
Parsons A.J., Newman J.A., Penning P.D., Harvey A. and Orr R.J., 1994. Diet preference of sheep: Effect of recent diet, physiological state and species abundance. In: *J. Anim. Ecol.*, 63. p. 465-478.
Pfister J.A., Stegelmeier B.L., Cheney C.D., Ralphs M.H. and Gardner D.R., 2002. Conditioning taste aversions to locoweed (*Oxytropis sericea*) in horses. In: *J. Anim. Sci.*, 80. p. 79-83.
Pfister J.A., Stegelmeier B.L., Cheney C.D. and Gardner D.R., 2007. Effect of previous locoweed (*Oxytropis sericea*) intoxication on conditioned taste aversions in horses and sheep. In: *J. Anim. Sci.*, 85. p. 1836-1841.
Pollan M., 2006. *The Omnivore's Dilemma*. New York, NY, USA: The Penguin Press.
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. In: *Small Rum. Res.*, 59. p. 281-288.
Provenza F.D., 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. In: *J. Range Manage.*, 48. p. 2-17.
Provenza F.D., 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. In: *J. Anim. Sci.*, 74. p. 2010-2020.
Provenza F.D., 2003a. *Foraging Behavior: Managing to Survive in a World of Change*. Logan, USA: Utah State Univ.
Provenza F.D., 2003b. Twenty-five years of paradox in plant-herbivore interactions and "sustainable" grazing management. In: *Rangelands*, 25. p. 4-15.
Provenza F.D., 2008. What does it mean to be locally adapted and who cares anyway?. In: *J. Anim. Sci.*, 86. p. E271-E284.
Provenza F.D., Bowns J.E., Urness P.J., Malechek J.C. and Butcher J.E., 1983. Biological manipulation of blackbrush by goat browsing. In: *J. Range Manage.*, 36. p. 513-518.
Provenza F.D., Kimball B.R. and Villalba J.J., 2000. Roles of odor, taste, and toxicity in the food preferences of lambs. In: *Oikos*, 88. p. 424-432.
Provenza F.D., Lynch J.J. and Nolan J.V., 1994a. Food aversion conditioned in anesthetized sheep. In: *Physiol. Behav.*, 55. p. 429-432.
Provenza F.D., Ortega-Reyes L., Scott C.B., Lynch J.J. and Burritt E.A., 1994b. Antiemetic drugs attenuate food aversions in sheep. In: *J. Anim. Sci.*, 72. p. 1989-1994.
Provenza F.D. and Villalba J.J., 2006. Foraging in domestic vertebrates: Linking the internal and external milieu. In: Bels V.L. (ed.). *Feeding in Domestic Vertebrates: From Structure to Function*. Oxfordshire, UK: CABI Publ. p. 210-240.
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. In: *Small Rum. Res.*, 49. p. 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. In: *Crop Sci.*, 47. p. 382-398.

Ralphs M.H., 1997. Persistence of aversion to larkspur in naive and native cattle. In: *J. Range. Manage.*, 50. p. 367-370.

Ralphs M.H. and Provenza F.D., 1999. Conditioned food aversions: Principles and practices, with special reference to social facilitation. In: *Proc. Nutr. Soc.*, 58. p. 813-820.

Rosenthal G.A. and Berenbaum M.R. (eds), 1992. *Herbivores: Their Interactions with Secondary Plant Metabolites*, 2nd ed. New York, NY, USA: Academic Press.

Rosenthal G.A. and Janzen D.H. (eds), 1979. *Herbivores: Their Interaction with Secondary Plant Metabolites*. New York, NY, USA: Academic Press.

Scott L.L. and Provenza F.D., 1998. Variety of foods and flavors affects selection of foraging locations by sheep. In: *Appl. Anim. Behav. Sci*., 61. p. 113-122.

Shaw R.A., Villalba J.J. and Provenza F.D., 2006. Resource availability and quality influence patterns of diet mixing by sheep. In: *J. Chem. Ecol.*, 32. p. 1267-1278.

Vasta V., Nudda A., Cannas A., Lanza M. and Priolo A., 2007. Alternative feed resources and their effects on the quality of meat and milk from small ruminants. In: *Anim. Feed Sci. Tech.* (in press).

Villalba J.J., Provenza F.D. and Banner R.E., 2002. Influence of macronutrients and activated charcoal on utilization of sagebrush by sheep and goats. In: *J. Anim. Sci.*, 80. p. 2099-2109.

Villalba J.J., Provenza F.D. and Han G.-D., 2004. Experience influences diet mixing by herbivores: Implications for plant biochemical diversity. In: *Oikos*, 107. p. 100-109.

Waghorn G.C., 1990. Beneficial effects of low concentrations of condensed tannins in forages fed to ruminants. In: Akin D.E., Ljungdahl L.G., Wilson J.R. and Harris P.J. (eds). *Microbial and Plant Opportunities to Improve Lignocellulose Utilization by Ruminants*. New York, NY,USA: Elsevier Sci. Publ. p. 137.

Waghorn G.C., 2008. Beneficial and detrimental effects of dietary condensed tannins for sustainable sheep and goat production – Progress and challenges. In: *Anim. Feed Sci. Technol.* (in press).

West N.E., 1999. Juniper-pinon savannas and woodlands of western North America. In: Anderson R.C., Fralish J.S. and Baskin J.M. (eds). *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. New York, NY, USA: Cambridge University Press. p. 288-308.

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. In: *J. Anim. Sci.*, 80. p. 2340-2348.

Woodland R.D., 2008. Influence of fall grazing by sheep on plant productivity, shrub age class structure and herbaceous species diversity in sagebrush steppe. MSc Thesis: Utah State University (Logan, UT, USA).

Woodward S.L., Waghorn G.C. and Laboyrie P.G., 2004. Condensed tannins in birdsfoot trefoil (*Lotus corniculatus*) reduce methane emissions from dairy cows. In: *Proceedings of the New Zealand Society of Animal Production*, 64. p. 160-164.