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Foraging Behavior: Managing to Survive in a World of Change : Behavioral Principles for Human, Animal, Vegetation, and Ecosystem Management

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Foraging Behavior: Managing to Survive in a World of Change

Behavioral Principles for Human, Animal, Vegetation, and Ecosystem Management

Frederick D. Provenza

Acknowledgments

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Back Cover - Mary Donahue (rock art), Jeff Henry (bison), File Photo (horse), Fred Provenza (goat)

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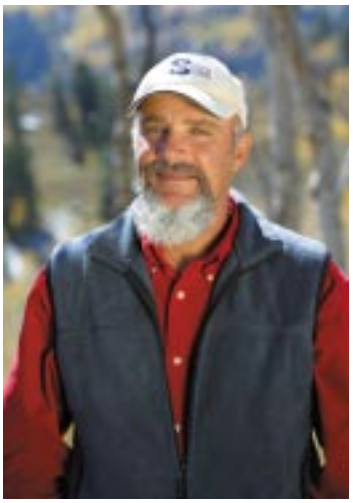


Gary Neuenswander

Dr. Frederick D. Provenza was born in Colorado Springs, Colorado, and began his career working with cattle, sheep, alfalfa, and grain on a ranch near Salida, Colorado. After earning his B.S. in Wildlife Biology in 1973 from Colorado State University, he became ranch manager. As a research assistant and technician at Utah State University, he earned his M.S. and Ph.D. in Range Science. He joined the faculty there in 1982 and is currently a professor in the Department of Forest, Range, and Wildlife Sciences. He has been recognized for his accomplishments in research and service as a mentor for students. In 1999, Dr. Provenza received the W.R. Chapline Research Award from the Society for Range Management for exceptional research accomplishments that enhance management of rangelands. The same year, he also received the University Outstanding Graduate Mentor award from Utah State University. In 1994, he received an Outstanding Achievement Award from the Society for Range Management. He was named Professor of the Year for the College of Natural Resources at Utah State University in 1989 and 2003.

Dr. Provenza's research focuses on understanding behavioral processes, and using that understanding to inform management. For the past two decades, his emphasis has been on the role of learning in food and habitat selection by herbivores. He has been senior or co-author of over 120 papers in peer-reviewed journals and an invited speaker at national and international conferences. In October 2001, he received a $4 million grant to establish a consortium that includes Utah State University, University of Arizona, University of Idaho, and Montana State University. Its goal is to increase the ability of producers, land managers, extension agents, and technical assistance personnel to use behavioral knowledge to better reconcile the ecological, economic, and social facets of management.

Preface

Why would anyone want to read ***Foraging Behavior: Managing to Survive in a World of Change***?

It is filled with new discoveries about the age-old topic of grazing animals and forage resource management. Cattle producers, dairy farmers, sheep producers, wildlife biologists, and anyone challenged with managing livestock, forages, wildlife, and natural resources can use the principles contained in this book.

Sheep eat what sheep eat because sheep are sheep, right? Well, not entirely, sheep as well as other animals learn what to eat in many different ways. They learn from their mothers before and after they are born. They learn from other sheep. They learn through trial and error.

Do all cows eat the same plants? Will cows from Florida know what to eat if taken to a South Texas ranch and surrounded by brush species? Can ranchers use livestock behavioral knowledge to select a herd that forages in different locations and on different plants? Can knowledge of foraging behavior improve animal performance? Do these things matter to the producer or the natural resource manager?

Read this booklet from cover to cover or read segments that seem to interest you, watch the companion video, then read it again. Put it aside and read it again in a few days. Think about what you have seen on your farm or ranch or someone else's place. You have seen things you couldn't explain, didn't understand, or simply didn't think about; things that can make a difference, if you understand how to manage them.

The principles in this booklet will provide you with a new understanding of why animals eat what they eat, why they forage where they forage, and why they act the way they act. The principles in this book, once understood, can make a difference in how you manage your land and animals or how you advise others to do so. These principles, when applied, can make a difference in animal performance, natural resource conditions, and farm and ranch profitability.

Dr. Larry D. Butler, Director
Grazing Lands Technology Institute
USDA Natural Resources Conservation Service
Fort Worth, Texas

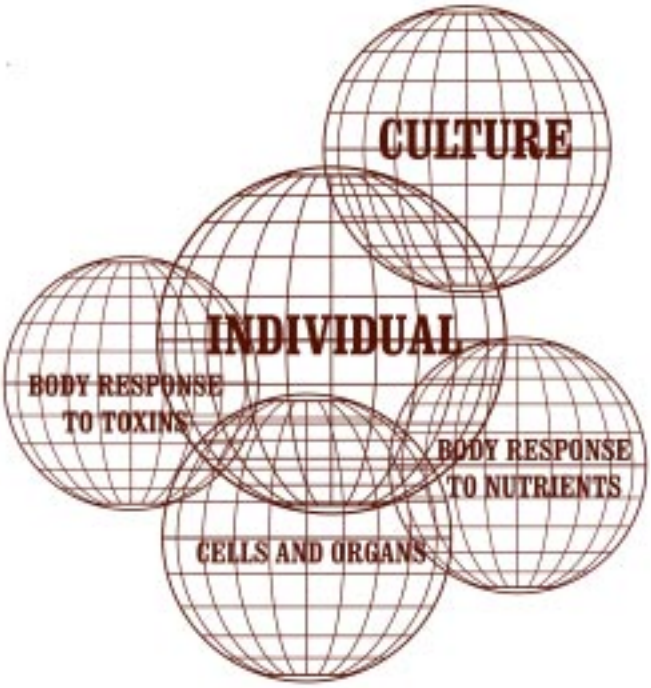
The Challenge

Have you ever considered why animals behave as they do and what it means for management? Why livestock moved from pastures or rangelands to confinement or vice versa lose their appetites, often get sick, and generally perform poorly for as little as a month or as long as 3 years, even when offered nutritious foods? Why wild and domestic animals moved to unfamiliar environments often suffer from predation, malnutrition and overingestion of toxic plants? Why livestock on pastures and rangelands with only a few plant species perform less well than when they have a wide variety of plants to eat? Why some individuals know exactly which toxic plants to avoid while others don't have a clue? Why animals can safely eat toxic plants under some conditions yet suffer dire consequences under others? Why changes in grazing management can reduce livestock performance for as many as 3 years?

Unfortunately, efforts to help people make a living often ignore how animals make their living. Without awareness of behavior in management, there can be no sustainability of ecological, cultural, or economic systems. Without consideration for behavioral principles in research, scientific conclusions often are inadequate. For the past two decades, we have attempted to develop behavioral principles related to food and habitat selection. Our work has shown how simple strategies that use knowledge of behavior can markedly improve the efficiency and profitability of agriculture, the quality of life for managers and their animals, and the integrity of the environment. The scientific research and real-life situations presented in this booklet provide insight into why animals act as they do, and how understanding their behavior can improve operations in any part of the country.

Life for herbivores exists at the boundary between order and chaos. Animals, humans included, learn habits to create order and predictability. The origins of food habits and habitat preferences involve interactions between the culture and the individual. Young animals learn how to behave through interactions with adults. The origins of preference also entail responses of the body to nutrients and toxins. Each cell and organ of the body is a world unto itself. These "worlds" interact and tell the palate which foods to like or dislike based on postingestive effects—feedback from cells and organs in response to nutrients and toxins. Although both people and herbivores strive for order, they also seek variety. Bodies satiate—get sick and tired—on familiarity and flourish on diversity. Satiety encourages creatures to explore novel foods and habitats, while culture encourages creatures to embrace familiar fares and haunts. This creates an ongoing tension between curiosity about things new and different and a suspicion of them.

The behavior and well being of animals has an immediate impact on an operation. Unfortunately, efforts to help managers make a living often ignore how animals make their living.



That's why it's often hard to change an animal's behavior—as the saying goes, you can't teach old dogs new tricks. Still, ongoing changes in social and physical environments challenge creatures to learn new tricks. Those who can adapt, survive. The key to survival for herbivores and the people who manage them is to continually explore new possibilities and to know when to adapt.

The key to survival for herbivores and the people who manage them is to continually explore new possiblities and to know when to adapt.

Thus, while the behavior of herbivores may appear to be little more than the idle wanderings of animals in search of food and a place to rest, foraging is a process that provides insights into an age-old dilemma faced by herbivores and humans alike: How do creatures of habit survive in a world whose only habit is change? The demands herbivores face in finding food to eat and a place to live are similar to those people face in making a living. These demands arise because climate, soils, plants, herbivores, and people are interrelated facets of systems that change constantly. Change requires that each component of the system continually adapt. Understanding the challenges herbivores face and how they cope can reduce stress and increase profitability.

Gary Neuenswander

Human foods have labels giving nutrient and toxin information. Grazing animals don't have it so easy.

Detecting nutrients

Whether they're confined or foraging on open ranges, animals traverse an ever-changing landscape. Like humans, herbivores must cope with changes in themselves and the environment. An animal's nutritional needs vary with age and physical activity. They change throughout pregnancy. They increase when animals are infected with parasites and when they're ill. These changes may transpire gradually during pregnancy or as parasites increase, or they may occur quickly with shifts in physical activity or a change in the weather. Unlike humans who acquire nutritious foods from familiar and predictable haunts—grocery stores, restaurants, gardens—herbivores must sift through an ever-changing landscape fraught with biochemical complexity. Nature constantly alters the quantity of energy, protein, and minerals in the foods herbivores require. Individuals must maneuver through these challenges, recognizing nutritional deficiencies in themselves and in the plants they eat. Individuals who do, survive. Those who don't, won't.

How do animals detect nutrients in foods and what can managers do to help them select nutritious diets?

Gary Neuenswander

Even so-called healthy and natural foods humans eat have toxins. Eating too much of one food may cause illness. Many of our vegetables and fruits have been bred to decrease the level of toxins present but interactions with the environment can increase toxin concentrations. For instance, potatoes that have been damaged, exposed to light, or sprouted have higher concentrations of two glycoalkaloids. Poison symptoms include gastric pain, weakness, nausea, vomiting, and labored breathing.

Minimizing ingestion of toxins

Plants also pose a toxic challenge. Most plants on pastures and rangelands produce toxins, often in high concentrations, that serve as chemical defenses against herbivores. Even garden vegetables—corn, tomatoes, potatoes, broccoli, spinach—contain toxins, but in low concentrations thanks to our efforts to select for low-toxin varieties of plants. There are tens of thousands of toxins, and they all vary in biochemical structures and activities. In animals, they interfere with

metabolic processes or reduce digestibility of foods. They can also cause death.

How do herbivores use plants that contain toxins and what does this mean for managers?

Physical attributes of plants

Herbivores also must deal with plant morphological characteristics, such as standing dead material in some grasses, thorns in forbs and woody plants, and differences in plant canopy shape and structure. Morphological characteristics can facilitate or inhibit foraging and increase or decrease ingestion rate, which in turn can influence foraging efficiency and food preferences. Any combination of plant physical and nutritional characteristics that optimizes nutrient intake is likely to be preferred. Animals that can navigate through such structural challenges can enhance their nutritional welfare.

How effective are herbivores at coping with plant morphological defenses, and what can managers do to maximize foraging efficiency for herbivores on pastures and rangelands?

Food on the move

Perhaps the trickiest challenge animals face is the fluctuation in nutrients, toxins, and physical characteristics of foods. While the biochemical composition of foods at the grocery store is relatively constant, the nutrient and toxin concentrations of plants on pastures and rangelands vary from morning to night, from day to day, from season to season, and from place to place. As plants mature, physical attributes that make foraging difficult increase while nutrient concentrations decline. An animal's challenge is to track these biochemical changes as they occur.

Can herbivores figure out where and when to eat to meet their needs for nutrients and avoid ingesting toxins, and, if so, what are the implications for managing pastures and rangelands?

Fred Provenza

Plant morphology counts! These leaves are too small to efficiently graze a good meal . . .

Fred Provenza

And these stems are too large . . .

Fred Provenza

But these leaves are just right. The bite-sized morsels of this plant make foraging a pleasure. Appropriate bite sizes decrease bite rates and time spent grazing, all of which make foraging more efficient.

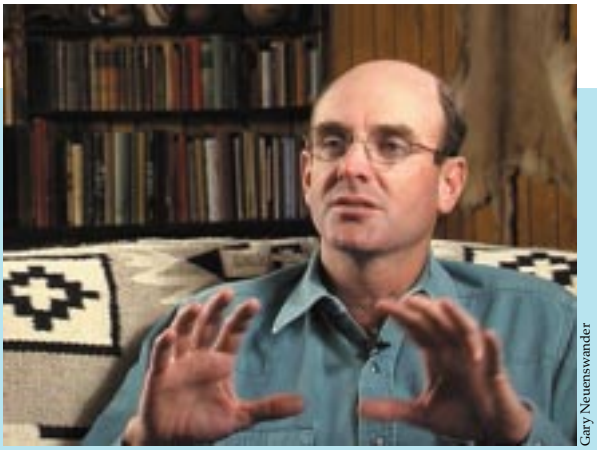
Animals on the move

Changes in terrain pose yet another challenge. Either by catastrophic events like floods and fires or by an animal's being moved to a new location, the environment regularly presents an unfamiliar smorgasbord to an animal. Like a person shopping for the first time in a foreign country, herbivores that adjust quickly to drastically altered terrain can reduce nutritional stress and greatly increase chances for survival.

How well do animals adapt to new foraging environments and how can managers help to reduce the stress of moving and thereby increase profitability?

Mary Donahue

A puzzling change in terrain . . . . These barn-raised cows in upstate New York are let out to the pasture for the first time. They ran around for awhile before trying to go back to the barn. It took them some time to figure out they should be eating the grass.



Gary Neuenswander

Jim Winder talks about the use of creative strategies to keep his southwest New Mexico ranch in business.

People on the move

Just as herbivores must adapt to constantly changing environments, changes in social and physical environments transform the beliefs and values of people. During the frontier days of the 1800s values were shaped largely by the challenge of eking a living from farms and ranches. During the past century, values have been shaped increasingly by life in the city. In the process, people have come to embrace lifestyles that emphasize recreation and conservation rather than production of commodities such as livestock. As a result, many of the practices ranchers have come to rely on to manage their animals have become socially unacceptable and prohibitively expensive. Nowadays, the challenge is to learn to manage landscapes in ways that blend culture, ecology, and economics.

Jim Winder, a rancher in southern New Mexico, blends environmental and economic values by managing livestock behavior. As Jim points out, once mastered, behavioral principles and practices provide an array of solutions to the problems faced in management and improve the economic viability of ranchers and the integrity of land. Unlike the infrastructure of a ranch such as corrals, fences, and water development, behavioral solutions cost very little to implement and are easily transferred from one situation to the next.

Unfortunately, scientists and managers often ignore the power of behavior to transform systems, despite compelling evidence. We know that the environment, continually interacting with the genome during the growth and development of an organism, is as important in shaping creatures as their genetic code. Though experiences during development in utero and early in life are especially critical, genome-environment interactions continue throughout life.

Thus, the issue isn't if animals are adapting to ongoing changes in social and physical 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 genomes to influence behavior, the potential benefits are virtually unlimited: improved economic viability and ecological integrity of pasture-based enterprises, enhanced and sustained biodiversity of rangelands, restored pastures and rangelands once dominated by weeds, mitigated livestock abuse of riparian areas, minimized wildlife damage to crops, pastures, and rangelands, improved ability to manage complex adaptive systems . . . .

As Winder maintains, the challenge is to understand why creatures do what they do, and then to use that understanding as the basis for managing landscapes. To do so requires integrating curiosity with careful observations and experimental manipulations. The rewards are great, but it’s not easy and it requires a change of perspective.

So what happens if we decide to make behavior an integral part of our management? We come to rely less on technology and tradition and more on behavioral adaptation and innovation. In this arena, there's a new sort of independence, where it's more gratifying to question than to confirm, more inviting to participate than to withdraw, and more rewarding to evolve than to hold on.

Origins of Preference

Pasture and rangeland researchers, as well as nutritionists and ecologists, typically consider foraging only in terms of how plant physical and chemical characteristics influence an animal's ability to achieve high rates of nutrient intake. This view of foraging is reinforced by a strong desire to use mathematics and computers to model and "predict" intake rates. Most literature in nutrition, physiology, psychology, and foraging behavior that relates to eating focuses on how much is eaten rather than what is eaten. The social environment, if it is considered at all, is seen as a nuisance variable that may only slightly moderate a process that is basically physically and chemically driven.

This is an unfortunate oversight because a young animal's interactions with its mother and peers have a lifelong influence on where it goes and what it eats. When managing pastures and rangelands that contain a variety of foods and terrain, managers must understand how social factors influence the foods eaten by creatures and the locations where they forage, both of which influence carrying capacity. As psychologist Paul Rozin points out for humans,

> Suppose one wishes to know as much as possible about the foods another person likes and eats and can ask only one question. What should that question be? There is no doubt about it, the question should be, "What is your culture or ethnic group?" There is no other single question that would even approach the informativeness of the answer to this question.

A young herbivore learns what kind of creature it will be through social interactions. The impact of social learning on adaptation helps account for why herbivores of the same species occur in diverse environments and survive on a variety of different foods. The flexibility of the process is illustrated by the variety of possible end points. 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. This same flexibility occurs for humans, as Rozin points out, "Consider the massive differences between the almost purely carnivorous diet of Eskimos and the plant-dominated diets of many tropical cultures, or between the elaborate cuisines of India or France and the relatively limited amounts of food processing carried out by some hunter-gatherers."

When it comes to managing pastures and rangelands that contain a variety of foods and terrain, managers must understand how social factors influence the foods creatures eat and the locations where they forage, both of which influence carrying capacity.

Fred Provenza

The terrain of Louisiana (above) creates an animal with much different behavior from an animal reared in Utah (below).

Randy Wiedmeier

Fred Provenza

Goats and blackbrush

We once worked with a group of goats on blackbrush rangeland in southern Utah. The goats were from northern Arizona and they had always been herded. They were familiar with grass, but they had never seen blackbrush. After 90 days, they had hardly moved from along the roadside where we placed them originally. When we measured how much blackbrush the goats had eaten, it was clear their foraging "excursions" had taken them only about one-fifth of the way into the pastures. Needless to say, those goats didn't fare well on blackbrush: they lost 16% of their initial body weight during the winter. The next year we worked with semi-feral goats from brush-dominated rangeland in South Texas. They were so wild we scarcely saw them during the 90-day season. They foraged throughout the blackbrush pastures and lost only 5% of their initial body weight during the winter. They were the same species—goat—but their previous experiences made them different creatures. The same is true for other domestic and wild herbivores.

Randy Wiedmeier

The importance of experience to production

To reduce the cost of ranch operation, researchers and producers in the western U.S. are exploring ways to feed low-cost foods like 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 for 60 days during their first 3 months of life, while the other half had never seen straw. Throughout the 3-year study, the experienced cows maintained higher body condition, produced more milk, lost less weight, and bred back sooner than cows with no exposure to straw as calves, even though they had not seen straw for 5 years.

The point of this example is simple to understand, but easy to overlook. Experiences of young animals have lifelong influences that affect the efficiency and profitability of production systems. Animals' histories must be considered if we wish to improve the efficiency of agricultural production, the welfare of livestock, and the well-being and profitability of managers. Young animals cope with change more readily than adults because their food and habitat preferences are more malleable. Thus, exposing young animals with their mothers to a variety of foods and locations, especially those they will experience later in life, can lessen problems with transitions.

Mother knows best

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

As offspring begin to forage, they 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 inexperienced lambs are exposed alone or not exposed at all. Lambs exposed with their mothers to various foods—grains like barley, forbs like alfalfa, shrubs like serviceberry—eat considerably more of these foods than lambs exposed without their mothers.

Research also shows that a mother can reduce 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 two palatable shrubs like mountain mahogany or serviceberry—one of which their mother was trained to avoid—show a marked preference for the shrub they ate with their mother. Through her actions, mother models appropriate foraging behaviors for her offspring.

Fred Provenza

Lambs exposed to various foods with their mothers, like this pair sampling serviceberry, will eat considerably more of those foods than lambs exposed without their mothers.

In the process of foraging with mother, young animals also learn foraging skills needed to efficiently ingest foods of different forms—grasses, forbs, shrubs. The rate at which goats and sheep are able to ingest grasses and shrubs increases with experience. In one study, bite rates tripled as experience increased during 30 days of browsing the shrub blackbrush. Younger animals 6 months of age learned foraging skills more readily than older animals 18 months of age.

Mother's most important role is helping her offspring become familiar with the environment where they will live so that when offspring encounter new foods or unusual circumstances, they stand out against a familiar background. Young animals who cautiously explore novel foods and circumstances are more likely to survive.

The peer group

As young animals age they interact increasingly with peers, who then become a major influence on one another's behavior.

Young animals encourage one another to explore new foods and environments. Cattle reared in different locations on summer range in Idaho roamed over a much broader area when they foraged together as yearlings, than when they foraged separately at 2 years of age and older.

Fred Provenza

"Hey, I dare you guys to eat that." Even foraging animals experience peer pressure. Young animals influence one another to explore new foods and environments.

In the process, adults also learn from offspring because young animals are more likely than adults to eat novel foods. Mature ewes learned to eat Douglas fir seedlings from lambs over a 4-year period as ewes and lambs grazed tree plantations on the West Coast. Initially, neither the ewes nor the lambs ate the seedlings. However, as young animals began to eat the flush of new growth on the trees, the ewes also began eating the trees.

Social influences are strong enough to override food aversions conditioned with high doses of toxins. Lambs and calves can easily be trained to avoid a particular food by administering to them a toxin dose after they ingest the food. After one or two food-toxicosis pairings, the animals no longer eat the food. However, if trained animals subsequently forage with animals that eat the food, the trained animals are much more likely to sample the food they were trained to avoid. When they sample the food and no longer receive a toxin dose, the positive effects of nutrients can quickly override the previously conditioned food aversion and increase preference for the food.

File Photo

Meeting the challenge

So how do young herbivores learn to cope with foraging challenges? There are four facets to the process of adaptation. They involve interactions between social learning from mother and peers and trial-and-error learning by individuals.

•Social interactions enable offspring to learn quickly to identify nutritious foods and to avoid those that are toxic, just as people learn to recognize the many foods in a grocery store.

•In the process of foraging with mother, young animals learn to discriminate the foods mother eats—familiar foods—from the foods mother avoids—novel foods. Young animals learn and remember specific foods, just as humans learn and remember plants in a store or garden.

•Animals are wary of the unfamiliar—unusual foods, places, and individuals of the same or different species. Careless individuals die young. There are simply too many hazards.

•Finally, animals associate the flavors of specific foods with their postingestive consequences. If the consequences are positive—satiating feedback from needed nutrients like energy and protein—animals gradually increase intake until the novel food becomes a part of the diet. If the consequences are negative—nauseating feedback from toxins—herbivores limit intake of the novel food in accord with the concentrations of the toxins in the food.

Advantages of social learning

Socializing enhances the learning efficiency of the group. Each creature no longer has to discover everything by itself. When an individual discovers a new resource, everybody benefits. Goats browsing blackbrush-dominated rangelands experience macronutrient (energy and nitrogen) deficiencies. When one goat discovers that the interior chambers of woodrat houses provide a good source of protein, all of the goats benefit. Likewise, when animals must learn to drink from a water device that requires pressing a lever, it takes only one individual to learn how to do it, and in no time all the others are drinking. The same is true for discovering the locations of new food resources in the environment.

Lynn Betts, USDA Natural Resource Conservation Service

Cattle come together at a nose pump to drink water in this southern Iowa pasture on a farm in Madison County. The cows use their nose to pump water from a nearby farm pond.

Unfamiliar environments

When managers move animals from familiar to unfamiliar environments they thwart one of the primary ways social creatures learn about environments—transgenerational learning from mother. In a new environment, animals must learn through trial and error about all of its facets—food, water, shelter, and predators—beginning with which foods to eat or avoid and where to forage. In the process, they are more susceptible to hazards. No wonder cattle moved to new areas in Louisiana break through fences and swim canals to return to familiar territory, and sheep have walked up to 150 km (90 miles) in search of familiar territory.

The importance of social interactions, and of the mother as an experienced model for her offspring, is illustrated in instances when wild and domestic animals are moved to unfamiliar environments. Research shows that animals new to an environment spend as much as 25% more time foraging but ingest 40% less food than animals reared in the environment. Inexperienced animals walk longer and farther. They also suffer more from predation, malnutrition, and ingestion of toxic plants. The net effect is greatly diminished reproductive rates and lower weaning weights. Little wonder ranchers often described the time when livestock were introduced into an unfamiliar environment as "the year from hell."

Ranchers with stocker enterprises accept the implications of placing young inexperienced animals in unfamiliar areas. However, the exploratory nature of these young animals produces a lesser degree of disruption than mature cows experience. Young animals cope with change more readily than adults because their food and habitat preferences are more malleable.

Mary Donahue

Butch Little and Khaki Trahan, two southern Louisiana cattle producers, tell how their cattle will swim canals to return to more familiar feeding areas after being moved. Below, left to right, Stuart Gardner, NRCS area range and pasture management specialist; Diane Borden-Billiot, wildlife biologist for the U.S. Fish and Wildlife Service; Johanna Pate, NRCS area range and pasture management specialist; and Clay Midkiff, NRCS district conservationist are the professionals who worked with Butch and Khaki.

Mary Donahue

Unfamiliar terrain for herbivores and managers

To reduce the high cost of feeding lactating dairy cows in confinement, many producers are using intensively managed pastures as a source of low-cost, high-quality forage. However, dairy cows reared in confinement perform poorly on pasture. Upset, perplexed producers typically report that cows don't eat grass and that milk production plummets. Conversely, livestock moved from pastures or rangelands to drylots or feedlots perform poorly. In both cases, animals have nutritious food freely available, but food intake is low, performance is poor, and animals are more likely to suffer diseases. What is the problem and what can be done to diminish the adverse effects on performance?

Mary Donahue

These dairy cows in upstate New York have just been released from the confinement barn and moved onto pasture for the first time. There was a lot of running and not much grazing.

For a dairy cow reared 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 distinct disadvantage when placed in new environments, like a pasture, and expected to harvest forages they have never seen. Although they may be quite hungry, they lack the knowledge and the skills to eat grass. Little wonder they stand at the gate to the barn and bellow to be fed. Grass isn't food and the pasture isn't home. For a beef cow reared on rangelands in the western U.S., riparian areas and uplands are habitat; a diverse array of 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.

The stress associated with novel foods and environments leads to marked decreases in food intake, which greatly increases the likelihood of illness. During that time, stress is high and intake and performance are poor. Nevertheless, mature cattle gradually increase intake of nutritious novel foods. In the process, they learn foraging skills. Experience increases foraging efficiency, and that means higher rates of food intake and greater production.

Exposing young animals to foods they will encounter later in life can alleviate these problems and increase the efficiency of production. For example, dairy cattle can be exposed to pasture forages early in life before they are expected to forage and produce milk from pastures. Mature dairy cattle reared in confinement should be exposed gradually to pasture forages—either as green chop in confinement or on pastures—before they are expected to forage extensively on pastures. Allowing inexperienced animals to forage with experienced animals can expedite the process provided the animals interact socially.

Easing transitions for herbivores and managers

Chronic stress inhibits immune responses, which increases illness and decreases performance of livestock and humans alike. Being moved from a familiar to an unfamiliar physical environment and placed with animals the individual may or may not know, causes such stress. Harsh handling exacerbates the problem. Lack of familiarity with foods is the final blow. Given this combination of circumstances, animals are much less able to resist diseases than when physical and social stressors are minimized.

Mary Donahue

Social or physical stress can inhibit an animal's resistance to disease.

As a rule, animals with no experience of the foods or environment make the transition to new terrain better when they are moved from resource-poor environments—where plants are scarce, dispersed over rough country, low in nutrients, and high in toxins—to resource-rich environments where nutritious plants are abundant. By the same token, animals reared in high-resource environments are at a distinct disadvantage—compared with animals reared in low-resource environments—when they are moved to low-resource environments.

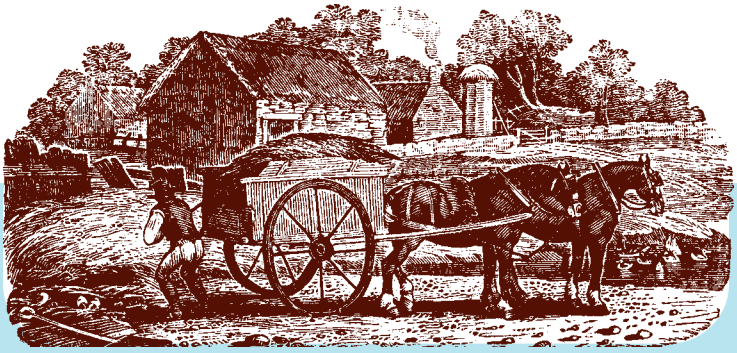
Animals make transitions from familiar to unfamiliar environments better if they are moved to areas where the foods and terrain are similar to what they have experienced. Some producers buy replacement animals only from areas similar to the ranges their animals inhabit. Still, no matter how similar a new area may be to a traditional area, animals have an affinity for familiar haunts. That's why many ranchers insist on raising their own replacement females—animals bought elsewhere and moved to new areas often are malnourished, lose weight, and reproduce poorly.

Preparing animals for foods they will eat in new environments increases intake and reduces illness. Exposing a young animal with its mother to foods that it will encounter in the feedlot increases efficiency. Young animals given only brief exposure with their mothers—1 hour per day for 5 days—remember foods for at least 3 years. Immediate acceptance of food in the feedlot helps to reduce stress and illness. Preconditioning combined with low-stress livestock handling techniques reduces stress on livestock and humans, and that increases performance and economic returns.

Mary Donahue

Mary Donahue

An animal raised in the low-resource environment of southwest New Mexico (top) would have an easier time adapting to the high-resource area of upstate New York (lower right) than an eastern animal moving to the West.



A load of hay

How can we help animals make transitions to new environments? In many cases, it is easier than you might think. It simply requires compassion for the plight of others. For example, a young man sold some fine bulls to a man in a neighboring state. After a few weeks, the irate new owner called to cuss and discuss the poor performance of the bulls. The young man was shocked and felt badly. He couldn't understand the problem—the bulls were fine when he sold them.

At that point, his grandfather suggested they take the new owner a load of familiar hay from the home place, a once-common practice. After they did, the condition of the bulls improved, and the bulls—and their new owner—were on their way to making the transition.

File Photo

The adaptation trough

The only constant in life is change. Unfortunately, change isn't easy. It takes time and it's painful. So why change? Because perpetual changes in physical and social environments require individuals, social groups, and species to adapt.

For the pessimist, change creates frightful problems and concerns—it represents forced adaptation with few alternatives for holding on to the past. For the optimist, change presents invigorating challenges and opportunities—it is a generative process with ample opportunities to create a new future. For both there really is no choice—we must all continually adapt or go extinct.

Changes in grazing regimens affect every facet of the system—soils, plants, herbivores, people—and as many as 3 or more years are required for systems to adapt to changes in management. It takes at least 3 years for soils to adapt to changes from inorganic to organic ways of farming. When rancher Ray Banister changed grazing management practices to enhance and maintain biodiversity of his rangelands in Montana, it took 3 years for his cows to adapt to the new diets they were required to eat and at least that many years for soils and plants to adapt (see sidebar, page 47, *Boom-bust management*). When rancher Bob Budd changed habitat selection patterns of his cattle herd from bottom dwellers in riparian areas to upland inhabitants, it took at least 3 years for his cows and his rangelands to adapt (see sidebar, pages 39–40, *Using behavior to manage for ecological, cultural, and economic integrity*).

In the end, productivity of each of these systems improved—soils and water were healthier, plant biodiversity was increased, and more animals were produced. During adaptation, however, animal performance—food intake, weight gains, reproductive rates—typically declines before it improves. The degree and duration of the decline depend on the magnitude and direction of change. The greater the change and the more challenging the terrain, the greater the impact.

More Than a Matter of Taste

What are the origins of preference? Certainly, mother and peers play an important role in the acquisition of behaviors. By doing what mother does, young animals learn quickly what and what not to eat and where and where not to go. Diet and habitat selection patterns develop as a result of these interactions. But is that the whole story? As every parent knows, no matter how good the advice, offspring must try everything for themselves. This is certainly the case for young herbivores.

While mother and peers facilitate the acquisition of behaviors, continuation of the behaviors depends on the consequences to the individual. In the case of food ingestion, consequences depend on the postingestive effects of nutrients and toxins. Thus, social influences interact with individual experiences to generate behaviors. For example, young goat kids forage near mother even when a food they prefer is located elsewhere, which illustrates the influence of mother on offsprings' food and habitat selection. When given a choice of the two foods, however, the kids eat the food they prefer, which illustrates the influence of postingestive effects of nutrients and toxins on food selection. Likewise, young lambs that experience mild toxicosis while ingesting food their mother prefers do not continue to eat the food, which illustrates that the consequence of toxicosis to the lambs is more influential on diet selection than mother's preference. The same is true for humans. Young people who are lactose-intolerant stop drinking milk and eating yogurt and cheese because the consequences are aversive, even though their parents may eat the foods.

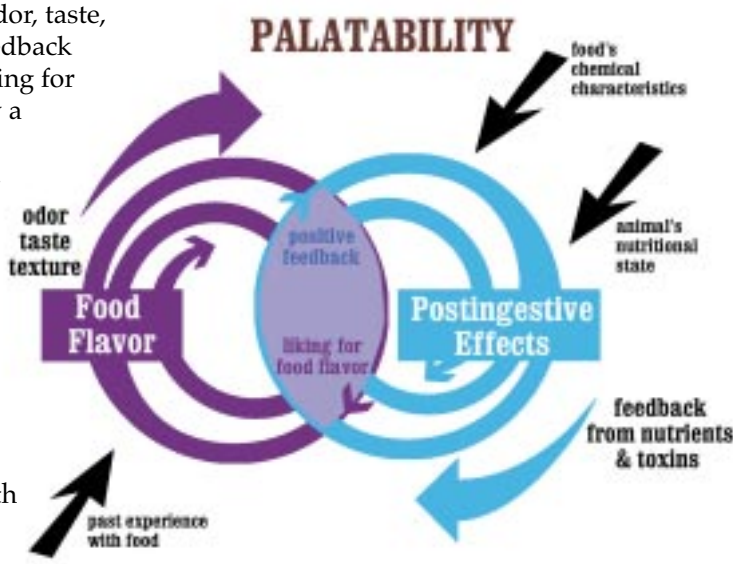
Why are ice cream sundaes so palatable? Most of us prefer them over celery.

Thus, the origins of food and habitat preference involve interactions between the culture and the individual, as well as responses of the body to nutrients and toxins. Each cell and organ of the body is a world unto itself. These "worlds" interact and tell the palate which foods to like or dislike based on postingestive feedback from nutrients and toxins.

Palatability is more than a matter of taste

Preferences for foods are typically thought to be influenced by palatability. What is palatability? It is a narrowly defined term that has many meanings. Webster defines palatable as pleasant or acceptable to the taste and hence fit to be eaten or drunk. Animal scientists usually explain palatability as the hedonic liking or affective responses from eating that depend on a food's flavor and texture, or the relish an animal shows when consuming a food or ration. Conversely, plant scientists describe palatability as plant attributes that alter preference, such as chemical composition, growth stage, and associated plants. All popular definitions focus on either a food's flavor or its physical and chemical characteristics.

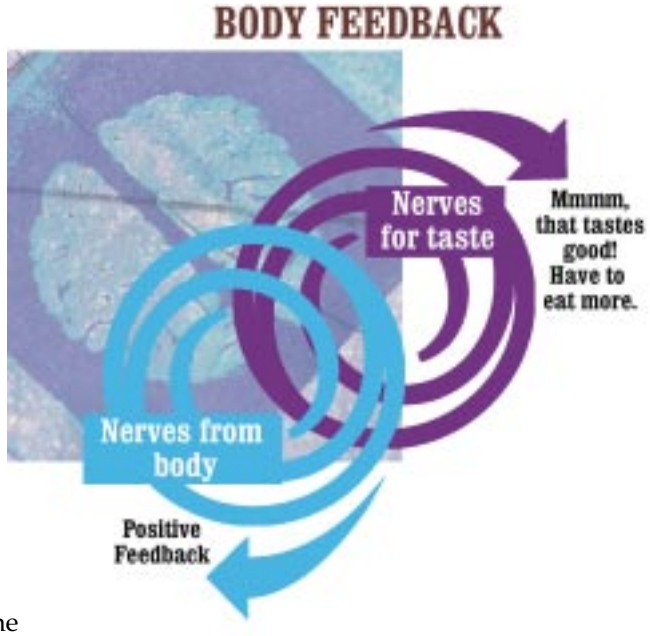
Research during the past two decades shows that palatability is the interrelationship between a food's flavor and its postingestive effects. Flavor is the integration of odor, taste, and texture. Postingestive effects are a result of feedback from nutrients and toxins. Feedback influences liking for flavor. Flavor-feedback interactions are affected by a food's chemical characteristics, an animal's nutritional state, and its past experiences with the food. The senses—smell, taste, sight—enable animals to discriminate among foods and provide the pleasant sensations—liking for a food's flavor—associated with eating. Postingestive feedback calibrates the sensory experiences—like or dislike—in accord with a food's utility to the body.



Feedback from the "body" to the senses is critical for health and well-being. Bodies are integrated societies of cells, organs, and organ systems all with nutritional needs. They interact with one another and with the external environment through feedback mediated by 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 relay throughout the central nervous system, from the brainstem to the limbic system to the cortex. Feedback from the body to the palate is how societies of cells and organs influence which foods and how much of those foods are eaten. Feedback from the body influences the senses—hedonics of taste, odor, sight—that are the interface between the body's internal environments and the external environments where animals forage.

The wisdom of the body

If palatability is more than a matter of taste, and it is, then how does the body discriminate among different foods based on flavor-feedback interactions during a meal? How does the body determine which foods have which postingestive effects?



The enteric (gut) and central (brain) nervous systems continually interact with one another and with the rest of the body to integrate a food's flavor with its postingestive effects. These interactions begin early in life. Because the body has a long memory, flavor-feedback interactions don't have to be re-learned each time an animal eats a food, any more than a human has to re-learn when different garden vegetables are ripe. Flavor-feedback relationships merely need to be updated when flavor or feedback change.

Several factors interact during these updates in which an animal's past experiences with a food are integrated with new information about food. These updates are based on the novelty of a food's flavor and the amount of each food eaten in a meal. Animals acquire aversions to novel foods when a meal of several familiar foods and a novel food is followed by toxicosis. Conversely, an animal that is nutrient deficient

associates recovery from the deficiency with a novel food after eating a meal of familiar and novel foods. The amount of each food eaten in a meal also enables the body to discriminate among foods in a meal. For example, when toxicosis follows a meal of blackbrush twigs, goats avoid either current-season or older-growth twigs depending on which they ate in the greater amount. Sheep must ingest a minimal amount of a novel food to discriminate among foods in a meal. Lambs offered novel foods for only 20 minutes a day actually preferred the less nutritious of two foods, presumably because it was most familiar, when they were eating a basal diet adequate in nutrients. However, the lambs quickly changed preferences to the most nutritious novel food when offered only the novel foods for 8 hours a day. Thus, lambs discriminated based on both the amount of food eaten and their nutritional state. Collectively, factors such as these influence palatability as food abundance, nutritional quality, and toxicity change daily and seasonally.

Bob Nichols, USDA Natural Resource Conservation Service

Carlos Rodriques (right), NRCS resource conservationist, assists in feeding Corriedale sheep on a ranch in Charlo, Mission Valley, Montana. Research shows that lambs discriminate among foods based on both the amount of food eaten and their nutritional state.

Changes in palatability are automatic

Changes in palatability through postingestive feedback occur automatically without the need for any overtly recognized (cognitive) association or conscious memory of the feedback event. The same is true for digestive processes. We don't have to tell the pancreas to release a dose of insulin after we eat a candy bar. Even when animals are deeply anesthetized or tranquilized, postingestive feedback still causes changes in the palatability of a food eaten just prior to anesthesia. When sheep eat a nutritious food and then receive a toxin dose during deep anesthesia, they acquire an aversion to the food because feedback changes palatability automatically in the absence of conscious awareness.

The body is typically unobtrusive in "instructing the creature" what and what not to eat. People consciously remember only those blatant feedback events that were traumatic, such as becoming violently ill from food poisoning. Through vomiting and nausea-induced decreases in palatability, the body tells us not to eat the food again. But the body typically works subtly and at a non-cognitive level to indicate its needs. If it didn't, animals would spend all their time figuring out what to eat, how to digest it, and how to change preferences based on ongoing changes in needs. It is remarkable to consider that so many complex interactions occur without a bit of thought.

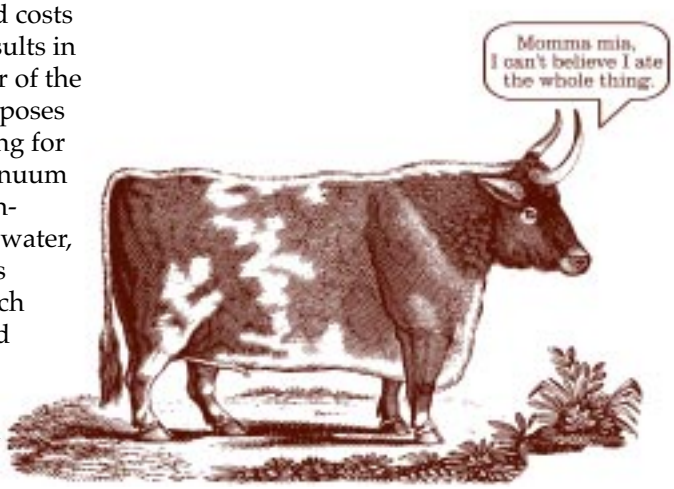
File Photo

As an animal eats, it is unaware of the thousands of messages traveling between the brain, the senses, and organs and between all the cells of the body.

The non-cognitive nature of flavor-feedback interactions is why palatability changes, even when food aversions make no rational sense. For example, humans often acquire strong aversions to foods eaten just prior to getting nauseated even in cases where the person knows for a fact that flu or wave-induced seasickness—not food—was responsible for the decrease in palatability.

Excesses and deficits

Satiety and malaise are the experience of the benefits and costs of eating. Ingesting nutrients in appropriate amounts results in benefits, experienced as satiety and a liking for the flavor of the food. Conversely, ingesting excess nutrients or toxins imposes physiological costs, experienced as malaise and a disliking for the flavor of the food. Palatability operates along a continuum to influence preference because virtually everything, if ingested in high enough doses, is toxic, including oxygen, water, and all nutrients. As the Swiss-born alchemist Paracelsus observed, "All substances are poisons; there is none which is not a poison. The right dose differentiates a poison and a remedy."



Animals typically show little preference for foods low in nutrients. Likewise, they eat limited amounts of foods too high in nutrients. Excesses or deficits of nutrients—protein, energy, minerals—decrease palatability. Humans experience this excess-nutrient effect when we eat high-energy foods that are too rich or high-sodium foods that are too salty. Research shows that herbivores experience these effects when they are forced to eat foods with excessive levels of minerals like phosphorus, sodium, sulfur, or macronutrients. For example, protein is required in moderate amounts every day, but excess protein causes dramatic decreases in palatability and intake because of excess production of ammonia, which is toxic. Energy is also a major nutrient, needed daily in far greater amounts than any other nutrient. However, too much energy from readily available sources of carbohydrates in foods like grains can cause malaise—acidosis—and diminish palatability. Both the ratio of protein to energy and the rates at which different sources of protein and energy ferment in the rumen have a strong influence on intake and palatability. Palatability declines if there is too much protein relative to energy or if the rates at which protein and energy ferment are not similar.

As the Swiss-born alchemist Paraclesus observed, "All substances are poisons; there is none which is not a poison. The right dose differentiates a poison and a remedy."

Over-ingesting toxins such as terpenes, alkaloids, and cyanogenic glycosides causes palatability to decrease. Research with toxic compounds shows that delivering high doses of toxins via a stomach tube—oral gavage—following food ingestion causes strong aversions to the food eaten just prior to toxicosis. When herbivores forage, however, over-ingestion of toxins is seldom a problem. Rapid postingestive feedback from toxins enables animals to limit the rate and amount of most toxic foods ingested, apparently in accord with the rates of detoxification they can sustain. Thus, the concentration of toxins in foods sets limits on the amount of a particular food animals can ingest. As toxin concentrations in a plant decline, intake of the plant increases. That is why, given a choice, herbivores are able to select more of foods that are high in macronutrients and low in toxins.

Fred Provenza

These Missouri cows stand in water trying to cool themselves down from fever brought on by toxic alkaloids. Grazing endophyte-infected fescue caused the over-ingestion of alkaloids.

All forages are not created equal

Pasture managers typically attempt to increase animal production by planting forages that maximize nutrient intake, but they don't always succeed. For instance, Greg Baer, a livestock producer in Missouri, planted a mixture of legumes, and nutritional analyses showed that the pastures were very high in energy and protein. To Greg's dismay, forage intake was low and cattle were losing weight. The animals even preferred moldy hay and endophyte-infected tall fescue high in toxic alkaloids to the forage legumes. The plants evidently contained excess protein and cyanogenic glycosides, which resulted in strong food aversions. When Greg planted strips of grass in the legume pastures, the abnormal feeding behaviors ceased and production improved because cattle were able to select a more balanced diet. Biochemical diversity adds spice to life for livestock, improves economic viability for producers, and maintains the ecological integrity of agricultural landscapes. To meet nutritional requirements, animals need a variety of foods.

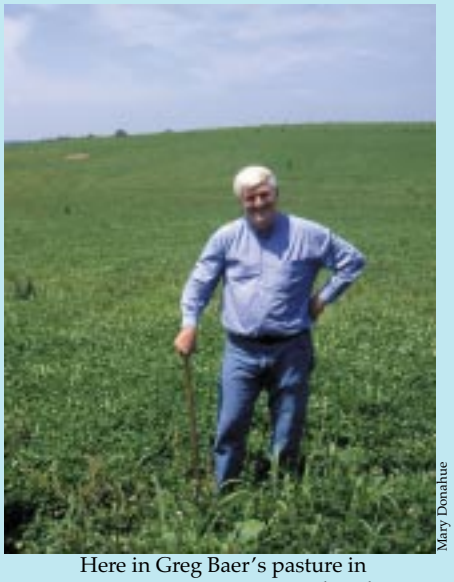
Gary Neuenswander

Missouri livestock producer, Greg Baer, was puzzled as to why his cattle were losing weight on carefully planted pasture that offered a mixture of legumes high in energy and protein.

The kinds and mixtures of plant species influence food intake and animal performance. Offering animals a variety of foods on pastures and rangelands helps each individual to meet its nutritional needs. Individual herbivores, when given a variety of foods, balance the ratio of macronutrients in their diet to meet their nutritional needs. Turnips in ryegrass pastures and grass-legume mixtures can help livestock maintain a better ratio of energy to protein while minimizing effects of toxic compounds in plants. Providing a variety of foods that differ in macronutrients also allows for changes in nutritional needs, such as changing demands for milk production and daily variation in activity and weather.

When foods contain different kinds of toxins that are complementary—that is they operate on the body and are detoxified in different ways—they may have a positive influence on food intake and animal performance. Forages like white clover contain cyanogenic compounds that limit intake by herbivores. Endophyte-infected tall fescue produces alkaloids that adversely affect food intake and livestock performance. Cattle in Missouri performed better on fescue and clover pastures than on legume-only pastures because the mixture contains complementary toxins. It may be beneficial to plant forbs like sanfoin that contain tannins together with legumes like alfalfa that cause bloat. That's because tannins and proteins that cause bloat form stable complexes in the intestinal tract, thereby reducing the amount of foams that cause bloat.

We have much to learn about how animals might mix their diets to reduce toxicosis. We also have much to learn about biochemical complementarity among plants in mixture and how concentrates fed in confinement affect selection of forages in pasture. No doubt our lack of knowledge contributes to observations that a plant is palatable under some conditions and unpalatable under others. Palatability depends on biochemical interactions among the mix of foods available.

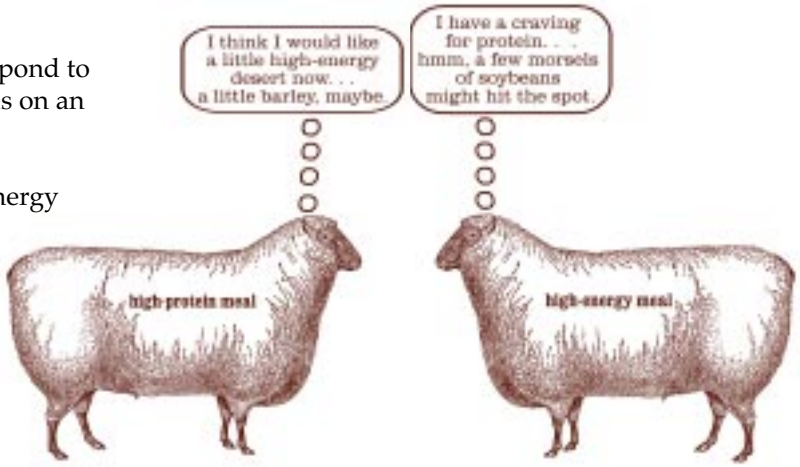


Mary Donahue

Here in Greg Baer's pasture in central Missouri, Bob Herschbach, NRCS grazing lands specialist, shows the variety of plant species that helped cattle to increase forage intake and gain weight.

Nutritional state

There is growing understanding that animals respond to specific nutrients. Thus, what's palatable depends on an animal's nutritional state.



Animals maintain a relatively constant ratio of energy to protein in their diets—when they can select from foods varying in macronutrients—because the body discriminates between feedback signals from energy and protein. Preference for food high in energy increases after a meal high in protein, while preference for food high in protein increases after a meal high in energy. Animals also increase intake of protein relative to energy as their needs for protein increase, for example, during growth, pregnancy, or parasite infections. Animals require nearly 5 times more energy than protein, and they can store excess energy in the form of fat. Thus, palatability is always strongly influenced by energy.

Limited evidence suggests that mineral needs also influence palatability. Managers have used salt to limit intake of macronutrient supplements for years. Research shows that when their mineral needs are met, sheep strongly prefer flavored straw alone to flavored straw paired with an oral gavage of NaCl. Conversely, when animals need salt, they strongly prefer mineral licks and trace-mineral salt blocks. Herbivores respond to deficits of sodium, phosphorus, and sulfur. In general, though, carefully conducted research is needed to determine if herbivores can rectify deficits of other required minerals.

Fred Provenza

This research found that when the mineral needs of sheep are met, they strongly preferred flavored straw alone to flavored straw paired with an oral dose of NaCl.

Interactions between nutrients and toxins

When animals eat foods high in toxins, their nutrient needs increase. When supplemented with needed nutrients, they are better able to ingest foods high in toxins. For example, sheep and goats eat more sagebrush, a shrub high in terpenoids, when they receive supplemental macronutrients, especially protein. The need for protein also increases when animals eat diets high in tannins. Conversely, animals supplemented with energy are better able to eat foods high in toxins like cyanogenic glycosides, which increase needs for energy.

Diets high in toxins increase mammals' acid loads. That has led to the idea that intake of foods with toxins is regulated by the rate of formation and disposal of hydrogen ions responsible for acidosis. Maintaining acid/base balance and excreting toxins increase amino acid catabolism and glucose depletion. Thus, the capacity to ingest toxins depends on an animal's macronutrient status because animals must biotransform and excrete toxins.

Mary Donahue

Gerald Menard, a rancher near Abbeville, Louisiana, explains how he likes to grow turnips with ryegrass to provide an energy source that complements the protein in the grass.

Fred Provenza

Contrary to the popular belief, getting livestock to eat undesirable plant species does not involve greater deprivation of food but better nutritional status. The better off nutritionally herbivores are, the more toxins they can handle in the plants they eat. The sheep above have eaten all the leafy spurge outside the fence.

Helping weed eaters

In the United States, the cost of controlling undesirable plants—so-called weedy and invasive species—is estimated at $12 billion annually. It is little wonder that weed specialists, range scientists, and plant ecologists are seeking ecologically viable ways to suppress undesirable plants and encourage more desirable species. The public is rightly concerned over the adverse environmental effects of herbicides, and specialists are concerned that herbicides alone cannot prevent the spread of weeds. On the other hand, interest is growing in using livestock to reduce the abundance of undesirable plants on pastures and rangelands.

Livestock have been used to control weeds and brush under a variety of conditions, even in urban areas. The city of Laguna Beach, California, each year pays nearly $2,700 per square kilometer for 500 to 800 goats to graze a 68-square-kilometer "fireproof moat" in chaparral vegetation around the city. Goats and sheep are even being used as weed eaters in cities like Denver and Vail, Colorado.

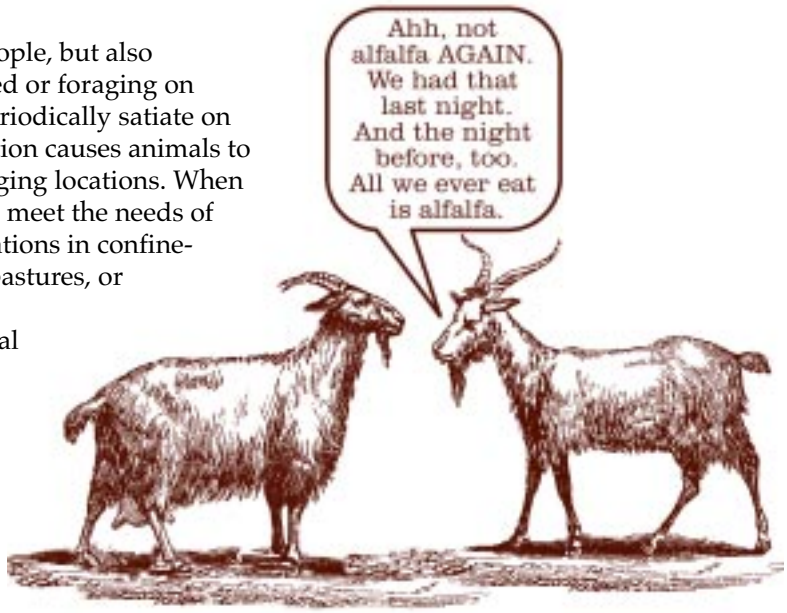
Livestock can be herded or fenced with temporary electric fencing, they recycle nutrients (urine and feces), and they pose no environmental hazards when managed properly because grazing is a natural process. In many cases, livestock can be used "surgically" to reduce plant species abundance by altering competitive relationships between less and more desirable plant species.

Bob Nichols, 1997, USDA Natural Resource Conservation Service

Trinete Bell (right), NRCS soil conservationist, assists Maeoloa Barber with fencing around a livestock area in South Carolina.

Despite their potential, using livestock to eat undesirable plant species presents challenges. Most plants—weeds included—are unpalatable because they contain toxins. The conventional wisdom is that the greater the level of food deprivation the more herbivores will eat unpalatable weeds. However, the better the nutritional status of herbivores, the better they are able to eat plants that contain toxins, as illustrated with foods such as sagebrush, which is high in terpenoids, and bitterbrush, which is high in tannins. Intake of these foods was nearly doubled in feeding trials when sheep and goats received supplemental energy and protein. These findings are counter-intuitive and suggest that understanding the nutritional and physiological needs that underlie the behaviors of herbivores grazing weeds can lead to more effective, efficient, and sustained weed control by livestock.

The Spice of Life



Variety is the spice of life, not only for people, but also for herbivores, whether they are confined or foraging on pastures or rangelands. Like us, they periodically satiate on familiarity and thrive on variety. That combination causes animals to continually investigate different foods and foraging locations. When we unduly constrain animals by mixing food to meet the needs of the "average" animal, by feeding total-mixed rations in confinement, by planting monocultures of forages on pastures, or by restricting the ability of animals to fully use rangelands, we will only meet the nutritional needs of a subset of individuals in a herd—and abuse lands in the process.

Variety of theories

Herbivores and omnivores are often referred to as generalists because they eat a wide variety of foods. Some experts believe that eating a variety of foods reduces the likelihood an animal will over-ingest toxins. They hypothesize that toxins limit the amount of any single food an animal can tolerate, and to meet needs for macronutrients, animals must consume small amounts of a variety of foods with different toxins, each of which presumably is detoxified by somewhat different means. Others believe animals eat a variety of foods to meet nutritional needs—no single food contains the required mix of macronutrients, minerals, and vitamins. Both theories are valid, but neither accounts for the fact that animals eat an assortment of foods even when toxins are not a concern and nutritional needs are met.

File Photo

Looking over clover

Sheep in the United Kingdom prefer to eat clover in the morning and grass in the afternoon, even though clover is more digestible and higher in protein than grass. Why? Animals prefer highly digestible foods because the delay between beginning to eat and nutrient reinforcement is short and the amount of reinforcement is high. However, if animals eat too much of a highly digestible food, and rates of fermentation are too high, they become ill and begin eating less digestible foods. When the immediate positive postingestive effects of nutrients are then followed by mild illness, the pattern of intake becomes cyclic: gradual increases followed by sharp declines. The more familiar an animal is with a food, and the greater the positive feedback from nutrients, the less likely the animal is to acquire a lasting aversion. This response is characteristic of nutritious foods like larkspur, which contains toxic alkaloids, or rapidly fermentable foods like grain (high in carbohydrates) and some pasture forages (high in protein).

Mary Donahue

This helps explain why sheep in the United Kingdom eat clover in the morning and switch to grass in the afternoon. Hungry sheep initially prefer clover because it is highly digestible compared with grass. As they continue to eat clover, however, sheep satiate—acquire a mild aversion—from the effects of soluble carbohydrates and proteins and from the effects of toxic cyanogenic compounds. The mild aversion causes them to seek the less nutritious grass, which is lower in nutrients and toxins, in the afternoon. During the afternoon and evening, the sheep recuperate from eating clover, and the aversion subsides. By morning, they're ready for more clover.

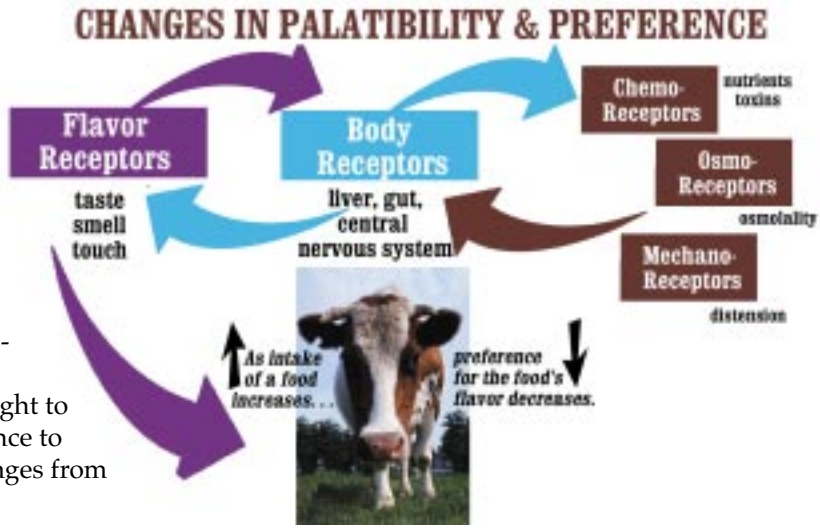
Why animals search for variety

Sheep and cattle prefer foods in different flavors, just as people who eat maple-flavored oatmeal for breakfast everyday eventually prefer a different flavor. Preference for particular foods declines as the foods are eaten. 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. Preference also drops if animals overingest a food on a particular day, just as a person's preference for turkey drops markedly following a Thanksgiving Day meal. When forced to eat the same food too frequently or excessively, people typically remark, "I'm sick of it." If livestock could speak, they would echo the sentiments, as their actions show.

Bob Nichols, USDA Natural Resource Conservation Service

Landowner Dorlene Rides at the Door Waln, and NRCS conservationist discuss the operation of the ranch. This Montana ranch supports approximately 2,000 head of Hereford and Black Angus cattle and 12,500 acres of wheat, barley, and oats.

Interactions between the senses and the body help to explain why palatability changes within meals and from meal to meal. Flavor-, nutrient-, and toxin-specific satiety refer to the decrease in preference for the flavor of a food during and after eating due to interactions involving a food's flavor and postingestive feedback from nutrients and toxins. Flavor receptors respond to taste (sweet, salt, sour, bitter), smell (a diversity of odors), and touch (astringency, pain, temperature). Flavor receptors interact with receptors in the body (liver, gut, central nervous system, and elsewhere) that respond to nutrients and toxins (chemo-receptors), osmolality (osmo-receptors), and distension (mechano-receptors). Preference for the flavor of a food declines automatically as that food is eaten because of interactions between the senses and the body. These interactions cause transient decreases in the preference for foods just eaten; interactions that can be understood as operating along a continuum of stimulation from slight to extreme—that is from aversion to preference to aversion as a food's utility to the body ranges from inadequate to adequate to excessive.



The decrease in preference is influenced by an animal's nutritional needs relative to a food's chemical characteristics. Animals fed nutritionally balanced food in one of two flavors for a day prefer the other flavor in a meal on subsequent days. The decrease in preference is more persistent when a food is either deficient or excessive in needed nutrients. Aversions may be pronounced when foods contain excess toxins or rapidly digestible nutrients, such as some forms of protein and energy. Aversions also occur when foods are deficient in specific nutrients. They even occur when animals eat nutritionally adequate foods, particularly if those foods are eaten too often or in too great an amount. Thus, eating any food to satiety causes a transient aversion to the flavor of that food. That's why people cook familiar foods in different ways using a variety of different flavors. How many ways can you cook ground beef?

Eating any food to satiety causes a transient aversion to the flavor of that food.

Tim McCabe, USDA Natural Resource Conservation Service

This South Dakota rancher rotates sheep from one cell to another in a cell-grazing system designed to manage range grasses.

Herding sheep

Many of the principles related to flavor-, nutrient-, and toxin-specific satiety have been used in human nutrition and in pastoral grazing systems, and they are important in understanding feeding behavior. The reasons might not have been clear but the effects were evident.

Herders in France use these principles to stimulate food intake and more fully use the range of plants available by herding in grazing circuits. The grazing circuit includes a moderation phase, which provides sheep 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. Daily grazing circuits are designed to stimulate intake and satisfy an animal's appetite for different nutrients and to ensure use of many different plant species, thereby enhancing plant biodiversity.

Moving animals to fresh pastures or moving them to new areas on rangelands is likely to have the same effect. The new areas offer nutritious forages and a change of scenery. Livestock producers have learned how easy it is to move animals to new pastures. Once the animals have learned the routine and experienced the benefits, they move themselves.

Humans, too, have developed culinary practices that combine foods grown locally to meet nutritional needs. Corn and beans, for example, are staples in the diets of many traditional American cultures and a major source of caloric intake. Both corn and beans are inadequate in certain essential amino acids, but the amino acids in short supply are complementary. Eaten in combination, corn and beans are an adequate source of amino acids and a great source of energy.

Variation among individuals

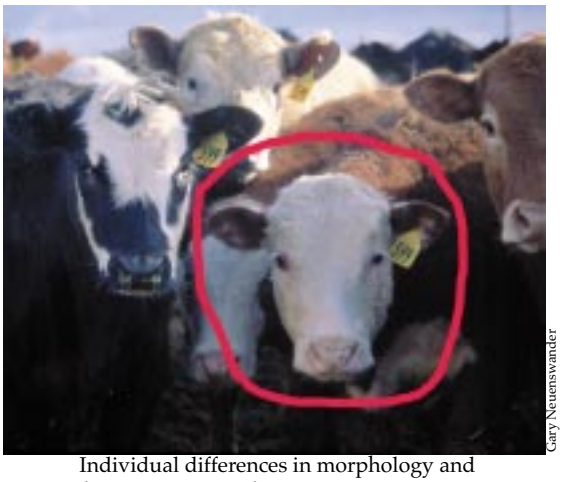
With the advent of statistics during the 20th century, researchers and managers have placed great emphasis on devising experiments to determine the response of the "average" animal to a particular treatment. While these experiments have enabled us to better understand biological processes, they have obscured the vital importance of variation among individuals. We make decisions based on "averages" obtained from "populations" rather than on individual responses.

Gary Neuenswander

In the real world, we all know there is no such thing as "average"—only a multitude of individuals.

From studies of behavior and nutrition, we typically determine nutritional needs and formulate rations (for animals in confinement) or make predictions of food preferences (for animals on rangelands) for the herd, not for individual members of the herd. The same is true for habitat use. We typically assess the carrying capacity of pastures and rangelands based on factors such as slope, site productivity, and

food preference of the "average" member of the herd. We calculate "means" but no such thing exists. There is no "mean" weather, soil, plant, herbivore, or person. Variations among individuals and the ongoing interactions among individual components of each sub-system virtually guarantee that systems will continually vary across time and space.



Cary Neuenswander

Individual differences in morphology and physiology among herbivores means varied food and habitat preferences.

Anyone studying nutrition or toxicology soon realizes the great degree of variation among individuals. Variations in dental structure and arrangement affect the foraging abilities of individual sheep and goats, as do differences in organ mass and how animals metabolize macronutrients. Lambs of uniform age, sex, and breed vary widely in their preferences for foods. Some lambs prefer foods high in energy, while others prefer foods with medium or even low energy. Doses of sodium propionate (sodium and energy) that condition preferences in some lambs condition aversions in others. Sheep, goats, and cattle show similar variation in susceptibility to toxins. Some sheep fed a high level of the plant goatsrue failed to show any symptoms of toxicosis; others were killed by a low dose. The point is that individual differences in morphology and physiology influence food and habitat preferences of individuals, and they provide a basis for "natural" and "artificial" selection. Diets and habitats that enable animals to select among alternative foods and locations enable *each individual* to best meet its needs.

Noted biochemist Roger Williams was convinced that each individual is "built in a distinctive way in every particular, and that this was the basis of individuality." Williams was aware of the functional significance of differences in people, and he articulated those notions:

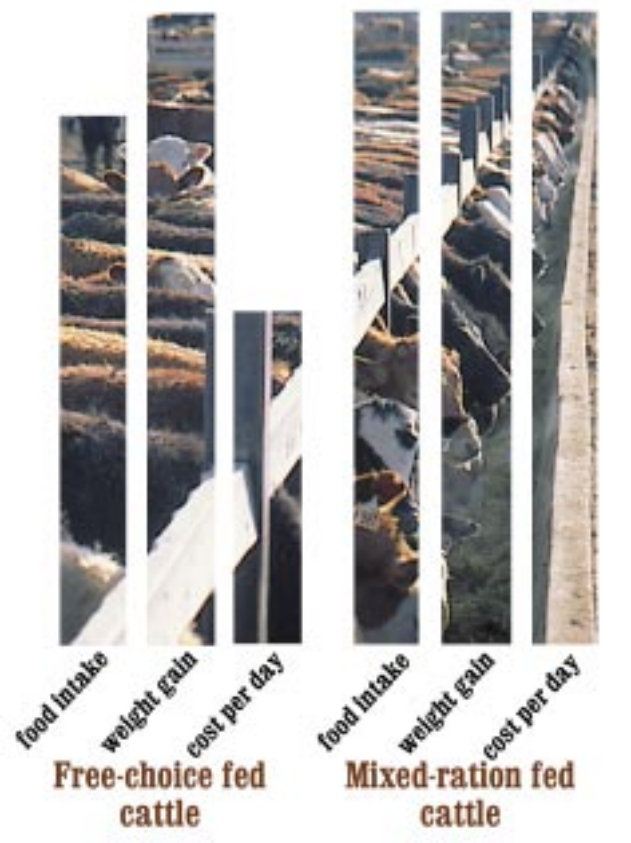
> Stomachs vary in size, shape and contour . . . . They also vary in operation . . . . A Mayo Foundation study of about 5000 people who had no known stomach ailment showed that the gastric juices varied at least a thousand fold in pepsin content . . . . Such differences are partly responsible for the fact that we tend not to eat with equal frequency or in equal amounts, nor to choose the same foods . . . . In fact, marked variations in normal anatomy are found wherever we look for them . . . . Some of the most far-reaching internal differences involve the endocrine glands—thyroids, parathyroids, adrenals, sex glands, pituitaries—which release different hormones into the blood. These, in turn, affect our metabolic health, our appetites for food, drink, amusement and sex, our emotions, instincts and psychological well-being . . . . Our nervous systems also show distinctiveness . . . . Since our nerve endings are our only source of information from the outside world, this means that the world is different for each of us.

Noted biochemist Roger Williams was convinced that each individual is "built in a distinctive way in every particular, and that this was the basis of individuality."

Confined and constrained

Animals in feedlots, dairies, or dairy/pasture operations are fed total-mixed rations of concentrates and roughages formulated to meet the needs of the "average" animal. We often feed total-mixed rations to animals in confinement because we're afraid they'll eat too much grain and we believe that they are unable to balance their own rations. What would happen to food intake, weight change, and the cost of food per day if animals could choose their own diets from a variety of concentrates and roughages? Conventional wisdom says animals will eat too much grain and perform poorly or die because they cannot balance their own rations.

But when goats, sheep, and cattle are offered a variety of foods, including grain concentrates, they seldom eat too much grain if they have time to adjust. Rather, they limit intake of grains and roughages and adjust intake according to nutritional needs. Indeed, they eat less grain than animals force-fed a total-mixed ration designed to maximize weight gain. Excess grain causes acidosis, which induces food aversions.



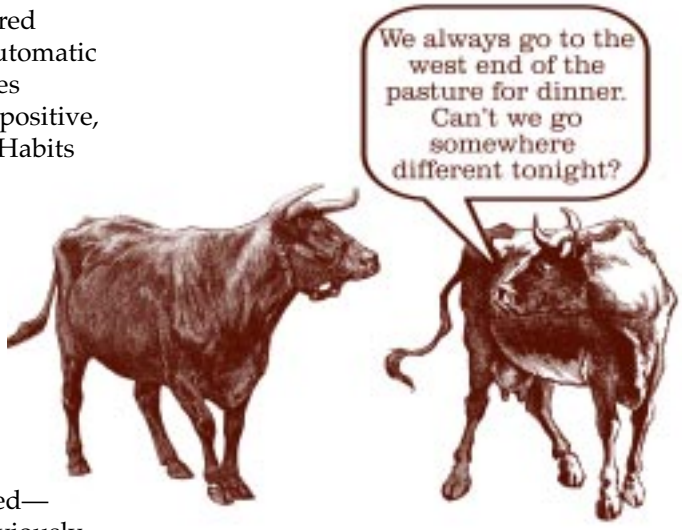
Even though cattle fed individual ingredients by free-choice ate slightly less food per day, the end result of reaching finished body condition was the same for both groups of cattle. However, the cost per day to feed the free-choice animals was much less because they ate less grain. In the end, the weight gained per amount eaten did not differ between the groups, nor did the cattle differ in grade at slaughter.

In a recent study, cattle fed barley, corn, alfalfa, and corn silage were compared with animals fed a chopped and mixed-ration of those ingredients. Food selection varied widely among individuals offered a choice of the four ingredients throughout the 63-day trial. Intake of dry matter, energy, and protein all changed from day to day, as did ratios of protein to energy for animals fed free-choice. On 21 of the 63 days, animals offered a choice had protein-to-energy ratios higher than animals fed the total-mixed ration. On 2 days the ratios were equal. On 40 of the 63 days they had protein-to-energy ratios lower than the animals fed the total-mixed ration. No 2 animals selected a diet similar to the total-mixed ration, and none consistently chose the same foods. Yet each animal apparently selected a diet that met its needs.

Averaged throughout the 63-day trial, animals offered the mixed-ration tended to eat more than animals offered a choice (109 vs 102 g/kg MBW/day), but they did not gain at a faster rate (0.89 vs 0.92 kg/day). Gain/unit food consumed also was similar for both groups (0.09 vs 0.10 kg/kg). However, food cost/day was less for animals offered a choice than for those fed the mixed-ration ($1.36 vs $1.58). Because animals offered a choice ate less, and they ate less of the more expensive grains, cost/kg gain was less for the choice than for the mixed-ration group ($1.49 vs $1.84). These findings suggest that: (1) individual animals can more efficiently meet their needs for macronutrients when offered a choice among dietary ingredients than when constrained to a single diet, even if it is nutritionally balanced; (2) transient food aversions compound the inefficiency of a single mixed diet by depressing intake even among "uniform" groups of animals suited to that nutritional profile; and (3) alternative feeding practices may allow producers to efficiently capitalize on the agency of animals, thus reducing illness and improving performance.

The Dilemma

All animals are creatures of habit. As Aristotle said, "We are what we repeatedly do. Excellence, then is not an act, but a habit." Habits are patterns of acquired behavior that have been repeated so often they are automatic and thus difficult to break. Behaving by consequences ensures habits; if the consequences of a behavior are positive, the likelihood of the behavior reoccurring increases. Habits add an element of predictability to an unpredictable world. They also increase efficiency.



The drawback to habit is that as the world changes, individuals must change or risk becoming obsolete. In the case of foraging behavior, as a result of selecting particular foods and foraging in specific locations, the responses of adults can become rigid to the point that habit is nature. There are two ways to escape this self-balancing feedback loop: changes within the animal that cause the creature to be satiated—get sick and tired—by the behavior, as discussed previously, or changes in social and physical environments that alter set patterns of behavior, as discussed in what follows.

If it ain't broke don't fix it

If variety adds spice to life, then what is the dilemma? The dilemma arises because habit can inhibit exploring new possibilities. Thus, an ongoing tension arises between curiosity about things new and different and a suspicion of them. From the standpoint of foraging, when nutritional and physiological conditions are adequate, familiarity breeds content and novelty breeds contempt.

As Aristotle said, "We are what we repeatedly do. Excellence, then is not an act, but a habit."

Well-fed animals are cautious of new things—that is they are neophobic. Mature animals typically eat small amounts of novel foods. They gradually increase intake of new foods if the foods are nutritious. Young animals also are neophobic, even while learning to forage with mother, but they are less neophobic than older animals. Declines in intake for young and mature animals alike are most dramatic when they are moved to novel environments and are offered novel foods. Sheep in unfamiliar environments prefer familiar to novel foods, even if the familiar foods previously have caused toxicosis. Cautious sampling of novel foods helps herbivores survive in a world where most foods contain toxins.

File Photo

Young animals are neophobic (cautious of the unfamiliar), even while learning to forage with mother, but they are less neophobic than older animals. Lambs are less neophobic when they are repeatedly offered only nutritious novel foods. However, they become markedly more neophobic when they experience toxicosis after eating novel foods.

If animals never experience the effects of toxins, neophobia decreases to a small degree. Lambs are less neophobic when they are repeatedly offered only nutritious novel foods. However, lambs become markedly more neophobic when they experience toxicosis after eating novel foods.

Neophobia also occurs with social interactions and habitat selection. Many herbivores—goats, sheep, cattle, deer, elk, moose, bison—live in subgroups of individuals that show fidelity to one another and to particular home ranges. They prefer to forage with companions on preferred foods in familiar locations. When subgroups of sheep with different food preferences forage in areas where preferred foods are distributed in patches, sheep reared together typically forage in the same locations on different foods, while sheep not reared together forage in different locations on preferred foods.

Necessity is the mother of invention

As discussed previously, animals satiate on familiarity, which is one mechanism that causes them to investigate the unfamiliar. They also are likely to change behaviors under risky survival conditions. The tendency to "explore" options that may or may not pay off is higher in animals that are nutritionally deficient than in those nutritionally satisfied. They eagerly sample new foods and habitats—that is they become neophyllic. As resources become scarce and nutritional conditions inadequate, familiarity breeds contempt and novelty breeds content.

Creatures begin exploring new options when conditions for survival depend on change. For example, lambs fed a basal diet inadequate in energy or protein readily eat novel foods, while lambs fed a basal diet adequate in energy and protein are neophobic. Sheep, goats, cattle, and many wild herbivores range more extensively in the late dry season than in the early and middle wet seasons, when food supplies are abundant and high in nutritional quality. When the going gets tough, survivors seek greener pastures. When forced to search for food, animals eat unfamiliar foods and move to unfamiliar terrain despite the hazards.

Fred Provenza

These elk are part of a small herd that come down from the hills every morning to their preferred breakfast location—the lawns of Mammoth Hot Springs Visitor Center in Yellowstone National Park.

As resources become scarce and nutritional conditions inadequate, familiarity breeds contempt and novelty breeds content.

Bob Nichols, USDA Natural Resource Conservation Service.

NRCS conservationist and farmer discuss pasture managment practices. It is important to take into account nutritional fluctuations in forage throughout the year. When resources get scarce, animals will seek out new, possibly dangerous foods.

The hazards of exploring new environments

Ignorance of behavior can be devastating. Mick Holder, a rancher in Arizona, writes, "Gila County is mercifully deficient in poisonous plants, but we have lupine and loco in small or moderate stands. In 30 years of ranching, I never had a problem with either. I leased rangeland in Apache County and moved a portion of my cattle to that location during a drought period and suffered severe losses to poisonous plants, while the sister cattle left here in Gila County on equally poor rangeland did not have one case of loco or lupine poisoning. Did they not recognize the plants because they had been relocated 100 miles east?"

Courtesy of Mick Holder

Mick Holder examines elk damage to desert vegetation on his ranch in southern Arizona.

It may seem strange, but animals prefer familiar to unfamiliar foods, even if the familiar foods are toxic, and this response is especially pronounced in unfamiliar environments. Cattle in Gila County preferred familiar, toxic foods to unfamiliar foods. Providing animals with familiar, nutritious foods while they are adapting to unfamiliar environments can mean the difference between life and death. Holder concluded that "The only plausible explanation I would make after reading your paper is that moving cattle to Apache County suspended their aversions to familiar plants—loco and lupine—due to the unfamiliar settings or the lack of diversity of browse found in the Pinyon-Juniper habitat . . . . [a] painful lesson for us both."

Fred Provenza

There also is evidence that the same dose of a toxin has a much greater effect in an unfamiliar environment compared to a familiar one. The added stress heightens the toxin's action on the animal, likely by diminishing the effectiveness of detoxification processes, much as stress suppresses immune responses. Thus, cattle may have ingested amounts of toxic plants that were sublethal in the familiar environment but lethal in the unfamiliar environment.

Correcting nutritional deficits

There has been a longstanding debate over the ability of animals to balance their diets nutritionally. Some contend herbivores are unable to prevent nutrient imbalances; others claim they innately recognize nutrients in foods. There is little evidence to support either position. However, there is ample evidence that animals forage to correct nutritional imbalances and deficiencies.

File Photo

There is evidence that animals forage to correct deficiencies.

Animals acquire aversions to nutrient-deficient diets. The reduced preference for the familiar diet depends on the severity of the deficiency. Aversions cause animals to sample other familiar foods or to sample novel foods. If the consequences of eating the novel foods are positive—they help to rectify the deficit—animals acquire a preference for the new foods and forage in the new locations. This "aversion-sample-preference" sequence helps animals to maintain nutrient balance, and it is a manifestation of the satiety hypothesis.

A decrease in preference for familiar over novel foods is the primary behavioral manifestation of a nutritional deficiency. For example, cattle, sheep, and goats deficient in phosphorus decrease intake of the familiar diet and increase their intake of novel alternatives including soil, bones, and rabbits. Lambs deficient in essential amino acids acquire strong aversions to the food(s) they were eating during the deficiency and acquire preferences for foods that rectify the deficits.

This combination of behaviors—aversion-sample-preference—may emerge in strange ways when animals are foraging on rangelands. The shrub blackbrush, for example, is deficient in macronutrients. Several years ago during a winter-grazing study, we confined Angora goats in groups of 11 goats to 6 adjacent blackbrush pastures. As the study progressed, goats became increasingly averse to blackbrush. In one pasture they began to eat woodrat houses. Goats acquired a preference for woodrat houses because chambers inside the dwellings contained a "cake" of urine-soaked (nitrogen-rich) vegetation that helped them to rectify their macronutrient deficit. By the end of the study, goats that ate woodrat houses had lost an average of 12% of body weight. Groups that had not discovered woodrat houses as a source of macronutrients had lost 20% of body weight.

Fred Provenza

All it took was one goat to discover that this woodrat house (above) provides a good source of nitrogen and other goats followed, which helped to rectify their macronutrient deficiency. Below, Angora goats graze amidst blackbrush.

Fred Provenza

The carnivorous herbivore

Animals sometimes engage in strange behaviors. In the case of foraging, cattle eat the flesh and bones of rabbits, deer eat antlers, goats eat woodrat houses, and bighorn sheep eat rodent middens. Various wild (caribou, red deer, white-tailed deer, bighorn sheep) and domestic (cattle, sheep, goats) herbivores eat other mammals (lemmings), birds (arctic terns, ptarmigan eggs), and fish. Livestock lick urine patches of rabbits and humans, chew wood, consume soil, and eat fecal pellets of rabbits. Why do herbivores eat these strange foods?

M. F. Wallis de Vries

A few cards short of a full deck or just short on nutrients? A nutrient deficiency caused this cow to exhibit the strange behavior of consuming rabbits.

Conventional wisdom says they're bored, but that doesn't fit with the finding that well-fed animals equally bored avoid eating strange foods. Herbivores deficient in nutrients acquire aversions to familiar foods. In essence, the deficiency "makes them

continued on next page. . .

The carnivorous herbivore continued. . .

File Photo

sick" and they associate the illness with the familiar diet. In turn, they readily sample novel foods.

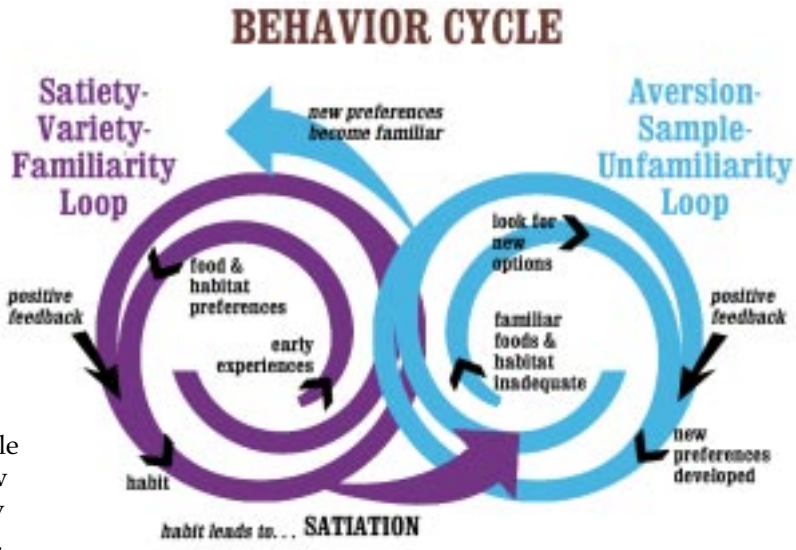
We once reared a group of lambs deficient in minerals. Their intake of the familiar diet began to decline, so we offered them another diet. Their intake of the new diet was high at first, but then declined. This pattern was repeated until we realized that they were deficient in minerals. Once we corrected the deficiency, intake of the basal diet and performance returned to formerly high levels. Cyclic patterns of intake are typical when animals are deficient in nutrients. They acquire an aversion to the familiar food and readily sample novel foods. When animals eat strange foods or when they spend inordinate time foraging, it indicates unmet nutritional needs.

File Photo

The question often arises as to the value of cafeteria-style mineral feeders. Strong scientific evidence shows that ruminants respond to excesses and deficits of energy, protein, sodium, phosphorus, and sulfur, and it is possible that they respond similarly to a broader array of minerals. Low concentrations of minerals limit intake, intermediate concentrations increase intake, and excessive amounts decrease intake. There are many anecdotal reports of animals in confinement, on pasture, and on rangelands selecting different minerals depending on their individual nutritional state and the chemical characteristics of the forage. Producers also report that ruminants decrease intake of specific minerals in free-choice feeders when those minerals are fed in confinement. For now, however, there is little scientific evidence to support or refute the contention. Carefully controlled studies that consider interactions between mineral nutrition and behavior are urgently needed.

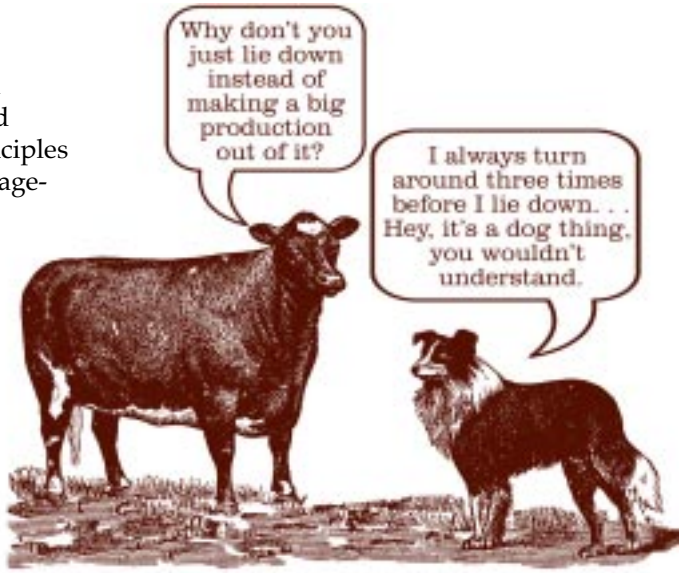
Cycles of behavior

Behavior, then, can be viewed as an ongoing dynamic that involves interactions between the familiar and the unfamiliar in two interacting feedback loops. (1) Satiety-Variety-Familiarity Loop: Experiences early in life cause preferences for foods and habitats; they are the origin of habits and the reason animals are reluctant to explore unfamiliar foods and habitats. Satiating on the same foods encourages animals to eat a variety of different familiar foods and to forage in various familiar locations.
(2) Aversion-Sample-Unfamiliarity Loop: If familiar foods and haunts become inadequate, animals investigate new options; old habits die and new habits are born. If they encounter suitable foods and habitats, they acquire preferences anew and move back into the satiety-variety-familiarity loop but with a broader repertoire of experiences.



Old Dogs, New Tricks

What influences behavior, be that of cells, organs, individuals, or social groups? Several principles pertain to the behavior of all creatures, from bacteria and insects to reptiles, birds, and mammals, including humans. Understanding these principles and how they influence behavior is key to effective management of systems. In the workplace, we can force employees to work hard because they need money, just as we can force animals to move through a chute with an electric prod. Alternatively, we can create environments where employees work hard because they like their job, as well as the money, just as we can create environments where cattle move, not because they are forced to move, but because they want to. To differentiate between the two approaches is to distinguish between positive (want to) and negative (have to) reinforcement, and knowledge of that difference can be used to teach old dogs new tricks in ways that increase profitability, reduce stress for animals and people, and improve the management of ecosystems.

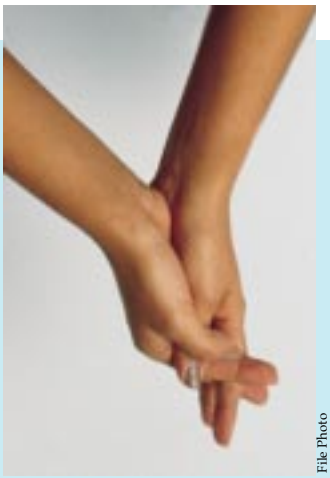


Behavior is a function of consequences

The variables that influence behavior of individuals are everywhere in the environment, from cells to organs to social and physical environments. At all these levels, behavior is a function of its consequences. If the probability of a behavior increases by delivery of some item or event, then that item or event, by definition, is a positive reinforcer, and the procedure is called reinforcement. When animals ingest a nutritious food or find nutritious foods in a particular location, the likelihood increases that they will eat the food and return to the location. If the probability of a response decreases after the contingent delivery of some item or event, that consequence is considered aversive and the procedure is called punishment. For example, if an animal is poisoned after eating a food or is attacked by a predator in a particular location, the likelihood decreases that the animal will eat the food or return to the location. Positive reinforcement increases response frequency, and punishment decreases response frequency. Nothing could be simpler or account for so much behavior at so many levels with so few assumptions.

Mary Donahue

Jim Winder, a rancher in southwest New Mexico, uses supplements to positively reinforce his cattle's behavior.



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Two hands clapping

Deborah Shouse describes the difference between positive reinforcement and punishment in an essay in *Newsweek* (May 1, 1995), "The Sound of Two Hands Clapping." She writes: "When I was growing up, I envied Sally Culver. Though she was five years younger, she had somehow managed to get herself a fan club. It began one summer evening, when Mrs. Culver brought her 1-year-old daughter, Sally, to our house.

"'I want to show you the most remarkable thing,' Mrs. Culver told my mother. She set the baby down on our driveway, and Sally, diaper rustling, took a step. 'Bravo!' Mrs. Culver said, clapping. 'Wasn't that just marvelous?' she asked, turning to me. I was standing back, my jump rope in hand, wondering why anyone would make such a big deal over walking.

"'Weren't her legs just the straightest things you've ever seen?' Mrs. Culver gushed to my mother. 'Her posture is exceptional,' my mother said. I took a breath and stood up straighter. My mother didn't notice. Sally took two steps before she plopped down. Again, applause. This time my mother joined in.

"I untangled my rope and jumped 10 more times. No one noticed. My mother was too busy clapping and cheering for Sally. It was my first experience with the power of applause."

Shouse goes on to describe how our personal lives are curiously devoid of tangible appreciation. Yet, if we don't experience positive reinforcement, how can we be expected to give it to others, be they people or livestock? Shouse developed a scenario—a day of two-hands clapping—for how such recognition might work: "I drive my children to school. As they collect their book bags, their extra tennis shoes, the book report that has already fallen in the mud, a team of mothers surrounds my car. 'Great job of getting your kids to school on time,' they say, applauding approvingly . . . . At work, my associates give me a standing ovation when I arrive. 'You are so responsible,' they say. I bask in the praise . . . . At the end of the workday, I drag myself through the grocery store. As I leave, the checkers and sackers stop to give their approval. 'Fabulous food gatherer,' they say encouragingly. 'What a wonderful mother and provider.'

"In my earlier life, I'd stagger into the house with bulging grocery sacks, only to have a daughter say, 'How come you didn't get chocolate-chip ripple ice cream? We never have anything good to eat.' Now, my daughters wait in the driveway, jumping up and down and cheering. 'Yeah, Mom. Thank you for guiding us nutritionally!' They stop their thunderous applause only to help me carry in the groceries.

"Do I really want to cook dinner after I've been solving problems, talking on the telephone, managing meetings all day? Sure, because as I carry the food to the table, my family applauds . . . . No wonder I'm thumbing through back issues of *Gourmet* magazine."

Shouse concludes with a anecdote that illustrates the power of positive reinforcement. "'This walkathon is not for sissies,' my friends warned me. After two hours, my new Walk-For-Life T-shirt was wet, my shoes were gnawing into my heels and my mouth felt like I'd licked 399 envelopes . . . . I was yearning for water, a fan and a new bottle of deodorant, when I heard "the sound." 'Yeah, you're great! You've come a long way. Only a few more miles to go. Great job!' The encouragement came from volunteers clustered at the intersection. Suddenly, my legs felt lighter, my mouth was moist. A gentle breeze dried my armpits. Someone had seen me—tired, sweaty and trying my best. Buoyed by the sounds of appreciation and praise, I knew I could walk a marathon."

At work, people are rewarded and punished throughout the day by all facets of the environment, just as a cow in a riparian area is rewarded and punished for her behaviors by insects, vegetation, water, shade, and social interactions. There are numerous occasions, for those with the time and interest, to encourage desirable behaviors and to discourage undesirable behaviors in people and in livestock. In so doing, we change the behavior of individuals and systems.

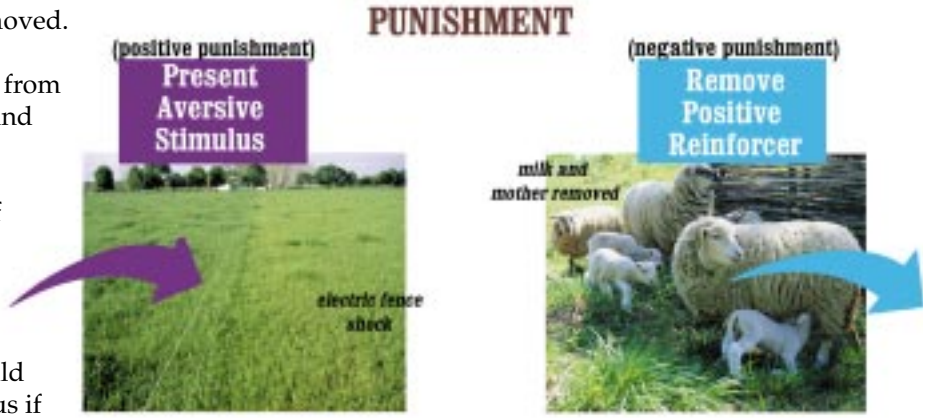
Reinforcement and punishment

Consequences can be divided into two categories—reinforcement and punishment. Behavior results from various combinations of these.

Reinforcement. Consequences that **increase** the likelihood of a behavior are called reinforcement, and they can be either positive (positive reinforcement) or negative (negative reinforcement). Creatures seek *positive reinforcers* and avoid negative reinforcers. When a hungry animal searches for a particular nutritious food, or a thirsty animal walks to water, or a hot animal seeks shade, they do so because food, water, and shade are positive reinforcers—they are things the animal wants. Conversely, animals avoid *negative reinforcers*. When a hungry animal searches for a nutritious food, or a thirsty animal walks to water, or a hot animal seeks shade, they also do so to get relief from an aversive stimuli—hunger, thirst, heat.

For long-term sustainability, behavior is better shaped by positive reinforcement than by negative reinforcement and punishment.

Punishment. Consequences that **decrease** the likelihood of a behavior are called *punishment*, and they can be based either on the presentation of an aversive stimulus (positive punishment) or on the removal of a positive reinforcer (negative punishment). *Positive punishment* is the presentation of an aversive stimulus. When livestock get shocked for touching an electric fence, they stop touching the fence. When employees are harassed for making suggestions, they stop proposing new ways to do business. *Negative punishment* is the removal of a positive reinforcer. When a goat eats a plant that was once nutritious but is no longer, or when a ewe walks away each time her lamb attempts to nurse during weaning, both the goat and the lamb decrease rates of responding (eating the plant, nursing) because a positive reinforcer (nutrients, milk) has been removed.



There is a growing movement away from reliance on negative reinforcement and punishment and toward the use of positive reinforcement. Punishment arouses anger and fear in animals. If strongly aversive stimuli are used, these emotions inhibit learning and actually lead to results opposite of those intended. A submissive dog may attack its owner if beaten. A child may become unduly shy and nervous if parental punishment is too severe. Punishment by withdrawing a positive reinforcer produces characteristic forms of emotional reaction—disappointment or depression—in people. Withdrawal of strong reinforcers may produce serious emotional reactions, the most obvious example being the death of a loved one. People who are close to us provide many reinforcers; when they die, those reinforcers are suddenly withdrawn. The same is true when animals are

moved from familiar to unfamiliar environments. All the positive reinforcers they have come to know are suddenly removed. No wonder they wander for miles, become malnourished and stressed, and don't reproduce. That's why it is so difficult to break old habits—all of the reinforcers are removed. Change, then, requires the death of old behaviors and the birth of new ones—no small task.

File Photo

Coercion doesn't work well for animals or people.

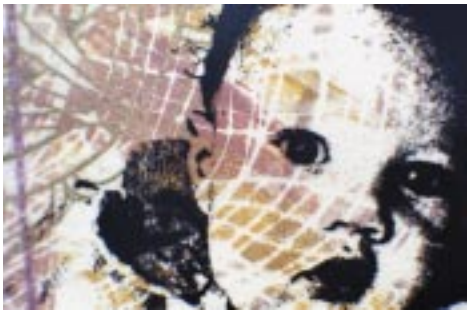
For long-term sustainability, behavior is better shaped by positive reinforcement than by negative reinforcement and punishment. While coercion can quickly change behavior, its long-term negative consequences —the desire to escape the circumstance and avoid anything remotely related—far outweigh its short-term benefits. People who work because they have to (negative reinforcement) are much less productive than people who work because they want to (positive reinforcement). Coercion causes stress, which reduces performance and profits. Livestock can be forced to move through chutes and in feedlots with hotshots, but that method will never cause animals to move freely. It may cause other unwanted behaviors like jumping and kicking. Livestock move readily when they are worked gently and rewarded for moving through chutes. It is less stressful on the animals and on the people.

"Nothing is more powerful than positive reinforcement. Everybody uses it. But top performers, almost alone, use it extensively."

Livestock handlers and trainers like Bud Williams advocate the use of gentle handling over harsh treatment. There is also a tendency, at least among those who publish books, to advocate use of positive reinforcement in business. It is virtually impossible to pick up a book on leadership and management that doesn't have at least one chapter, if not the entire book, devoted to encouraging people. In their book *In Search of Excellence*, Thomas Peters and Robert Waterman, Jr. state that "Nothing is more powerful than positive reinforcement. Everybody uses it. But top performers, almost alone, use it extensively."

Consequences depend on nature and nurture

What causes consequences to be positive or aversive? There has been a long-standing debate over which is more important—nature (genes) or nurture (experience). The argument is pointless because both are involved in behavior. Behavior is the ongoing integration of nature and nurture.



Behavior is the ongoing integration of nature and nurture.

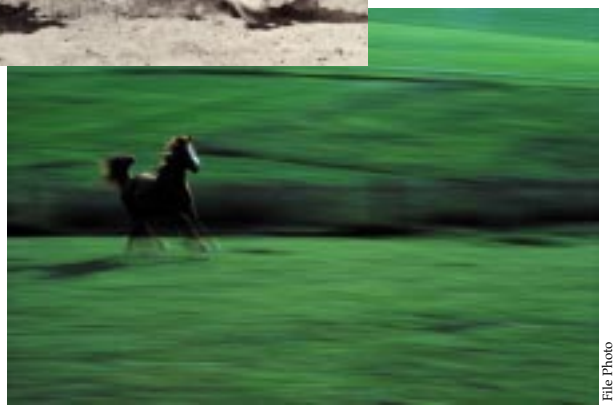
At conception, each individual inherits a genotype with instructions for its development, morphologically and physiologically. Morphology and physiology set limits within which an animal must function. For example, to continue to live all animals must ingest nutrients, and to avoid premature death all animals can ingest only limited amounts of toxins.

To facilitate adaptation, nature has constructed creatures so that nurture—social and environmental experiences—can help individuals adapt to the ever-changing conditions they encounter throughout life, even to the degree that experience influences gene expression. From conception on, each

individual interacts with a social and physical environment that influences its development. As cells, organs, individuals, and social groups interact with their respective environments they are themselves changed in the process. For example, all animals are born with muscles, but their ongoing development and stamina depend on how the muscles are used. This is true with all facets of behavior, including food and habitat selection. Neural development and patterns of firing, gut morphology, and digestive physiology all are influenced by what an animal eats. Thus, ongoing interactions continually transform both the individual and the environment. Nurture complements nature by allowing an animal of a given morphological form and physiological function to learn which combinations of foods are palatable and which combinations are not, based on experience and flavor-feedback interactions. Ongoing learning and adaptation are critical for survival because foods and habitats appear in such diverse forms across time and space and over the lifetime of the individual and the species. Flexibility means that what is "palatable" to one individual may not be "palatable" to the next, depending on each animal's genotype and its past experiences with particular foods and habitats—"one critter's meat is the next critter's poison."

File Photo

All animals are born with muscles but their ongoing development and stamina depend on how the muscles are used. The same is true with all facets of behavior, including food and habitat selection.



File Photo

"One critter's meat is the next critter's poison."

Using behavior to manage for ecological, cultural, and economic integrity

Some 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 to 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 our own behavior and that of livestock.

Gary Neuenswander

Red Canyon Ranch near Lander, Wyoming.

Cattle can be trained to prefer uplands over riparian areas, but only if people manage using behavioral principles. 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 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.

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Using behavior continued. . .

Gary Neuenswander

Bob Budd, manager of Red Canyon Ranch near Lander, Wyoming, believes a rider on horseback can train cattle to use uplands by consistently moving them to desired locations.

Bob Budd, an innovator who manages Red Canyon Ranch near Lander, Wyoming, for The Nature Conservancy, and his co-workers have been using these techniques for several years. They have increased cattle use of uplands and improved riparian areas. He 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.

Fred Provenza

Riders at Red Canyon Ranch herd cattle away from riparian areas and cull individuals who persist in using sensitive areas.

While riding has proved effective for controlling livestock distribution, a rider must consider social behavior. As Budd points out, most "wrecks" occur because animals aren't ready to move. For example, a cow without her calf moves slowly and eventually runs back, taking most of the herd with her. Cattle subgroups should be dispersed as a unit, otherwise individuals separated from their subgroup will return to their former location. A rider should purposely relocate subgroups to desirable sites. Upon arrival at the new site, the animals should be shown the locations of palatable forage, salt, and water. When moving cattle to a new site in familiar territory, it is best to move them before they have fed and watered; at the new site, they experience the positive reinforcement that comes from eating nutritious foods in the area. It also helps to plan moves to coincide with a decrease in nutritious forage in one location, which is aversive, and an abundance of food in the new location, which is positive. If done repeatedly, cattle learn to move because good things happen when they do. When moving them to new loafing areas, it is best to move them soon after they have fed and watered; a large meal is typically followed by muscular relaxation and drowsiness.

A rider also can identify cows and calves that consistently use riparian areas so individuals that exhibit repeated undesirable behaviors can be culled. Not all animals in a herd prefer the same foods or the same locations. Within any group, some individuals will never conform to management needs concerning food or habitat selection criteria while others will conform well. 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.

Skin and gut defenses

On rangelands, just one plant may stand between an herbivore and its use of a foraging environment. In some habitats, the obstacle is a poisonous plant, like locoweed or larkspur. Though palatable, it is toxic, preventing animals from using otherwise abundant and nutritious forage. In other areas, the barrier is a tasty plant that has high agronomic value, such as apple, cherry, or Douglas fir trees. Livestock could easily graze fruit orchards and forest plantations, even improving fruit harvest and tree growth, if only they could be persuaded not to eat the trees. In such cases, the key is to teach the critters that the preferred food is harmful.

Mary Donahue

Johnny Boudreaux, a cattle producer near Perry in southern Louisiana, uses a faithful dog to move his cattle and an electric fence to contain them.

How can livestock managers accomplish this useful trick? Say a manager wants to train herbivores to avoid a particular food, for example a field of barley or fruit trees in an orchard. Two fundamentally different techniques can accomplish the task. One is to teach the animal to avoid the place with dogs or an electric fence—place aversion. Animals learn quickly to avoid electric fences. When placed in a "training pen," they learn to avoid the wire; when they touch it, the shocking consequences are always aversive. The procedure is easy and cost-effective.

The other technique is to train herbivores to avoid the food with the use of toxins—food aversion. Animals quickly learn to avoid a food when its ingestion is followed by toxicosis. This can be induced by giving a toxin dose in a capsule with a balling gun immediately after the animal eats the food. Unlike a properly functioning electric fence, however, if an animal eats the food while foraging on pasture and does not experience toxicosis, the positive consequences of nutrients will diminish the food aversion—it is as if the electric fence no longer contains electricity.

Fred Provenza

Beth Burritt, Utah State University research associate, demonstrates the use of a balling gun.

Therein lies the challenge with food aversions. How can one create aversions strong enough to ensure that animals will never sample the food? The person who discovers the solution to this problem will certainly prosper. The findings will apply not only to livestock, but also to wildlife depredation, which results in the loss of millions of dollars annually. Here's food for thought on the matter.

Anyone who has ever trained animals has wondered what they learn from different experiences. For instance, a person walks into a pen of animals that have just been fed, catches a lamb or calf, and puts a balling gun containing a capsule with a toxin into its throat. The animal soon will experience toxicosis, but will it associate the toxicosis with the person who just attacked it or with the food it just ate? What mechanisms enable animals to learn to differentiate between the consequences of different stimuli—food and place aversions—in the environment?

Animals learn about foods and places in different ways. As preeminent psychologist John Garcia points out, "All organisms have evolved coping mechanisms for obtaining nutrients and protective mechanisms to keep from becoming nutrients." In many birds and most mammals, *auditory* and *visual* stimuli and sensations of pain and satisfaction are associated with the so-called skin-defense system, evolved in response to predation. The *taste* of food and sensations of nausea and satiety are part of the so-called gut-defense system evolved in response to toxins and nutrients in foods. *Odors* are readily associated with skin- or gut-defense systems. The odor of predators forewarns the skin-defense system, while the odor of food serves as a cue for the gut-defense system.

"All organisms have evolved coping mechanisms for obtaining nutrients and protective mechanisms to keep from becoming nutrients."

The way skin- and gut-defense systems work is illustrated in trials with hawks fed distinctively colored or flavored mice. When hawks normally fed white mice were given a black mouse, followed by an injection of a toxin, the hawks would eat neither black nor white mice. They were not discriminating between mice as a food item based on color. Rather, they were discriminating based on taste, which was the same for black and white mice. Thus, when a distinct taste was added to black mice, hawks learned to avoid black mice on sight after a single black mouse–toxicosis event. The hawks were discriminating between food sources based on taste.

These experiments show that not all cues are associated readily with all consequences. Animals made ill following exposure to audiovisual and taste cues show much stronger aversions to the taste than to the audiovisual cue. In contrast, if they receive a foot-shock following the same cues, they show much stronger aversions to the audiovisual than to the taste cues.

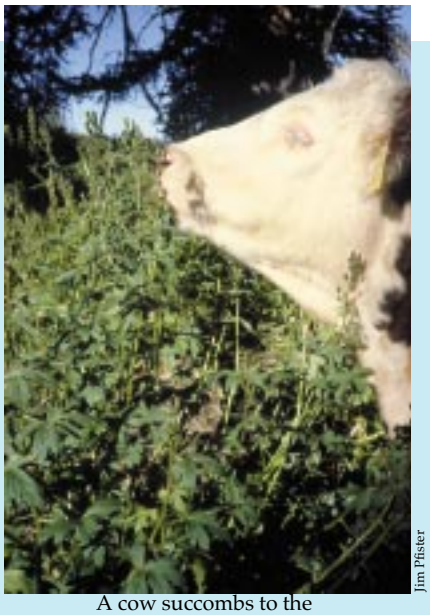
The same kind of response has been demonstrated for food and place aversions. Toxins decrease palatability, but they do not necessarily cause animals to avoid the place where they ate a particular food; this is the essence of the hawk-mice-toxicosis experiment. Conversely, an attack by a predator may cause animals to avoid the place where they were eating, but it does not decrease the palatability of the food. While place aversions are specific to the site, food aversions depend on the food and are generally independent of the location where the food was eaten.

Thus, when a person walks into a pen of animals, catches one, and puts a balling gun containing a capsule with a toxin in its throat, the animal will associate the person with the attack and its skin-defense system will respond, but it will associate the food ingestion with toxicosis and its gut-defense system will respond. The automatic, non-cognitive pairing of foods with postingestive consequences means that even if the person could explain to the animal that the capsule of toxin—not the food—was the cause of the toxicosis, it would still be averse to the food. The gut-defense system is designed to pair food ingestion with postingestive effects regardless of what the animal "thinks" caused the illness.

In trials, hawks normally fed white mice were fed black mice followed by an injection of toxin and they would eat neither black nor white mice. However, when a distinct taste was added to black mice, the hawks learned after a single black mouse–toxicosis event to avoid black mice on sight. Taste helps to create a much stronger aversion regarding food.

Teaching herbivores about toxic foods

Most plants contain toxins of one sort or another—even plants grown in gardens. They are simply present in low amounts because people have selected for low-toxin varieties of plants. By and large, herbivores have little trouble limiting intake of toxic plants to tolerable levels, as long as they have nutritious alternatives. Poisonous plants are typically a problem only when animals lack nutritious alternatives. However, some plants like larkspur and locoweed are a problem even when alternatives are available. Training livestock to avoid poisonous plants is one alternative to the economic losses from poisonous plant deaths.



Jim Pfister

A cow succombs to the temptation of larkspur.

The best way to an animal's palate is through its stomach, and the best way to teach an animal not to eat a food is to pair its ingestion with toxicosis. In a typical training protocol, animals are allowed to eat the food then given a dose of a toxin like lithium chloride. Lithium chloride is ideal for inducing food aversions because it can be administered in doses high enough to condition strong aversions without fear of death. Toxins cause food aversions by stimulating the emetic system, which is responsible for nausea in humans. Aversions to plants like larkspur and locoweed have persisted for as long as 3 years with cattle herds of up to 75 individuals. Aversions to shrubs like serviceberry and mountain mahogany have persisted for at least 1 year in sheep. Animals are usually trained in pens then allowed to forage on pastures or rangelands. Several principles pertain to food-avoidance conditioning for poisonous plants or trees in fruit orchards or pine plantations.

Jim Pfister

A field of locoweed, pretty to look at but deadly for horses.

Novelty of the food and dose of the toxin

The strength of an aversion depends on the strength of the flavor—its novelty—and the dose of the toxin. Generally, the stronger and more novel the flavor and the higher the dose of the toxin, the stronger and more persistent the food aversion. Animals most strongly avoid eating novel foods when their ingestion is consistently followed by a bout of toxicosis. That's how plants deter herbivores—the most noxious plants have strong, novel flavors and maintain high levels of toxins. Herbivores get the message the first time they eat the plant and every time thereafter. It is much harder to condition a lasting aversion to a previously eaten food—especially a nutritious food—because animals are more likely to re-sample the food. If they sample the food and do not experience toxicosis, the nutritional benefits the plant provides will quickly counter-condition the food aversion.

Frequency of flavor-toxicosis pairings

The strength of an aversion also depends on the frequency of the flavor-feedback consequence. It is important to allow the animals to eat (re-sample) the novel food over several days, always following food ingestion with toxicosis. Animals often sample some of the target plant on the day following toxicosis, even with a high dose of a toxin like lithium

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Teaching herbivores continued. . .

chloride, though intake of the food is greatly reduced. They often eat a little on the second day, but after the third day they typically show no interest in the plant.

Nutritious alternatives

Once an aversion is in place, it is critical that animals have access to abundant, nutritious alternatives while foraging. It is not enough to simply cause an aversion to the target plant to punish unwanted behaviors. One must also provide attractive alternatives. When the option is to eat the target plant or starve, animals eat even when plants are poisonous.

Jim Pfister

Larkspur—cattle can be trained to avoid it.

Age of animal

Younger animals can be more difficult to train than mature animals to persistently avoid a novel food. Young animals re-sample novel foods previously paired with toxicosis more readily than adults. They are more neophyllic. When a young animal eats the target food while foraging on pasture, the aversion quickly diminishes in the absence of toxicosis.

Social facilitation

Finally, trained animals should not be allowed to forage with untrained animals that eat the plant. When trained and untrained animals forage together, the trained animals are more likely to sample the plant, which allows nutritional benefits of eating the food to counter-condition the aversion. Mike Ralphs, range scientist with the Agricultural Research Service, Poisonous Plants Research Laboratory, trained one group of cattle to avoid larkspur, and the aversion persisted for 3 years. When he placed trained and untrained animals in the same pasture, the aversion to larkspur was gone within a month.

Creating cultures that enhance biodiversity

The dependence of ecosystem function and stability on biological diversity has been an integral part of ecological theory for over a century, but we are just beginning to understand the *biochemical links* between herbivores, plant diversity, and the sustainability of ecosystems. Biochemical diversity increases resiliency, adaptability, and productivity of ecosystems by creating options for plants, herbivores, and people.

Herbivores satiate on nutrients and toxins, and nutrient-toxin interactions limit the amount of any particular food an herbivore can ingest. Most plants contain toxins so ingesting plants with toxins is not simply a case of avoidance, but a matter of regulation. The ability to consume toxic plants depends on the quantity and quality of nutrients and the kinds of toxins.

Fred Provenza

A variety of plant life indicates biological diversity. This produces biochemical diversity increasing the resiliency, adaptability, and productivity of the ecosystem.

Herbivores are likely to optimize intake of nutrients and toxins in a manner consistent with the *chemistry of the foods* on offer and with their *previous experiences mixing those foods*. If animals are familiar with only some of the foods, and those foods provide adequate nutrition, herbivores are unlikely to eat other foods and are less likely to learn about the possible benefits of mixing different foods. Rather, they will probably eat all of the familiar foods in an area before they accept unfamiliar foods and mix the foods so as to balance nutrients and toxins. On the other hand, if herbivores are repeatedly forced to eat all plants they may learn to eat mixtures that mitigate toxicity, if appropriate choices are available.

Fred Provenza

Over 39 million hectares of the western landscape is now dominated by sagebrush and juniper, greatly decreasing plant diversity in sagebrush-steppe ecosystems.

Grazing sagebrush-steppe

Even though grazing can enhance plant diversity in sagebrush-steppe ecosystems, diversity generally declined during the past century as toxin-containing woody plants such as sagebrush (*Artemisia spp.*) and juniper (*Juniperus spp.*) came to dominate over 39 million hectares of land in the western U.S. This domination reflects the dearth of herbivores and changes in grazing patterns associated with grazers, such as cattle and elk, instead of mixed feeders and browsers, such as sheep, goats, deer, and antelope. Livestock often are confined and graze the same herbs repeatedly, particularly during spring on sagebrush-steppe landscapes. The decrease in grasses and forbs reduces fine fuels for fires and creates conditions that favor severe fire storms that reduce biodiversity. The problem has been exacerbated by fire suppression policies and lack of prescribed burning.

The decline in diversity adversely affects sagebrush-steppe ecosystems. Less water is available for other plant species because sagebrush transpires year-round. Nutrient cycling, plant production, and herbivore nutrition all are badly affected because sagebrush contains high concentrations of terpenoids, compounds that are toxic to soil and rumen microbes and to ruminants. To reverse these trends, managers must decrease—but not eliminate—the dominance of sagebrush and maintain a mixture of plant species.

Fred Provenza

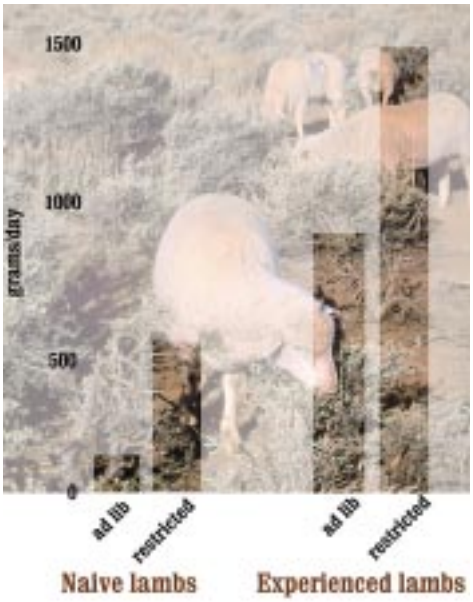
Sheep and goats supplemented with energy and protein eat much more sagebrush than unsupplemented animals. Macronutrients like energy and protein facilitate detoxification.

Grazing by livestock may be the most economical means to accomplish both objectives. Intensive grazing by sheep for short periods during the fall, when herbs are dormant, may increase diversity. Sheep and goats supplemented with macronutrients—energy and protein—eat much more sagebrush than unsupplemented animals, evidently because macronutrients facilitate detoxification. Thus, intake of sagebrush may be increased, and the adverse impacts of sagebrush on sheep mitigated, if large numbers of supplemented sheep graze sagebrush for short periods.

Finally, through grazing management that encourages use of all plants, herbivores may learn to mix their diets to achieve more even use of all plants, thereby maintaining plant diversity. Herbivores learn to optimize intakes of nutrients and toxins in a manner consistent with their previous experiences and with the mix of foods offered. If allowed to eat only the most preferred plants, herbivores are unlikely to learn about the consequences of mixing foods high in nutrients with foods high in toxins. On the other hand, herbivores repeatedly forced to eat all plants in an area may learn to eat mixtures of nutritious and toxic plants in ways that mitigate toxicity, assuming appropriate choices are available, given that nutrients facilitate detoxification processes.

We have begun to investigate the relationship between herbivore experience and availability of foods that vary in toxins and nutrients. In pen trials, lambs who learned to eat ground rations that contained tannins, terpenes, and oxalates ate more when they had a choice of two of the foods offered simultaneously—food with tannins/terpenes, tannins/oxalates, or terpenes/oxalates—than lambs offered only one food, and lambs offered the three-way combination—tannins/terpenes/oxalates—ate more than lambs offered any of the two-way combinations.

We then compared food intake by lambs with 3 months of experience mixing foods that contained the different toxins with lambs naive to the toxin-containing foods. Lambs were offered 5 foods, 2 of them familiar to all of the lambs—ground alfalfa and a 50:50 mix of ground alfalfa and ground barley—and 3 of them familiar only to experienced lambs—ground rations with either tannins, terpenes, or oxalates. Each day, half of the lambs were offered the familiar foods ad libitum, whereas the other half of the lambs were offered only a small amount (200 g) of the familiar foods.



In both cases, lambs with experience mixing foods that contain different toxins ate significantly more of the foods with toxins than naive lambs. Experience and availability of nutritious alternatives were both factors in food choices.

Experience and availability of nutritious alternatives both influenced food choice. Naive lambs ate much less of the foods with toxins if they had ad libitum rather than restricted access to the nutritious alternatives (66 vs 549 g/day). Experienced lambs also ate less of the foods with toxins if they had ad libitum as opposed to restricted access to the nutritious alternatives (809 vs 1497 g/day). In both cases, lambs with experience ate significantly more than naive lambs of the foods with toxins whether they had ad libitum (811 vs 71 g/day) or restricted (1509 vs 607 g/day) access to the alfalfa-barley alternatives.

These findings have implications for grazing management. Different systems of management cause animals to forage in different ways. Light stocking encourages selective foraging, whereas heavy stocking for short periods encourages diet mixing. What was traditionally considered proper grazing management—rotational grazing at low stock densities—may have trained generations of livestock and their offspring to "eat the best and leave the rest" thus inadvertently accelerating a decline in biodiversity and an increase in the abundance of less desirable plant species. By changing grazing practices, managers may be able to train their animals to "mix the best with the rest."

Fred Provenza

Heavy stocking for short periods encourages diet mixing and, along with learned patterns of foraging behavior, may, in the long run, lead to maintaining the biodiversity of landscpes.

Such learned patterns of foraging behavior are transmitted culturally from one generation to the next. Experiences early in life with mother influence preferences for foods and habitats. That knowledge, critical for the survival of individuals, may also be essential for maintaining the biodiversity of landscapes.

Fred Provenza

Gary Neuenswander

Ray Banister of eastern Montana looks at the least palatable plant species as indicators of when to move his cattle to a new pasture.

Boom-bust management

Ray Banister manages 7,200 acres of rangeland in eastern Montana. His management style has 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 2 growing seasons of rest. Ray's boom-bust grazing management stresses systems—soils, plants, and herbivores—with intensive grazing pressure, then allows them to recover. Ray believes that stress, and recovery from stress, strengthens systems.

The change to boom-bust grazing challenged the Hereford cattle on his ranch. The cattle were no longer allowed to eat only the most palatable plants as they had under the rotational grazing system. 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 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.

Fred Provenza

Ray Banister improved his rangeland in eastern Montana through boom-bust management. Occasional disturbance followed by rest creates and maintains a diversity of habitats and abundant plant cover.

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 well over 500 pounds to 350 pounds, then rebounded back to over 500 pounds.

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. Cattle likely mitigate the aversive effects of toxins by eating palatable plants high in nutrients along with unpalatable species high in toxins.

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.

Ray has improved the land through boom-bust management. 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 even during years of drought. 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.

Gary Neuenswander

Bob Jackson and Sharon Magee manage bison and land on the basis of the small bison family unit maintained by the group matriarch.

Culture, social organization, and grazing management

Bob Jackson and Sharon Magee own a bison operation in Iowa. They also have lived and worked in the back country of Yellowstone Park for many years where they spent considerable time observing social animals. They understand the interrelationships among culture, social organization, and grazing management. Intact family units—offspring, mothers, fathers, grandmothers, grandfathers—are the basis of their operation.

Frank Mayer and Charles Roth describe these social units in *The Buffalo Harvest*. "Do you remember reading about buffalo herds millions strong, moving in a solid mass, and stopping trains and wagons? . . . . Of course the herd, this vast mass of animals, would be under the leadership of a grand old buffalo bull, who would trot serenely at its head, issuing orders and demanding instant and complete obedience." But as they point out, these are misconceptions. "Most of the herds would run from 3 to 60 animals, with an average of around 15. In these small herds the buffalo traveled and fed, scattered over the plains, but each one separate and apart from the other herds. Whenever they stampeded they did come together and charged as one vast, solid herd. But when the fright passed they'd separate into their peculiar small herd formation . . . . (whose) leader wasn't a bull at all . . . . It was a cow, a sagacious old cow who by the power of her intellect had made herself a leader. Buffalo society, you see, was a matriarchy, and the cow was queen."

Bob and Sharon manage bison and land on the basis of these "peculiar small herds" under the leadership of matriarchs. They contend that bison family units are necessary for proper management. Young animals benefit from the knowledge of social behavior, food, and habitat selection of older generations. Bison culture, as with other social species like goats, sheep, cattle, deer, elk, and elephants, is a repository of knowledge about social and physical environments.

Jeff Henry

Part of a small family unit of bison graze in Yellowstone National Park, where Bob Jackson is a backcountry ranger and first began to study bison.

Members of family groups learn how to mix diets and achieve uniform use of different plant species, which enhances biodiversity. Bob and Sharon contend that managers who use family groups achieve the same outcome as those who use management-intensive grazing: more uniform use of all plant species. Competition among family groups promotes rotational grazing, without the need for fencing, as family groups displace one another while grazing across landscapes.

Social interactions also discourage the over-use of riparian areas. Matriarchs maintain identity of family groups by moving from riparian areas when other families enter the area, ensuring groups do not linger along watering points. Historical accounts

continued on next page. . .

Culture, social organization, and grazing management continued. . .

in Yellowstone and elsewhere indicate that riparian areas were heavily used primarily during the winter, when families tolerated more contact as they were forced to forage along riparian areas.

Such use of these environments is not possible when family order is disrupted or when domestic or wild animals are moved to unfamiliar environments. When cultures are disrupted, either by breaking up family groups or by moving families to unfamiliar environments, animals suffer from malnutrition, poisonous plants, and predation. This painful lesson, learned by many ranchers as they have attempted to move animals to unfamiliar haunts, is now being learned by conservation biologists who are attempting to re-introduce wild animals into habitats formerly occupied by other members of their species.

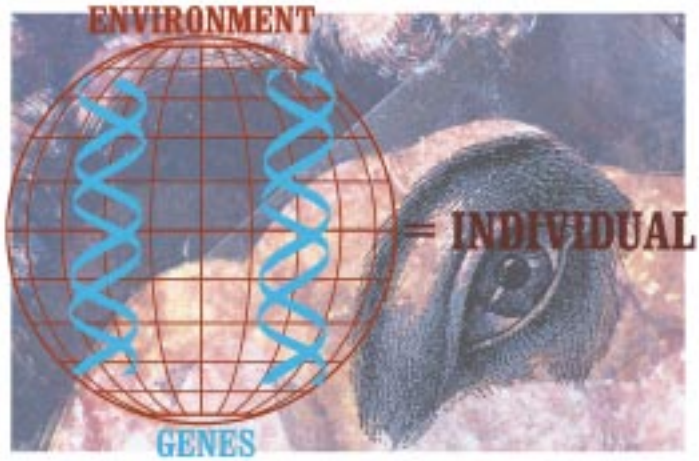
Fred Provenza

Bison in Yellowstone National Park allowed to remain in their small family units, above, versus a herd, below, where the family units are broken up and the bison behave more like cattle in their grazing movements.

Jeff Henry

Behave

In this booklet, I have discussed how behavioral principles influence food and habitat selection. I have attempted to show how simple strategies can be used to improve the efficiency and profitability of agriculture, the quality of life for managers and their animals, and the integrity of the environment, thereby enhancing the long-term sustainability of natural resources on private and public lands.



Scientists and managers often ignore the power of behavior to transform systems in spite of compelling evidence of the significance of environment in behavior. It now appears that there are only about one-third the number of human genes previously thought—roughly 20,000 to 40,000 total. Only a few hundred genes distinguish humans from mice. Geneticists say "blueprint" is not an appropriate metaphor for the genome. According to Craig Venter, president and chief scientific officer of Celera Genomics Inc., "We know that the environment acting on biological steps may be as important in making us what we are as the genetic code." Yoshiyuki Sakaki of the Riken Genome Sciences Center adds, "For companies that have concentrated solely on genetics, [these results] are bad news." On the other hand, the potential is virtually unlimited for those willing to understand how environment interacts with the genome to influence behavior.

"Scientists and managers often ignore the power of behavior to transform systems in spite of compelling evidence of the significance of environment in behavior."

Understanding the behavior of any creature is simple: behavior is a function of its consequences. Favorable consequences increase and aversive consequences decrease the likelihood of a behavior. This seemingly simple principle has enormously complex manifestations because consequences evolve from the ongoing integration of heredity and environment. At conception, each individual receives genetic "instructions" for its morphological and physiological development. To facilitate adaptation, these instructions can be modified by social and environmental experiences, and experiences early in life can influence gene expression. The uniqueness of these interactions makes each individual different. The plasticity of these processes lets animals adapt to ever-changing environments, and lets people use behavior to transform systems.

File Photos

Once mastered, behavioral principles become a part of the "infrastructure" of the person, not the place, so they are readily transferred from one locale to another. Such knowledge can be used to improve economic viability and ecological integrity of confinement-, pasture-, and range-based enterprises; to enhance and maintain biodiversity of

rangelands; to restore pastures and rangelands dominated by weeds; to alleviate livestock abuse of riparian areas; to anticipate the influence of behavior on systems; and 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.

Twentieth-century physics has shown that there is no absolute truth in science, that all concepts and theories are limited and approximate. Science is a quest for understanding, for truth, an attempt to account for observable phenomena in the physical and biological worlds, but science cannot be perceived as "true" or "final" in any absolute sense. It is merely a tentative organization of working hypotheses that, for the moment, best account for the facts concerning physical and biological processes whose interconnections are the fabric of a web characterized by change.

Managers confront a similar challenge: How does one manage ongoing interrelationships among facets of complex and poorly understood ecological, cultural, and economic systems, in light of a future not known or predictable, in ways that won't diminish options for future generations?

"All boundaries" as Peter Senge writes, "are fundamentally arbitrary. We invent them and then, ironically, we find ourselves trapped within them."

The best way to predict the future is to create it, and in the arena of constant transformation, anything is possible if we dare to engage one another and the environment in ways that nurture creativity. Creativity comes from venturing into the unknown. The familiar—comforting, orderly, generally predictable—often lacks creative zeal. The unfamiliar—obscure, potentially dangerous, always unpredictable—typically bestows creative opportunities.

Creativity comes from unions of opposites, from compassion, from opening up to that which is different from oneself. The contemporary world of natural resource management is filled with passion, but often devoid of compassion. The challenge is to transcend the boundaries we create. "All boundaries" as Peter Senge writes, "are fundamentally arbitrary. We invent them and then, ironically, we find ourselves trapped within them." Ultimately, the courage to love is the courage to transcend boundaries and traditions, and it is the source of creativity.

Illustration - Mary Donahue

Glossary of Terms

affective processes. Involuntary processes that do not require conscious thought. Breathing, digestion, and changes in palatability, for example, occur even while an animal sleeps or is anesthetized. They are intimately involved in changes in liking for foods.

aversion. Dislike for a food or place causing avoidance or rejection.

chaos. Lack of predictability in time and space.

cognitive processes. Voluntary processes that require conscious thought. Selecting particular foods or locations to forage, for example, are cognitive processes. Choosing to remain with the group or to forage alone involves the interplay between affective and cognitive processes.

contiguity. Proximity of a behavior and its consequences in time and space. Dynamic complexity arises when behaviors (actions) and consequences (outcomes) are detached in time and space.

contingency. Actions whose occurrence depend on specific environmental conditions that are subject to chance occurrences and hence probabilistic rather than deterministic. Behavior is contingent upon history of the social and physical environment, necessity, and chance.

continuum. A continuous whole whose parts cannot be separated. Nutrients and toxins interact in a dose-dependent manner along continuua from bodily benefit (experienced as satiety) to bodily harm (experienced as malaise). The behavior of any individual is a continuum formed by the interaction of the genotype (history of the species passed down through the ages) and the environment (individual's experience of social and physical conditions beginning at conception).

culture. Social influences on behaviors such as food and habitat selection that involve learning behaviors from social models such as a mother.

discriminate. The ability to distinguish between similar stimuli based on different consequences. Goats, for example, discriminate between current season's and older growth twigs from the shrub blackbrush based on differences in their flavor and postingestive effects.

emetic system. System responsible for malaise—nausea, vomiting—in animals. It is a critical component of the affective (involuntary) system and plays a role in the formation of conditioned taste aversions to forages too high in toxins or nutrients.

enteric. Intestinal or more generally of the digestive system.

feedback. A process in which the factors that produce a result are themselves modified by that result. Behavior, for example, is a function of its consequences.

flavor. Integration within the central nervous system of a food's taste and odor.

fluctuation. The process of continually changing or varying in an erratic way.

generalize. A transfer of the effects of conditioning to similar stimuli. Lambs, for example, that have learned food preferences or aversions based on a flavor such as cinnamon generalize preferences and aversions to different foods (e.g., wheat and rice) that contain cinnamon.

hedonic shift. A shift in palatability following positive or aversive postingestive feedback from nutrients or toxins. Hedonic shifts are manifest as increases or as decreases in intake or preference for a particular food.

herbivore. Any of a diverse group of animals with special adaptations for eating plants as the primary component of their diets.

intake. Amount of food eaten.

macronutrient Nutrients such as energy and protein required in large amounts by animals on a daily basis. They have a large influence on palatability.

malaise. Aversive postingestive feedback due to excessive intake of nutrients or toxins, experienced as nausea or feelings of physical discomfort.

metaphor. The application of a word or phrase to an object or concept it does not literally denote, implying comparison with that object or concept.

morphology. Branch of biology that deals with the form and structure of animals and plants.

nature. The influence of the genotype, as manifest morphologically and physiologically, on behavior.

negative punishment. Decrease in the rate of a behavior due to removal of a positive reinforcer. Creatures placed in unfamiliar environments are punished (i.e., all of the familiar positive reinforcers have been removed).

negative reinforcement. Increase in the rate of a behavior to avoid an aversive consequence. Livestock move away from people to avoid aversive contact.
neophobia. Avoidance of anything new or different.
neophyllia. Ready acceptance of anything new or different.
neurology. Branch of biology that deals with the structure and function of the nervous system.
novel food. Any food that is new or different and unfamiliar.
nurture. The influence of the environment, beginning at conception, on behavior.
nutrient-specific satiety. Decrease in preference for the flavor of a food based on postingestive feedback from nutrients. Sensory-, nutrient-, and toxin-specific satiety interact to influence palatability and preference for different foods.
palatability. The interrelationship between a food's flavor (recognizable features including odor, taste, and texture) and its postingestive effects caused by nutrients and toxins (postingestive feedback). The relationship between flavor and feedback is influenced by a food's chemical characteristics and an animal's nutritional state and past experiences with the food.
perturbation. Something that causes disturbance and disorder or confusion.
physiology. Branch of biology that deals with the functions and vital processes of living organisms including their cells and organs.
positive punishment. Decrease in the rate of occurrence of a behavior due to aversive consequences.
positive reinforcement. Increase in the rate of occurrence of a behavior due to positive consequences.
postingestive feedback. Feedback from the cells and organs of the body to the central nervous system. The central nervous system integrates a food's flavor with its postingestive effects, due to nutrients and toxins, through postingestive feedback. Nerves for taste (hypoglossal, glossopharyngeal, and trigeminal nerves innervate the buccal cavity and pharynx) converge with nerves from the viscera (vagal and splanchnic nerves innervate the pharynx, respiratory and gastrointestinal tracts) in the solitary nucleus of the brainstem. From there, they synapse and relay throughout the brainstem, limbic system, and cortex. Thus, the central nervous system integrates the external (social and physical) and internal (cells and organs) environments.
preference. The choices an animal makes when given alternatives. Preference indices are typically calculated as the amount of a particular food eaten in a meal divided by the total amount of all foods eaten in the meal.
ruminant. Any of a suborder of cud-chewing mammals (e.g., giraffe, camel, cattle, bison, elk, sheep, goats, deer, antelope) having a stomach with four chambers (rumen, reticulum, omasum, abomasum).
satiate (satiety). Having had enough or more than enough so that all pleasure or desire is lost.
self-organization. The outcome of feedback-driven functions—in far-from-equilibrium systems—whose outcomes are structured at bifurcation points, determined by probabilistic laws.
sensory-specific satiety. Decrease in preference for the flavor of a food as it is consumed. Sensory-, nutrient-, and toxin-specific satiety interact to influence palatability and preference for different foods.
social facilitation. The performance of a pattern of behavior already in an individual's repertoire, as a consequence of the performance of the same behavior by other individuals.
social learning. Acquiring new behaviors through social interactions.
toxin. Any compound capable of producing toxicosis by impairing some aspect of animal metabolism. Everything is toxic, including oxygen, water, and all nutrients if ingested in high enough doses. Most plants, grasses included, contain toxins. Toxins typically set a limit on the amount of food an animal can ingest. They do not produce harmful effects if ingested in limited amounts. Under certain circumstances, animals have difficulty refraining from overingesting certain plants that contain toxins—the so-called poisonous plants.
toxin-specific satiety. Decrease in preference for the flavor of a food based on postingestive feedback from toxins. Sensory-, nutrient-, and toxin-specific satiety interact to influence palatability and preference for different foods.

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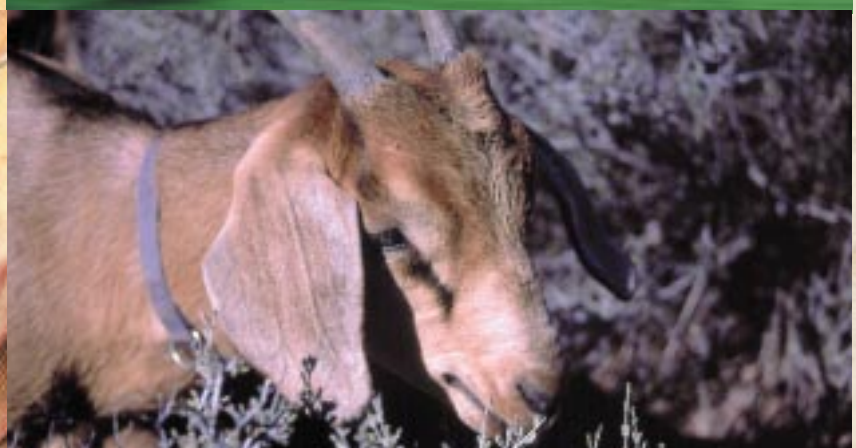
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