Foraging on the Edge of Chaos

Frederick D. Provenza and Karen L. Launchbaugh

Abstract

The foraging behavior of herbivores may appear to be little more than the idle wanderings of animals in search of food and a place to rest. A closer look reveals a sophisticated process by which herbivores survive in a tremendously complex, dynamic, and unpredictable habitat. How do creatures of habit, survive in a world where the only certainty is change? Most do fairly well despite the difficulties they encounter. These predicaments arise because climate, soils, plants, herbivores, and people are interrelated facets of a dynamic system. Continuous change demands that each component of the system continually react and adapt. This dynamic milieu causes problems for individuals which are inflexible but, adaptive behavioral processes can turn nature from an adversary to an ally.

Animals face several challenges in selecting foods and habitats in which to live. How animals cope with change, make foraging decisions, and overcome dilemmas they encounter illustrate behavioral processes as old as life. Understanding that variety is the spice of life and that adaptive behaviors allow old dogs to learn new tricks, can give natural resource managers new tools to help animals deal with dynamic environments and create more desirable environments. In short, understanding the behavioral processes that allow animals to deal with their daily foraging crises, can help us to better anticipate and manage the dynamics of living systems.

The Challenge

Herbivores face several challenges while foraging (Provenza and Balph 1990). The nutritional needs of animals change constantly as a consequence of age, physiological state, and environmental conditions. The quantities of energy, protein, and minerals in plants also vary constantly. The kind and amount of toxins in different plants and plant parts vary as do morphological defenses, such as standing dead material in some grasses, thorns in forbs and woody plants, and differences in canopy shape and architecture. Nutrients and toxins in plants also vary spatially and temporally. Additionally, animals encounter unfamiliar environments through dispersal, migration, or forced immigration. Given these dynamics, animals that can assess forage resources quickly and appropriately adjust nutrient intake, clearly have an advantage for survival and reproduction.

Fred D. Provenza is Professor of Rangeland Resources, Utah State University, Logan, UT, 84322-5230. Karen Launchbaugh is Professor of Rangeland Ecology & Managment, University of Idaho, Moscow, ID, 83844-1135.

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Coping with Change

Most of what we know about foraging behavior comes from controlled experiments, yet if properly described, the principles of behavior apply to all herbivores. The variables that influence animal behavior reside throughout the environment, from cells and organs to social and physical environment (Provenza et al. 1998; Figure 1). If the probability of a behavior occurring increases, due to the contingent delivery of some item or event, then that item or event is termed a positive reinforcer and the procedure is called reinforcement. 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. Positive reinforcement increases response frequency and punishment decreases response frequency (McSweeney this volume). Each individual behaves uniquely because interactions with its environment shape its behavior, beginning at conception and continually unceasingly until death. Animals behave because they are alive (nerves fire, organs, glands, muscles, and bones respond). Animals are alive because they behave. The concepts of learned behavior give us insight into how animals cope with the immense dynamism that characterizes the world around them.

Food for thought

The year from hell. Moving wildlife and livestock to new areas is often necessary to reach management objectives, but when animals are relocated, they face several potentially life-threatening challenges: new predators, toxic plants, and unfamiliar topographic features. Managers describe with horror and disbelief how animals ride the fences, refuse to eat highly nutri-

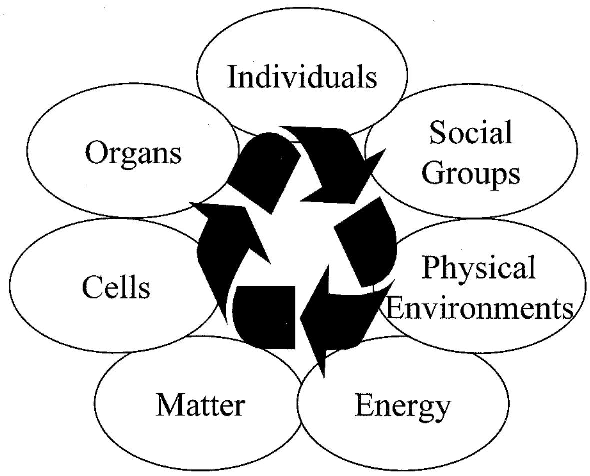

Figure 1. Life is interconnected and dynamic. Changes at any level in the environment lead to changes in behavior at all other levels. For instance, for responses (behavior) of a cell, independent environmental variables emerge from cellular, organ, individual, social, and physical processes, and the cell is the arbiter of consequences; for individual responses, the independent variables emerge from cellular, organ, social, and physical processes, and the individual is the arbiter of consequences; for responses of a social group, independent variables emerge from cellular, organ, individual, and physical processes, and the social group arbitrates consequences. In turn, cells, individuals and social groups influence environments, which in turn influence cells, individuals and social groups. The ever-changing nature of these relationships, involving the continual exchange of energy and matter, enables perpetually novel forms and behaviors to emerge at all levels of organization.

tious foods, and die from overingesting poisonous plants when introduced to a new environment. This situation often comes to be known as the "year from hell", and if herbivores could speak they would surely agree! Why do critters behave so? The conventional wisdom, that animals are unable to adapt to new environments, is inconsistent with the observation that both livestock and wildlife do well in the environment where they were reared.

Dairy dilemmas. To reduce the high cost of feeding lactating dairy cows in confinement, many producers are beginning to use intensively managed pastures as a source of low-cost, high-quality forage. A producer may optimistically turn a herd of lactating dairy cows, previously fed all their lives in confinement, onto a pasture with nutritious forage. Unfortunately, despite the abundance of high-quality food, the cows are likely to huddle at the gate and bellow. The highly upset producer reports that the cows are not eating and milk production is falling precipitously. Why do the cows behave in this manner and what can be done to rectify the problem? The conventional explanation, that the pasture is unpalatable, doesn't reconcile with the fact that dairy cattle in other areas readily eat similar plants and produce ample milk.

From range to feedlots. Livestock moved from pastures or rangelands to confinement in feedlots usually perform poorly during the first few weeks. Despite the fact that they have nutritious foods available *ad libitum*, food intake is low, animal performance is poor, and animals are likely to succumb to diseases. What are the problems and what can be done to reduce their adverse influences on animal performance? The conventional wisdom, that livestock are responding to the stress of being transported, cannot fully account for the decreases in food intake and performance.

Scientific perspective

Learning to eat. Gregarious animals learn many of their preferences through social interactions. For social animals, the transition from neonate to experienced forager occurs through interactions with mother and peers. Interactions with social models help young animals learn about the kinds and locations of foods, sources of water, and nature of hazards in their environment.

The influence of mother and peers on foraging behavior depends on the animal's age. Younger animals are influenced more by mother and less by peers than older animals (Mirza and Provenza 1992). Learning from mother about foods begins with flavors transferred in the uterus and in milk. Preferences for flavors become apparent as young animals begin to forage (Nolte et al. 1990, 1992, Nolte and Provenza 1992a, b). Lambs are most attentive to mother's grazing behavior from 4 to 8 weeks of age, a time when lambs begin to rely more on forage and less on milk (Mirza and Provenza 1992). The close proximity of the lamb to its mother during weaning may enhance learning by the lamb (Squibb et al. 1990). As lambs age, they interact increasingly with peers, affecting each other's behavior (Ralphs and Provenza 1999).

Eating to learn. Animals also must acquire foraging skills. Lambs reared on shrubs are more efficient at eating shrubs (they have higher intake rates) than lambs naive to shrubs (Flores et al. 1989a). Likewise, lambs that learned to eat grass in either vegetative or reproductive stages are more efficient at harvesting grass in the phenological stage to which they are accustomed (Flores et al. 1989b). Lambs that learned to harvest large leaves from serviceberry (*Amelanchier alnifolia*) shrubs were not as efficient at eating crested wheatgrass (*Agropyron cristatum*) stems as lambs reared on grass pastures (Flores et al. 1989c). On the other hand, animals that learned to eat twigs from shrubs like blackbrush (*Coleogyne ramosissima*) easily generalize their skills to other shrubs with large leaves (e.g., serviceberry) and to grasses and forbs with reproductive stems (Ortega-Reyes and Provenza 1993a). In general, the more structurally similar the plants, the greater the degree of generalization of skills between different plant species.

Age and amount of experience influence the development of foraging skills (Ortega-Reyes and Provenza 1993b). Young goats consistently maintained higher bite rates than adult goats. Bite rates increased with more experience browsing on pasture, but increments were higher in young than in adult goats. Bite rates increased only slightly after 20 days of browsing experience in adult goats, while bite rates were still increasing after 30 days in young goats. Browsing wildlife must certainly acquire foraging skills just as sheep and goats do. The age and amount of experience undoubtedly affects the acquisition of foraging skills in all grazers and browsers.

The lay of the land. Experiences of youth also shape habitat and die preferences. Wild herbivores of the same species often occupy different home ranges within an area (Provenza 1995a). Cross-fostering research with calves and lambs shows that where an animal is reared has a much greater influence on habitat selection than the genetic make-up of its natural or foster mother (Key and MacIver 1980, Howery et al. 1998). Offspring typically remain near where they were reared, unless drought or lack of forage force them to move to new locations, and even then, animals are generally reluctant to leave familiar surroundings for long. Peers can also affect habitat use, especially when offspring are yearlings. The effect of peers is observed in an increase in distance from mother, and by a higher association among yearlings. Nevertheless, as animals age, they often are found near where they were reared. Thus, experiences with both mother and peers affect distribution, but experiences early in life with mother have a more persistent influence.

Creatures of habit. As a result of selecting particular foods in certain locations, and not eating other foods in different locations, the responses of adults can become rigid and appear to be genetically fixed. Experiences early in life cause neurological changes in animals which may explain why some habits are difficult to break. Goats reared from 1 to 4 months of age with their mothers on blackbrush-dominated rangelands ate twice as much blackbrush as goats naive to blackbrush (when compared at 4 months of age; Distel and Provenza 1991). Nine months later, after both groups of goats foraged on pasture and naive goats had 1 month practice feeding on blackbrush, experienced goats still ate 27% more blackbrush than naive goats when only blackbrush was offered and they ate 30% more when blackbrush was given as a choice with alfalfa pellets.

These experienced and naive goats differed physiologically and morphologically immediately following exposure. Goats reared on blackbrush were excreting 63% more uronic acids than inexperienced goats, an indication of enhanced detoxification from eating high-tannin blackbrush. The rumen mass of goats reared on blackbrush was 30% greater than that of inexperienced goats. Collectively, experience affects diet and habitat selection, and in the process influences neurological, physiological, and morphological processes.

Noticing novelty. Experiences early in life lead to familiar-novel dichotomies that are manifest behaviorally in several ways: animals prefer familiar to novel foods, they prefer to be in familiar rather than unfamiliar environments, and they prefer to be with companions rather than strangers. Wariness of the unfamiliar does not indicate that animals "innately know" what is harmful or beneficial. Rather, it reflects that survival depends on their showing cautious regard for anything novel until its attributes can be discerned.

Management implications

Back to the year from hell. Animals born and raised in one place have difficulty adjusting to new foraging environments even if the new habitat has abundant forage resources. Unfamiliar environments are potentially dangerous, because animals must learn new locations for food, water, shelter, and in the process they are more susceptible to hazards like toxic plants, predators, and treacherous terrain. Young animals learn about these hazards from their mother and peers. The importance of social interactions, especially with mother, are clearly illustrated in instances when wild and domesticated animals are moved to unfamiliar environments. Compared with experienced animals reared in the environment, naive animals spend more time foraging but eat less food, more time walking greater distances, and suffer more predation, malnutrition, and ingestion of toxic plants (Provenza et al. 1992).

Animals encounter new environments when they are moved to new pastures as part of livestock management practices or when environments change rapidly because of abiotic or catastrophic events like fire or rain which can distinctly alter vegetation. 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 in the past. Some producers buy replacement animals only from areas similar to the ranges their animals inhabit. Similarly, wildlife biologists like to introduce animals into areas similar to their location of origin. Regardless of how similar a new area is to the area where animals were raised, there is still much information that does not transfer from one environment to the next. Animals must learn, through trial-and-error, the new environment beginning with which foods to eat or avoid and where to go to forage. Overcoming this herbivore version of "homesickness" typically takes about a year; the year from hell.

Back to dairy dilemmas. Mature dairy cattle, reared in confinement on processed foods, are at a distinct disadvantage when placed in a pasture, and expected to harvest forages they have never seen. Initially, they have neither the appetite nor the skills to ingest the grass. They require some time, typically several weeks, to become familiar with novel foods (pasture plants) and habitats (the pasture), and to acquire the skills needed to forage. This is especially true when animals are reared in confinement, as they have few opportunities to learn about different forages or practice harvesting these forage plants.

Animals are neophobic; they fear new foods and places (Provenza et al. 1998). The lowest intake occur when animals are offered novel foods in unfamiliar locations (Burritt and Provenza 1997). For cattle reared in confinement, the pasture is a new environment. Nevertheless, cattle gradually increase intake of nutritious novel foods, and in the process, they learn new foraging skills. Experience increases foraging efficiency and leads to higher intake rates and greater production.

Young animals cope with change more readily than adults, as do animals with a broad range of experiences, because their food and habitat preferences are more malleable. Exposing young animals to a variety of foods and locations, can minimize problems with transitions. Dairy cattle can be exposed to pasture forages early in life, as green chop in confinement or on pastures, before they are expected to forage and produce milk from pastures. Allowing young animals to forage on pastures with experienced animals can also alleviate the problem, and is somewhat akin to so-called "soft releases" in wildlife introductions.

Back to feedlots. Animals moved to feedlots have the skills needed to eat processed foods, but they have no experience with the food. They will require time, usually about 3 weeks, to adapt to the new diets. Exposing a young animal with its mother to foods it will encounter later in the feedlot greatly increases learning efficiency and enhances performance in feedlots (Ortega-Reyes et al. 1992). Exposure does not need to be long to be effective; as little as one hour per day for five days is sufficient. Young animals learn quickly from their mothers, and what they learn they remember for a long time; as long as three years with only brief exposure at six months of age (Green et al. 1984).

Conclusion

Animals learn based on the consequences of their actions - positive consequences increase the likelihood of the behavior, whereas aversive consequences decrease the likelihood of the behavior. Social interactions with mother and peers also play a key role in the development of food and habitat preferences. Experiences of youth profoundly affect an animal's ability to adapt to changing environments. To ensure that animals adapt to change, natural or human-induced, we must prepare them with proper early life experiences. Finally, we need to be patient. Herbivores possess behavioral tools to help them survive in dynamic environments, but adaptation takes time.

Making Tough Choices

Many people believe animals are genetically programmed to respond to the environment. As a result, animal behavior is viewed as inflexible. When we encounter problems with animals, we often assume that we must change the environment to suit the animal, rather than vice-versa, because animal behavior is unalterable. The reality is that food choices are flexible and based on several factors: the animal's genetic make-up, individual history, and foraging environment.

Food for thought

Wildly selective critters. The careful study of animals foraging in the wild has time and time again confirmed the observation that herbivores forage selectively; they eat diets higher in nutrients and lower in toxins than the average of what is available in the environment. They do this by wisely selecting among plant species, plant parts, and foraging locations. How do herbivores know what to eat and where to go? The conventional wisdom is that animals instinctively know what plants have the "good stuff" and know where to get them. This contention is not necessarily consistent with observed animal behaviors, especially when animals are in unfamiliar environments. What can be done to protect plant communities from potential damage of selective grazing and still allow for the selective grazing needed by herbivores to survive and reproduce?

Blackbrush browsing. Blackbrush is a small shrub that grows in dense stands on millions of acres in the southwestern United States. Current season's twigs are more nutritious than older twigs, but goats, deer and bighorn sheep strongly prefer older to younger twigs. Why? The conventional wisdom is that plant palatability is correlated through evolutionary forces with an animal's nutritional needs. Therefore, herbivores simply eat foods that taste good, and avoid foods that taste bad. Yet, in the case of blackbrush, animals apparently make unwise nutritional choices.

Carnivorous herbivores. Herbivores eat strange foods on occasion. For instance, cattle eat the flesh and bones of rabbits, deer eat antlers, goats eat woodrat houses, and bighorn sheep eat rodent middens. Various wild and domesticated herbivores eat other mammals (lemmings), birds (arctic terns, ptarmigan eggs), and fish. Livestock occasionally lick urine patches of rabbits and man, chew wood, consume soil, eat fecal pellets of rabbits, and ingest non-food items such as plastic, feathers, bones, cinders, sacks, and tins. Why do herbivores eat these strange foods? The conventional wisdom, that animals are bored, does not fit with the observation that well-fed animals typically avoid eating strange foods, especially if the foods are novel.

Scientific perspective

Palatability. All animals forage selectively, and their preferences for foods typically are attributed to plant palatability. Unfortunately, palatability is a nebulous term. Animal scientists explain palatability as the hedonic response of an animal to its food depending on flavor and texture and the relish an animal shows when consuming a food or ration. Plant scientists describe palatability as plant attributes that alter acceptability or "attractiveness" to animals, including chemical composition, growth stage, and associated plants. These definitions focus on either a food's flavor or its chemical characteristics, but they rarely integrate both concepts.

Palatability is the interrelationship between a food's flavor (odor, taste, and texture) and the postingestive effects of nutrients and toxins; both are influenced by a plant's chemical characteristics and an animal's nutritional state and past experiences with the food (Provenza 1995b). The senses (smell, taste, sight) enable animals to discriminate among foods and provide hedonic sensations associated with eating. Postingestive feedback calibrates the senses (hedonic sensations) with a food's hemostatic value.

Excesses and deficits. Excesses or deficits of nutrients (energy, protein, minerals) cause palatability to decrease (Provenza 1995b). It is generally accepted that animals show little preference for foods low in nutrients, but it is also true that animals avoid foods with excessive amounts of nutrients or energy (Smith et al. this volume, abstract). Protein and energy are important resources, but excesses of protein or energy cause dramatic decreases in preference and intake (Villalba and Provenza 1997a, b). The ratio of protein to energy has a strong influence on 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 (Kyriazakis and Oldham 1997).

Excesses of toxins (e.g., terpenes, alkaloids, cyanogenic glycosides) cause palatability to decrease (Provenza 1995b). Animals typically limit intake of nutritious foods that contain toxins to the amount of a particular toxin they can detoxify; as toxin concentrations decline, intake increases (Launchbaugh et al. 1993). When macronutrient and toxin concentrations vary, herbivores prefer foods high in nutrients and low in toxins, regardless of a food's flavor or physical characteristics (Wang and Provenza 1997, Villalba and Provenza 1999a).

Nutritional state. Palatability depends on an animal's nutritional state (Provenza et al. 1998). Palatability of foods high in energy increases after a meal high in protein, whereas palatability of foods high in protein increases after a meal high in energy (Villalba and Provenza 1999b). Lambs maintain a relatively constant ratio of energy to protein in their diets when they can select from foods varying in macronutrients. On a daily basis, animals require nearly five times more energy than protein, and they can store excess energy in fat. Thus, palatability is always strongly influenced by energy. Mineral needs also influence palatability. For instance, sheep strongly prefer flavored straw alone to flavored straw paired with a gavage of sodium chloride when their mineral needs are met (Villalba and Provenza 1996).

Nutritional state also influences responses to novelty. When nutritional and physiological conditions are adequate, animals prefer familiar food to novel ones (i.e., animals are neophobic). Conversely, when nutritional and physiological conditions are inadequate, animals avoid familiar foods in favor of novel ones (i.e.,animals are neophyllic). Lambs fed diets inadequate in macronutrients readily ingest novel foods high in protein or energy (Wang and Provenza 1996). Cattle and sheep also range more extensively in the late dry season than in the early- and mid-wet seasons, when plants are abundant and of high nutritional quality (Dudzinski et al. 1978, 1982). The tendency to "explore" novel food options could reveal nutritional resource. This exploration may be worth the risk to animals that are nutritionally deficient but not to animals that are meeting their nutritional needs.

Sampling foods in the environment is an adaptive behavior. Even with brief eating bouts sheep discriminate accurately and exhibit little permanent preferences or aversions for foods readily or reluctantly eaten. Sheep remain in an unbiased testing mode, readily sampling plants. This is adaptive because the toxin and nutrient contents of plants vary with season and location. Most studies emphasize the permanence of food preferences and aversions, and miss the power of dynamic sampling that enables animals to continually adapt.

Variety is the spice of life. Palatability is dynamic. Interactions between the senses and the body help to explain why palatability changes, within meals and from meal-to-meal (Provenza, 1996). Sensory receptors respond to gustatory (i.e., sweet, salt, sour, bitter), olfactory (i.e., a diversity of odors), and tactile (e.g., astringency, roughness, pain) stimuli. These receptors then interact with visceral receptors that respond to nutrients and toxins (chemo-receptors), osmolality (osmo-receptors), and distension (mechano-receptors). These processes affect palatability. The degree of neural activation sets limits. Within these limits, palatability increases when foods contain needed macronutrients. Beyond these limits, nutrient excesses and deficits and excesses of toxins reduce palatability. Responses to nutrients and toxins operate along a continuum from preference to aversion, depending on the frequency and intensity of stimulation. Cyclic patterns of intake reflect interactions among flavors, nutrients, and toxins along a time continuum.

Management implications

Back to wildly selective critters. The postingestive effects of macronutrients (e.g., energy and protein) condition food preferences. Animals discriminate between foods that vary in macronutrients, even when the differences are as small as 1 or 2 percent. The energy content of hay is slightly higher in the afternoon than in the morning, and as a result, cattle, sheep, and goats prefer, eat more, and perform better when fed hay harvested in the afternoon as opposed to the morning (Fisher et al. 1997). Spraying thistles with energy sources like molasses increases preference.

Animals prefer nutritious foods, they avoid foods high in toxins, and they forage in locations where they can readily ingest nutritious foods. This can be of concern when domestic animals are confined by fences, and not allowed to move to new locations when the nutritional quality of the vegetation changes; for instance, to move to higher elevations as plants at lower elevations mature. In such cases, overgrazing can lead to a decrease in the abundance of nutritious plants, and an increase in low quality or toxic plants. Taken to an extreme, overgrazing can decimate perennial plant populations, decrease nutrient cycling, accelerate soil erosion, and decrease animal performance.

Back to blackbrush. Most plants contain toxins of one kind or another that deter herbivory. Animals can quickly detect the presence of most toxins in plants, through flavor-postingestive feedback interactions. Toxins set intake limits on an otherwise nutritious food. It may be possible to increase use of plants like blackbrush and sagebrush with anti-toxicants or nutritional supplementation. For example, polyethylene glycol increases intake of tannin-containing plants by cattle, sheep and goats, because polyethylene glycol mitigates the aversive effects of tannins (Titus et al. 1999ab). Supplementing with activated charcoal increases intake of sagebrush by sheep, because charcoal absorbs terpenes (Banner et al. 1999). Supplemental macronutrients can also increase intake by facilitating detoxification processes (Launchbaugh 1996, Pfister this volume). Thus, it may be possible to formulate nutritious supplements that alleviate the adverse effects of plant allelochemicals, thereby improving food intake and animal performance and providing for more uniform use of plants in an area.

Back to carnivorous herbivores. Carnivorous herbivores are an extreme example of animals eating varied diets because of nutrient deficits. A key concept in the hypothesis regarding varied diets is aversion, defined as the decrease in amount of foods consumed as a result of nearing or exceeding tolerance limits for sensory (smell, taste, texture) and postingestive effects (e.g., nutrients and toxins acting on chemo-, osmo-, and mechano-receptors). After eating any food too frequently or excessively, animals will be more likely to eat alternate foods. Aversions may be pronounced when foods contain toxins or excessive levels of rapidly digestible nutrients such as some forms of nitrogen and energy (Early and Provenza 1998). However, they also occur when foods are deficient in specific nutrients (Atwood and Provenza 1999ab).

Animals eat a variety of foods because of sensory-, nutrient-, and toxin-specific satieties. The variety of familiar foods offered to animals is likely to be important in efforts to increase intake and performance in confinement, on pastures, and on rangelands. Offering different foods of similar nutritional value, offering foods of different nutritional value, and offering the same food in different flavors are all means of changing preference and potentially increasing food intake and animal performance (Atwood et al. 1999b). Offering a variety of foods also is a way to enable each individual to select the diet that best meets its needs. Finally, understanding why animals eat varied diets might help us to control depredation by livestock and wildlife. Losses to wildlife exceed $3 billion annually in the U.S., much of it involving agricultural crops. Providing nutritious alternates is one way to help alleviate wildlife depredation (Nolte this volume). Variety may also be an important consideration when training animals to avoid foods, such as trees in orchards or plantations or poisonous plants; providing a desirable mix of alternative foods could enhance the persistence of aversions.

Conclusion

We typically consider that animals instinctively know what and what not to eat and we often do not give them much credit for being nutritionally wise. Nevertheless, research during the past two decades shows that animals learn and are adept to select foods high in nutrients and low in toxins. In most cases where animals were presumably making nutritionally unwise choices, such as goats preferring older over current season's twigs in blackbrush, we found that the choices were influenced by both toxins and nutrients in foods. The fact that herbivores learn food selection behaviors, provides ample opportunities for creative management.

Teaching Old Dogs New Tricks

Life endures in a background of ceaseless change ever clinging to its current form forever challenged to change forms. The most general challenge of all, faced by herbivores and humans alike, is how to participate fully in the moment, yet recognize when the time is right to transform, to change the rules, and to invent a new existence. Proficient animal management usually involves staying out of the way and letting the natural foraging abilities of animals prevail. However, to meet some management goals, we might sometimes want to encourage dietary change and set the stage for transformation.

Food for thought

Benevolent brainwashing. Sometimes just one plant stands between the herbivore and a healthy or useful foraging environment. In some habitat, the obstacle is a poisonous plant, like locoweed (*Astragalus* spp. or *Oxytropis* spp.) or larkspur (*Delphinium* spp.), that is quite palatable, but deadly if eaten. In other foraging environments, the barrier is a tasty plant that has high agronomic value such as apple or cherry trees. Livestock could easily graze orchards and even improve fruit harvest if only they could be convinced not to eat the fruit trees. In cases such as these, the key is to change the critters mind into thinking a preferred food is aversive. How could livestock managers accomplish this useful trick?

Riparian riddles. Excessive livestock grazing can adversely affect soils and plants in uplands, and along streams and meadows commonly referred to as riparian areas. Overuse of uplands and riparian areas can adversely influence soil stability, water quantity and quality, and diminish habitat quality for many plants and animals which rely on riparian areas for survival. Because of abundance of nutritious forage, water, and shade, cattle often reside in riparian areas, but this is not always the case. For instance, some sub-groups of cattle frequent riparian areas only for water and then walk for miles to preferred areas to forage and rest. Why do livestock show differential use or overuse riparian areas? How can we improve use of rangelands by livestock? The conventional wisdom is that cattle innately prefer riparian areas and therefore riparian areas either must be fenced, or livestock removed from the land to mitigate the problem.

Scientific perspective

How animals learn. Genes are the cumulative memory of how environment has shaped a species through millennia. Skin- and gut-defense systems are part of these genetic instructions in all species from fruit flies to humans; and the way they work provides insights into how animals behave.

Animals process environmental information (e.g., sights and sounds, odors and tastes) in different ways. In many birds and mammals, auditory and visual stimuli and sensations of pain are associated with the skin-defense system, evolved in response to predation. The taste of food and sensations of nausea and satiety are part of the gut-defense system evolved, in response to toxins and nutrients in foods. All organisms, as John Garcia (1989) points out, 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 experiments conducted with hawks and distinctively colored or flavored mice (Garcia and Garcia-Robertson 1985). Hawks fed on white mice with impunity, but occasionally given a black mouse followed by an injection of the toxicant lithium chloride, would not eat either black or white mice presumably because both mice taste the same. When a distinctive flavor was added to black mice, hawks learned to avoid black mice on sight after a single black mouse-toxicosis pairing. The taste cue potentiated the color cue.

These experiments show that all cues are not readily associated with all consequences. Cue-consequence specificity occurs, because animals made ill following exposure to audiovisual and taste cues, show much stronger aversions to the taste than to the audiovisual stimuli. In contrast, if they receive foot-shock following the same cues, they show much stronger aversions to the audiovisual than to the taste cues (Garcia et al. 1985). 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. Conversely, an attack by a predator may cause animals to avoid the place where they were eating, but it does not decrease palatability of the food.

Transformations. All animals must ingest foods high in nutrients and avoid over-ingesting toxins, but exactly which foods an animal eats and where animals obtain foods are acquired behaviors. Animals must learn preferences for foods, develop foraging skills, and learn preferences for foraging locations. Changing habits takes time and effort because it involves changing the animals (neurologically, morphologically, and physiologically) and their relationship with the social and physical environment (Provenza et al. 1999). Herbivores are capable of such changes; and it is remarkable that, given time, they can change food and habitats.

Variation among individuals. Individual variation occurs because the genotype and the environment function in concert to influence animal growth and development. An individual's morphology and physiology influence its interactions with the environment, which in turn alter each individual's morphology and physiology (Provenza et al. 1998, 1999, Launchbaugh et al. this volume). These interactive processes are true for every nerve, muscle, and organ in the body. Thus, the body determines the structure of experience which determines the structure of the body, and the process is ongoing throughout life. The axiom "use it or lose it" applies equally to herbivores and people.

Every person is unique. As Williams (1978) points out, "Stomachs vary in size, shape and contour. . . . They also vary in operation . . . 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."

Like people, every herbivore is unique. Variation in dental structure affects the foraging abilities of individual sheep and goats (Gordon et al. 1996), as do differences in organ mass and how animals metabolize macronutrients (Konarzewski and Diamond 1994). Lambs of uniform age, sex, and breed vary in their preferences for foods. Some lambs prefer foods high in energy, whereas others prefer foods of medium or even low energy (Provenza et al. 1996). Doses of sodium propionate (sodium and energy) that condition preferences in some lambs condition aversions in others (Villalba and Provenza 1996). Responses to toxins also vary (Provenza et al. 1992). Some sheep fed a high level of goats rue (*Galega officinalis*) failed to show any symptoms of toxicosis, whereas others were killed by a low dose (Keeler et al. 1988). Sheep show similar variation in susceptibility to golden crownbeard (*Verbesina encelioides*; Keeler et al. 1992), as do goats to condensed tannins in blackbrush (Provenza et al. 1990). Thus, morphological and physiological factors influence food and habitat preferences as individuals interact with physical and social environments.

Management implications

Back to benevolent brainwashing. The best way to an animal's palate is through its stomach. Herbivores can be trained to avoid foods paired with toxicosis. In a typical training protocol, animals are allowed to eat the food, then given a dose of a toxin that induce gastrointestinal malaise; the herbivores mistakenly associates the illness with the target plant. A commonly used toxin is lithium chloride, because it induces strong food aversions, presumably by stimulating the brain's emetic system (i.e., the areas of the brain responsible for nausea in humans; Provenza et al. 1994). Animals are usually trained in pens and then allowed to forage on pastures. Aversions to plants like larkspur and locoweed have persisted for as long as three years with herds of cattle up to 75 individuals; and aversions to shrubs like serviceberry and mountain mahogany have persisted for at least one year (Ralphs and Provenza 1999).

Several principles pertain to effective training (Ralphs and Provenza 1999). Conditioning is most effective if animals have never eaten the food before. It is much harder to condition a lasting aversion when the food is familiar rather than novel. It is also more difficult to train young animals to persistently avoid a food than mature animals. Young animals sample novel foods and foods previously paired with toxicosis more readily than adults. It is also important to allow the animals to eat, and re-sample the food over several days, always following food ingestion with toxicosis. Toxins like lithium chloride are ideal for causing aversions because they can be safely administered in doses high enough to condition strong aversions, without fear of death. After inducing an aversion, it is critical that animals have access to nutritious plant alternatives, and that they don't forage with animals that have not acquired an aversion to the target plant.

Back to riparian riddles. Fences set boundaries, but unless streams are excluded from grazing, fences do not limit use of riparian areas. The high cost of fencing riparian areas is making it increasingly necessary to look for new alternatives. Training livestock to use particular locations through strategic herding is an alternative. Despite its potential advantages over fencing, herding typically has not been used to enhance cattle dispersion. Herding can change animal behavior. By encouraging cows and calves to use uplands, and discouraging their use of riparian areas, it is possible to enhance dispersion, and thereby obtain more uniform use of all lands within an allotment.

Herding may be less costly and more effective than conventional means of livestock control, like fencing. A rider on horseback can train adult cows and their offspring to use uplands more and riparian areas less. A herder can also identify cows and calves that consistently use riparian or upland areas so that undesirable individuals can be culled and desirable individuals can be retained (Baily this volume). The costs associated with herding are offset by the benefits from additional forage, herd health, and better riparian areas. Given time, the amount of time required for riding will diminish as the herd becomes dominated by replacement heifers trained to use the new foods and habitats.

Conclusion

The fact that animals learn food and habitat selection, creates opportunities for managers. Animals can be taught which foods to eat and which to avoid, and be trained to use uplands more and riparian areas less. Animals also can be culled and selected based on food and habitat selection behaviors. Old dogs can learn new tricks. They just don't learn as quickly as young dogs. Young dogs constantly taught new tricks learn new tricks more readily as adults.

Summary

As we've seen, the scheme of things is seldom as we perceive it. Though knowable, the processes of nature are inherently dynamic and not necessarily predictable. Life never was the way it was and it never will be again. For creatures of habit, the notions of constant change and unpredictability are neither reassuring nor comforting. On the other hand, uncompromising rigidity in the face of change leads to demise, be that of individuals, social groups, or species. The only alternative, illustrated throughout this paper, is to constantly adapt in the face of change. The opportunities are limitless for those willing to constantly adapt. Whether herbivore or human, the choice may be simple: adapt to live, don't and die.

Literature Cited

Atwood, S.B., F.D. Provenza, R.D. Wiedmeier and R.E. Banner. 1999a. Changes in preferences of gestating heifers fed untreated or ammoniated straw in different preferences. J. anim. Sci. accepted.

Atwood, S.B., F.D. Provenza, R.D. Wiedmeier and R.E. Banner. 1999b. Influence of free-choice versus mixed-ration diets on food intake and performance of fattening cattle. J. Anim. Sci. accepted.

Banner, R.E., J. Rogosic, E.A. Burritt and F.D. Provenza. 1999. Supplemental barley and activated charcoal increase intake of sagebrush (Artemisia tridentata ssp.) by lambs. J. Range Manage. accepted.

Burritt, E.A. and F.D. Provenza. 1997. Effect of an unfamiliar location on the consumption of novel and familiar foods by sheep. Appl. Anim. Behav. Sci. 54:317-325.

Distel, R.A. and F.D. Provenza. 1991. Experience early in life affects voluntary intake of blackbrush by goats. J. Chem. Ecol. 17:431-450.

Dudzinski, M.L., W.J. Muller, W.A. Low and H.J. Schuh. 1982. Relationship between dispersion behaviour of free-ranging cattle and forage conditions. Appl. Anim. Ethol. 8:225-241.

Dudzinski, M.L., H.J. Schuh, D.G. Wilcox, H.G. Gardiner and J.G. Morrisey. 1978. Statistical and probabilistic estimators of forage conditions from grazing behaviour of merino sheep in a semi-arid environment. Appl. Anim. Ethol. 4:357-368.

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

Fisher, D.S., J.C. Burns and H.F. Mayland. 1997. Variation in preference for morning or afternoon harvested hay in sheep, goats, and cattle. J. Anim. Sci. 75 (Suppl.), 201.

Flores, E.R., F.D. Provenza and D.F. Balph. 1989a. Role of experience in the development of foraging skills of lambs browsing the shrub serviceberry. Appl. Anim. Behav. Sci. 23:271-278.

Flores, E.R., F.D. Provenza and D.F. Balph. 1989b. Relationship between plant maturity and foraging experience of lambs grazing hycrest crested wheatgrass. Appl. Anim. Behav. Sci. 23:279-284.

Flores, E.R., F.D. Provenza and D.F. Balph. 1989c. The effect of experience on the foraging skill of lambs: importance of plant form. Appl. Anim. Behav. Sci. 23:285-291.

Garcia, J. 1989. Food for Tolman: cognition and cathexis in concert. p. 45-85. In T. Archer and L. Nilsson (eds.) Aversion, avoidance and anxiety. Erlbaum. Hillsdale, New Jersey.

Garcia, J., and R. Garcia-Robertson. 1985. Evolution of learning mechanisms, pp. 191-242, in B.L Hammonds (ed.). The Master Lecture Series, Psychology and Learning. American Psychological Association, Washington, D.C.

Garcia, J., Lasiter, P.A., F. Bermudez-Rattoni, and D.A. Deems. 1985. A general theory of aversion learning. pp. 8-21, in: N.S. Braveman and P. Bronstein (eds.). Experimental Assessments and Clinical Applications of Conditioned Food Aversions. New York Acad. Sci.

Gordon, I.J., A.W. Illius and J.D. Milne. 1996. Sources of variation in the foraging efficiency of grazing ruminants. Functional Ecol. 10:219-226.

Green, G.C., R.L. Elwin, B.E. Mottershead, R.G. Keogh and J.J. Lynch. 1984. Long-term effects of early experience to supplementary feeding in sheep. Proceedings Aust. Soc. Anim. Prod. 15:373-375.

Howery, L.D., F.D. Provenza, R.E. Banner and C.B. Scott. 1996. Differences in home range and habitat use among individuals in a cattle herd. Appl. Anim. Behav. Sci. 49:305-320.

Keeler, R.F., D.C. Baker and J.O. Evans. 1988. Individual animal susceptibility and its relationship to induced adaptation or tolerance in sheep to Galea officinalis. Letters Vet. Human Toxic. 30:420-423.

Keeler, R.F., D.C. Baker and K.E. Panter. 1992. Concentration of galegine in Verbesina enceliodes and Galega officinalis and the toxic and pathologic effects induced by the plants. J. Enviro. Path., Toxic. and Onc. 11:75-81.

Key, C., and R.M. MacIver. 1980. The effects of maternal influences on sheep: Breed differences in grazing, resting and courtship behavior. Appl. Anim. Ethol. 6:33-48.

Konarzewski M. and J. Diamond. 1994. Peak sustained metabolic rate and its individual variation in cold-stressed mice. Physiol. Zool. 67:1186-1212.

Kyriazakis, I. and J.D. Oldham. 1997. Food intake and diet selection of sheep: the effect of manipulating the rates of digestion of carbohydrates and protein of the foods offered as a choice. Br. J. Nutr. 77:243-254.

Launchbaugh, K.L., F.D. Provenza and E.A. Burritt. 1993. How herbivores track variable environments: Response to variability of phytoxins. J. of Chem. Ecol. 19:1047-1056.

Launchbaugh, K.L. 1996. Biochemical aspects of grazing behavior. p. 159-183 In: J. Hodgson, and A.W. Illius (eds.) The Ecology and Management of Grazing Systems. CAB International, Wallingford, U.K.

Mirza, S.N. and F.D. Provenza. 1992. Effects of age and conditions of exposure on maternally mediated food selection in lambs. Appl. Anim. Behav. Sci. 33:35-42.

Nolte, D.L., F.D. Provenza and D.F. Balph. 1990. The establishment and persistence of food preferences in lambs exposed to selected foods. J. Anim. Sci. 68:998-1002.

Nolte, D.L., F.D. Provenza, R. Callan and K.E. Panter. 1992. Garlic in the ovine fetal environment. Physiol. Behav. 52:1091-1093.

Nolte, D.L. and F.D. Provenza. 1992a. Food preferences in lambs after exposure to flavors in milk. Appl. Anim. Behav. Sci. 32:381-389.

Nolte, D.L. and F.D. Provenza. 1992b. Food preferences in lambs after exposure to flavors in solid foods. Appl. Anim. Behav. Sci. 32:337-347.

Ortega Reyes, L., F.D. Provenza, C.F. Parker and P.G. Hatfield. 1992. Drylot performance and ruminal papillae development of lambs exposed to a high concentrate diet while nursing. Small Rum. Res. 7:101-112.

Ortega-Reyes L. and F.D. Provenza. 1993a. Experience with blackbrush affects ingestion of shrub live oak by goats. J. Anim. Sci. 71:380-383.

Ortega-Reyes L. and F.D. Provenza. 1993b. Amount of experience and age affect the development of foraging skills of goats browsing blackbrush (Coleogyne ramosissima). Appl. Anim. Behav. Sci. 36:169-183.

Provenza, F.D. 1995a. Tracking variable environments: There is more than one kind of memory. J. Chem. Ecol. 21:911-923.

Provenza, F.D. 1995b. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range Manage. 48:2-17.

Provenza, F.D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. J. Anim. Sci. 74:2010-2020.

Provenza, F.D. and D.F. Balph. 1990. Applicability of five diet-selection models to various foraging challenges ruminants encounters. Pages 423-459 In: R.N. Hughes (ed.) Behavioural Mechanisms of Food Selection. NATO ASI Series G: Ecological Sciences, Vol. 20. Springer-Verlag, Berlin, Heildelberg.

Provenza, F.D., L. Ortega-Reyes, C.B. Scott, J.J. Lynch and E.A. Burritt. 1994. Antiemetic drugs attenuate food aversions in sheep. J. Anim. Sci. 72:1989-1994.

Provenza, F.D., E.A. Burritt, T.P. Clausen, J.P. Bryant, P.B. Reichardt and R.A. Distel. 1990. Conditioned flavor aversion: a mechanism for goats to avoid condensed tannins in blackbrush. Am. Nat. 136:810-828.

Provenza, F.D., J.A. Pfister and C.D. Cheney. 1992. Mechanisms of learning in diet selection with reference to phytotoxicosis in herbivores. J. Range Manage. 45:36-45.

Provenza, F.D., C.B. Scott, T.S. Phy and J.J. Lynch. 1996. Preference of sheep for foods varying in flavors and nutrients. J. Anim. Sci. 74:2355-2361.

Provenza, F.D., J.J. Villalba, C.D. Cheney and S.J. Werner. 1998. Self-organization of foraging behavior: from simplicity to complexity without goals. Nutr. Res. Rev. 11:1-24.

Provenza, F.D., J.J. Villalba and M. Augner. 1999. The physics of foraging. In press in Proceedings of the XVIII International Grassland Congress.

Ralphs, M.H. and F.D. Provenza. 1999. Conditioned food aversions: principles and practices with reference to social facilitation. Proc. Nutr. Soc. in press.

Squibb, R.C., F.D. Provenza and D.F. Balph. 1990. Effect of age of exposure on consumption of a shrub by sheep. J. Anim. Sci. 68:987-997.

Titus, C.H., F.D. Provenza, E.A. Burritt, A. Perevolotsky and N. Silanikove. 1999a. Preferences for foods varying in macronutrients and tannins by lambs supplemented with polyethylene glycol. J. Chem. Ecol. submitted.

Titus, C.H., F.D. Provenza, A. Perevolotsky, N. Silanikove and J. Rogosic. 1999b. Preference for current season's and older growth blackbrush twigs by goats supplemented with polyethylene glycol. J. Chem. Ecol. submitted.

Villalba, J.J. and F.D. Provenza. 1996. Preference for flavored wheat straw by lambs conditioned with intraruminal administrations of sodium propionate. J. Anim. Sci. 74:2362-2368.

Villalba, J.J. and F.D. Provenza. 1997a. Preference for flavoured foods by lambs conditioned with intraruminal administration of nitrogen. Br. J. Nutr. 78:545-561.

Villalba, J.J. and F.D. Provenza. 1997b. Preference for flavored wheat straw by lambs conditioned with intraruminal infusions of acetate and propionate. J. Anim. Sci. 75:2905-2914.

Villalba, J.J. and F.D. Provenza. 1999a. Effects of food structure and nutritional quality and animal nutritional state on intake behaviour and food preferences of sheep. Appl. Anim. Behav. Sci., in press.

Villalba, J.J. and F.D. Provenza. 1999b. Nutrient-specific preferences by lambs conditioned with intraruminal infusions of starch, casein, and water. J. Anim. Sci. in press.

Wang, J. and F.D. Provenza. 1996. Food preference and acceptance of novel foods by lambs depend on the composition of the basal diet. J. Anim. Sci. 74:2349-2354.

Wang, J. and F.D. Provenza. 1997. Dynamics of preference by sheep offered foods varying in flavors, nutrients, and a toxin. J. Chem. Ecol. 23:275-288.

Williams, R.J. 1978. You are extraordinary, Pages 121-123 in The art of living. Berkeley Books, New York, NY.