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Rangeland Herbivores Learn to Forage in a World Where the Only Constant is Change

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Introduction

When we go to the grocery store it is a fairly easy task to select and purchase nutritious meals. A readily available, predictable food supply is conveniently organized and displayed in the aisles. The nutritional composition of most foods is clearly labeled so you can immediately know what nutrients (and perhaps, toxins) you will be consuming.

In contrast, rangeland animals live in a world where nutrients and toxins are constantly changing across space and time. For example, there may be 10's to 100's of plant species growing on a single acre, and each plant can differ widely in the kinds and amounts of nutrients and toxins it offers to free-ranging herbivores. Even at the level of the individual plant, plant parts vary in their concentration of nutrients and toxins. Leaves, stems, and flowers, all differ in the kinds and amounts of nutrients and toxins they contain. Nutrient and toxin content of the same plant species can also vary depending on where it grows (in the sun vs. shade, on a wet vs. dry site, on a fertile vs. infertile site, etc.). Mother Nature can also drastically alter foraging environments as a result of natural disasters like floods, fires, or droughts. Wild animals may find themselves in unfamiliar environments during their natural migration patterns. Range and wildlife management practices can also place wild and domestic herbivores in unfamiliar environments via relocation and reintroduction programs or via grazing management practices.

Despite all these challenges, rangeland herbivores are remarkably adept at selecting plants that meet their nutritional needs while largely avoiding plants that do not. The fact that animals preferentially select plant species that are more nutritious than what is available, on average, is strong evidence that animals are able to somehow detect nutrient and toxin levels in plants as they change across space and time. In this paper, we examine recent important discoveries that underscore the importance of learning as a critical mechanism which allows rangeland herbivores to survive in a world where the only constant is change (Provenza, 2003; **www.behave.net**).

Photo by F. D. Provenza

Photo 1. Mother can have a profound influence on her offspring's dietary preferences

Exposure to foods with mother at an early age has long-term effects on diet selection

We have all heard the old adage "mother knows best." Is it true for rangeland herbivores (Photo 1). Green et al. (1984) published one of the first experiments to demonstrate the importance of early experience with mother. These researchers exposed 6-week-old lambs to wheat for a very short period of time (1 hour per day for 5 days). One group of lambs ate wheat alone, a second group ate wheat with their mothers, while a third group (control) received no exposure to wheat. Later, researchers tested all 3 groups when the lambs were 3 and 34 months of age. Lambs that had previously eaten wheat with their mothers ate over twice as much of the high-quality grain during both test phases (3 and 34 months of age) compared to the other 2 groups.

Another study demonstrated that a mother could also influence her offspring to eat more of a low-quality food (Distel and Provenza, 1991). Researchers exposed goat kids to blackbrush (*Coleogyne ramosissima*) either with (treatment group) or without their mothers (control group). Similar to the previous study with lambs and wheat, early exposure to blackbrush with mother caused goat kids to consume about twice as much of the poor quality shrub (<6% crude protein), compared to the control group, when the kids were 4 and 13 months old. The group that had been exposed to blackbrush with mother continued to eat more of the shrub than the control group even as increasing levels of nutritious alfalfa pellets were offered alongside blackbrush. Thus, early exposure to blackbrush influenced total intake, as well as relative preference, of the low-quality shrub even when a high-quality food alternative was available.

Rangeland animals must play the foraging hand that is dealt to them. Some rangeland herbivores are fortunate enough to be raised in high-quality environments while others must survive in low-quality environments. For example, in the blackbrush experiment, young animals continued to eat more of the food that mother ate even though blackbrush is a very low quality food. The important point is that mother provides her offspring an initial repertoire of food choices unique to the foraging environment during the year in which the animal happens to be born. At weaning, young animals already have a familiar set of safe foods they learned to eat while foraging alongside their mothers. But learning about ever-changing rangeland foraging environments can not and does not suddenly end after weaning.

Animals possess a "hard-wired" (Pavlovian) system which provides flexibility to make "soft-wired" decisions in foraging environments where the only constant is change

Have you ever noticed that some folks love the taste of certain foods while others consider the same food to be absolutely wretched? For example, some people like potato salad while others despise it. In fact, some individuals find potato salad so disgusting they risk offending friends and family members by passing on Mom's or Aunt Gen's world famous dish. So why do some people loathe the same dish that others savor? Possible answers might be revealed by examining an individual's early cultural experiences with the food. Those that despise potato salad may have had an experience where they ate some after it had "gone south." Or, maybe they ingested it when their emetic system (the system in animals that causes nausea) was experiencing turmoil, perhaps due to a case of the flu or even motion sickness. In the former case, maybe they could blame Mom or Aunt Gen, but the latter case might be a simple case of bad timing. Either way, the body "remembers" early negative post-ingestive experiences with "bad" foods, and no amount of hearing "try it you'll like it" can convince certain people that potato salad tastes good. On the other hand, those that like potato salad could have grown to relish the dish as youngsters because their mothers and peers liked it and because they experienced positive rather than negative feedback after ingesting the food.

Conditioned aversions occur when an animal *learns* to associate the taste or flavor (flavor = taste + odor) of a food with nausea, or, to a lesser extent, when a food does not provide the nutrients an animal requires given its current physiological state and nutritional plane. Conversely, conditioned preferences occur when an animal *learns* to associate the taste or flavor of a food with satiety, i.e., when a food provides the nutrients an animal requires. Both conditioned aversions and preferences occur without any cognitive thought, even while animals are asleep or deeply anesthetized. The degree to which a food is despised or coveted depends on the animal's prior experiences with the food and whether or not the food meets the animal's needs. First impressions matter, and novel foods typically get blamed or credited for aversions or preferences, respectively, depending on whether the post-ingestive feedback (PIF) is negative (due to illness or malnutrition) or positive (due to needed nutrients or medicines). Thus, what makes a food taste good or bad depends on PIF from the gut to the brain after a food is ingested. If PIF is negative, intake decreases, and vice versa. This "conditioned response" phenomenon is pervasive throughout the animal kingdom and has been shown to occur in mammals, birds, and reptiles (Provenza, 1995).

So why are these discoveries important to rangeland herbivores? Conditioned aversions and preferences provide a "hard-wired" means for rangeland herbivores to learn in a world where the toxin and nutrient content of rangeland forages is constantly changing. Animals don't have to "think about" or "remember" how they acquire food aversions and preferences any more than they have to think about or remember how to take their next breath or to make their heart take its next beat. Thus, animals do possess "nutritional wisdom" but it comes from an involuntary system that affords maximum flexibility for animals to learn about the inevitable nutritional changes that occur in rangeland forages across space and time. These findings are also important because people have used this knowledge to train sheep to forage in vineyards without eating grape leaves (**http://www.news.ucdavis.edu/search/printable_news.lasso?id=8200&table=news**), train cattle and horses not to eat poisonous plants such as larkspur (cattle) and locoweed (horses) (Ralphs and Provenza, 1999), train cattle to eat weeds (**http://www.livestockforlandscapes.com**), and train sheep and cattle to eat sagebrush or blackbrush (Banner et al., 2000; Photo 2).

Photo by F. D. Provenza

Photo 2. Early dietary experiences with low quality foods like sagebrush or blackbrush (shown here) can help animals to tolerate more of these kinds of foods later in life.

Rangeland herbivores carefully sample rangeland forages to detect subtle changes in nutrient and toxin content

Have you ever tried to poison a rat? Rats, like most animals, are naturally suspicious of "novel" (new) foods and flavors. Rats are very keen at consuming sub-lethal amounts of a poisonous bait, associating negative post-ingestive consequences (malaise) with the bait's flavor, and then avoiding the bait after just one negative experience. In other words, rats will carefully sample a toxic bait, get sick, and then avoid it much in the same way some folks avoid Mom's potato salad. On the other hand, if a nutritious food meets a rat's nutritional needs, intake of the food gradually increases as the food's flavor and its positive post-ingestive consequences become less novel, more familiar, more "safe", and more preferred. When a food is novel, aversions (or preferences) intensify with the degree of illness (or positive feelings) that follows ingestion of the food.

But how can a free-ranging ruminant foraging in a pasture that contains 10's to 100's of plant species possibly associate PIF with that many foods? Well, its like the great philosopher, Yogi Berra once said, "You can observe a lot just by watch'n." The answer comes by observing how ruminants forage within a meal. Rangeland herbivores are akin to large rats with hooves when it comes to avoiding plants that are harmful or ones that are low in nutrients. Like rats, rangeland ruminants are very picky about what they eat. Even though there may be 10's to 100's of plant species available, rangeland herbivores typically will eat only a small fraction of those species (about 6-12) within a 2-3 hour meal (known as a "foraging bout" in the scientific literature). Most of these few species are familiar foods that have been previously confirmed to have relatively positive PIF. However, animals also carefully sample a few novel plants in small amounts until the relationship between the flavor and post-ingestive consequences of new foods can be confirmed. Foods that cause illness are avoided while foods that satisfy are sought. Thus, rangeland herbivores, like rats, are constantly, and mostly unconsciously, regulating their intake according to whether the flavors of foods are associated with negative or positive consequences. Foraging like a rat is a critical strategy that rangeland herbivores use to track variable foraging environments.

Animals have a long-term memory when it comes to remembering the consequences of eating good and bad foods

Do animals (elephants notwithstanding) ever forget a food? Several studies have shown that animals have long-term memories when it comes to remembering the consequences of eating foods. Recall the lamb study with wheat and the goat kid study with blackbrush. Animals learned very quickly at an early age to eat what mother ate and then remembered that information for at least 3 years.

Another study serendipitously revealed how early experience with a low-quality food was remembered by cattle for at least 5 years. Dr. Randy Wiedmeir from Utah State University was feeding ammoniated straw to cattle during winter as a means to reduce winter feeding costs (Wiedmeier et al., 2002). During a 3-year trial, 32 cows, 5-8 years old, were fed ammoniated straw from December to May. As the results of the study started coming in, Randy was surprised to learn that half the cows were performing poorly, while the other half exceeded expectations in several animal production categories. Why did these two groups of cows, purposely selected to be similar "experimental units", perform so differently on the ammoniated straw? This was a question that Randy pondered until he consulted one of his technicians who had kept detailed records on the dietary history of the 32 cows since birth. Records revealed that half of the cows had been exposed to straw with their mothers during their first 3 months of life, while the other half had never seen straw. Even though the experienced cows had not seen straw for at least 5 years, they maintained higher body condition, produced more milk, lost less weight, and bred back sooner than cows with no exposure to straw. Randy's study demonstrated two important lessons for both managers and scientists. First, early experience matters, especially with mother. Second, animals can remember what they learned early in life for at least 5 years.

Peers are role models too

Randy's study, the previously described studies with lambs and goat kids, and many other studies have demonstrated the importance of mother in influencing the early dietary preferences of her offspring. But what about peers? If you have children, especially teenagers, no one has to tell you that peer pressure can be either a good or a bad thing depending on the circumstances. Is the same true for livestock? The following two studies illustrate the importance of peer pressure in livestock: one with goats on Martinique, an island in the French West Indies, and a second with cattle grazing larkspur (a poisonous plant) on high elevation rangeland in Utah.

The vegetation composition on the island of Martinique can be characterized as a diverse tropical savanna. In this study, 4 groups of goats that had been reared in 4 different areas of the island were placed in a diverse pasture comprised of about 100 plant species (Biquand and Biquand-Guyot, 1992). Diet selection patterns of individuals in the combined herd were then closely monitored in the common pasture for 4 consecutive years. During the first year of the study, each group continued to select diets that mirrored their original location on the island. However, with each successive goat generation over the next 4 years, diets gradually converged across the 4 goat groups. Nevertheless, each successive generation of goats still preferred a few key plant species that could be traced back to the original goats that grazed the common pasture the first year of the study. The researchers concluded, "Diet selection in goats is thus influenced both by the composition of pastures grazed during the first year of life and by the social environment including family and peers (Photo 3)."

PHOTO BY F. D. PROVENZA

Photo 3. Goat peer groups can influence diet and habitat selection.

In the Utah study, researchers examined whether lithium chloride (LiCl), a compound that produces conditioned taste aversions, could be used to avert cattle to larkspur (*Delphinium* spp.), a highly nutritious, yet poisonous plant that commonly grows at high elevations throughout the western U.S. (Ralphs, 1997). During this 3-year study, one group of cows was averted to larkspur using LiCl (averted group) while a second group of cattle was not averted to larkspur (control group). During all 3 years of the study the 2 groups of cows grazed separate pastures that contained similar amounts of larkspur. As long as the averted and control groups were kept in separate pastures, averted cows mostly avoided larkspur while the control group grazed larkspur at much higher levels. However, during the last month of the 3rd year of the study, researchers placed averted and control animals in the same pasture, at which point averted animals began grazing larkspur at levels similar to the control animals.

What an animal eats changes its insides, which, in turn, influences what an animal is willing and able to eat

Why are some animals within a species or breed able to eat more foods that contain toxins than others? The following quote from noted biochemist Dr. Roger Williams conveys that what, how much, and how often humans eat has a lot to do with what is going on inside a particular individual's digestive tract (Williams, 1978).

"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 1000-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."

Dr. Williams' statement refers to humans but the same phenomenon applies to ruminants and other animals. Animal organs are not fixed entities. Several studies have demonstrated that rats and domestic ruminants experience neurological, morphological, and physiological changes that help them cope with the specific diets they ingest. For example, rat pups that were exposed to the odor of peppermint had greater brain activity when they were exposed to peppermint as adults compared to control rats (Coppersmith and Leon, 1984). Goats that ate blackbrush from 1 to 4 months of age had larger rumens and their livers excreted more glucuronic acid (a sign of liver detoxification) compared to goats that were not exposed to blackbrush until 4 months of age (Distel and Provenza, 1991; Photo 4). Sheep reared on low-quality roughage also have enhanced ability to recycle nitrogen (Distel et al., 1994, 1996). Lambs that were exposed to grain when they were 6-weeks old had denser and longer rumen papillae, and their rumens had more mineral deposits, compared to lambs that received no exposure to grain (Ortega Reyes et al., 1992).

PHOTO BY F. D. PROVENZA

Photo 4. Internal organs (e.g., rumens, shown below) of animals can vary morphologically and physiologically due to previous dietary experiences.

These examples once again demonstrate that early experience with certain foods can play a deterministic role in the kinds and amounts of foods animals are willing and able to ingest later in life. This can explain why animals that are raised on irrigated pasture from birth would likely have a difficult time surviving on a blackbrush monoculture, and vice versa. Adaptive feedback is again an important player. Experience with specific foods changes an animal's insides, and changes to an animal's insides greatly influence the "palatability" and "preference" of specific foods.

Necessity is the mother of invention and variety is the spice of life

One question you hear fairly often when discussing issues concerning animal foraging behavior is, "Why would an animal ever eat *that*?", or conversely, "Why doesn't that animal want to eat a nutritious food?" Some food preferences (or aversions) that animals exhibit may not seem "rational" to us. But they might make more sense if we knew the animal's current physiological condition, nutritional plane, and its past history and experiences with foods. As discussed earlier, animals suspiciously sample small amounts of novel, nutritious foods until flavor-PIF relationships can be confirmed. Animals that are pregnant and/or lactating exhibit different dietary preferences than non-pregnant, non-lactating animals.

Young, growing animals have relatively higher nutritional requirements than adults. Females, males, and castrated animals may have different dietary needs. Animals that are malnourished or in poor body condition, and animals with excessive parasite loads display different dietary preferences than animals without such maladies. These examples illustrate that foraging behavior is a *process* involving iterative feedback loops between animals and their environment. Provenza and Cincotta (1993) coined the phrase "positive feedback traps" to describe instances where animals use information from their foraging environment to generate their own "environment of information." Following are a few examples to illustrate this point.

Animals deficient in nutrients seek out new foods. Animals form preferences for foods, no matter how odd, if the food corrects the imbalance. For example, during a winter-grazing study in southwestern Utah, Dr. Fred Provenza confined 6 groups of Angora goats in 6 adjacent blackbrush pastures. Goats became increasingly averse to blackbrush due to its high condensed tannin and low protein composition. As the study progressed, goats in one of the pastures discovered woodrat houses and began to devour them like hot cakes. Why? Woodrat houses contained a "cake" of urine-soaked (nitrogen-rich) vegetation that helped goats mediate their protein deficit and attenuate the toxic effects of condensed tannins in the blackbrush. By the end of the study, goats that did not eat woodrat houses lost nearly twice as much weight as goats that ate woodrat houses. Individual learning by one goat and social learning by others were critical processes to introduce and perpetuate this adaptive behavior.

Have you ever seen a cow eat a rabbit (Photo 5). A Netherlands researcher placed one group of steers in a heathland pasture that was deficient in Na and P (WallisDeVries, 1996). He then compared foraging behavior in the heathland steers to steers foraging in pastures that were "nutrient rich". Steers in the heathland pasture licked urine patches, ingested soil, feces, wood, stones, bones, plastic, and occasionally consumed entire dead rabbits. Other examples of "carnivorous herbivores" include 1) sheep eating arctic terns, 2) red deer eating manx shearwaters, 3) white-tailed deer eating fish, and 4) consumption of dead lemmings, rabbits, and birds by red deer, caribou, and duiker. Researchers postulated that mineral deficiencies (e.g., Na, Ca, P, Mg) elicited the carnivorous behavior observed in these ruminants (Bazely, 1989; WallisDeVries, 1996).

Photo by M. F. WallisDeVries

Photo 5. Holstein eating a dead rabbit. Herbivores can become carnivorous in the face of nutrient deficiencies.

Yet another reason animals may exhibit inexplicable dietary choices is due to their need to balance the rate of energy vs. protein digestion or their need for variety. For example, sheep pastured in England prefer to eat clover in the morning and grass in the afternoon (Newman et al., 1992; Parsons et al., 1994). Clover is far more digestible and nutrient dense than grass so common sense would dictate that sheep should want to eat clover all the time, right? Indeed, research has shown that animals, as a general rule, do prefer highly digestible foods because the time interval between food ingestion and positive post-ingestive feedback is short. However, if animals eat too much of a highly digestible food, fermentation rates become toxic which apparently causes a mild aversion (acidosis = reduced intake) to the high-quality food. Sheep then switch to grass which is lower in digestible nutrients and toxins than clover (clover also contains toxins such as cyanogenic glycocides). The slower digesting grass apparently acts as a "medicine" that facilitates recovery from the mild aversion to clover. By the next morning, the hungry sheep are once again ready to consume the highly digestible clover.

The desire for variety has also been demonstrated for flavor when two distinct flavors are paired with the same nutritious food on alternating days. For example, sheep and cattle that eat a coconut-flavored nutritious food on one day prefer the same food flavored with maple the next, and vice versa (Early and Provenza, 1998; Atwood et al., 2001). Humans apparently exhibit their need for flavor variety when they use products like "hamburger helper" to alter the flavor of protein-rich hamburger dishes (e.g., spaghetti flavor one night, beef stroganoff the next).

Animals protect themselves against digestive and external threats through 2 different (but intertwined) systems

Behavior is a function of its consequences (Skinner, 1981). However, external and internal consequences are processed by animals via different time scales and via different senses using what is collectively known as the skin-gut system (Garcia and Holder, 1985). Sight, hearing, and feelings of pain and comfort are part of the skin defense system which evolved in response to insults to the skin (e.g., predation events). Conversely, the taste of food and feelings of nausea or satiety are part of the gut defense system which evolved in response to nutrient and toxin ingestion. The sense of smell bridges both systems (e.g., predator odors = skin defense; food odors = gut defense). Pre-eminent psychologist Dr. John Garcia characterized the skin-gut defense system this way: "All organisms have evolved coping mechanisms for obtaining nutrients [gut defense] and protective mechanisms to keep from becoming nutrients [skin defense]."

The first study to illustrate how the skin-gut defense system works was conducted on rats (Garcia and Koelling, 1966). As a consequence of these two systems, rats more easily associate taste stimuli with illness and audio-visual stimuli with shock. Moreover, rats avoid the place where they eat a particular food, but not the food, when the place is associated with electrical shock. Conversely, rats avoid the food, but not the place where the food is ingested, when food ingestion is paired with a toxin. Dr. Andres Cibils, a rangeland scientist, and his colleagues conducted a similar version of the Garcia and Koelling experiment with cattle (Cibils et al., 2004). They found cattle performed similarly to rats except LiCl treated steers avoided both the food and the place where they ate the food. Cibils et al. concluded that the high LiCl dose (200mg/kg BW) administered immediately after food ingestion was sufficient to elicit both a food and location aversion.

Skin and gut-defense systems operate on different time scales. For animals to learn from the skin defense system, the event and consequence must occur closely in time (seconds). For example, cattle quickly learn that an electric fence provides a painful shock and should be avoided. Animals would likely not learn not to touch the fence if they were shocked minutes or hours after touching it. The ability of animals to associate insults to the skin with immediate consequences is a very important component of the skin defense system that, according to Garcia, evolved as a protective mechanism against predator attacks. On the other hand, the consequences of ingesting a food can be learned even when food ingestion and PIF are separated by several hours. For example, sheep avoid foods that cause illness for up to 8 hours following ingestion. The ability of animals to associate food ingestion with delayed PIF is a crucial component of the gut-defense system because the process of digestion takes place over minutes to several hours.

Animals not only have to learn "what to eat" but "how to eat"

You have read about how animals must learn *what* to eat from their mothers, peers, and from individual experience (Photo 6). But did you know that animals also have to learn *how* to eat? In one study, goats nearly doubled their bite rate (bites/minute) as they gained experience browsing the shrub blackbrush (Ortega-Reyes and Provenza, 1993). Younger experienced goats were also more adept at selecting leaves over stems than older, less experienced goats. Younger animals (6 months old) learned foraging skills more quickly than older animals (18 months old). Younger animals also continued to increase their biting rate after 30 days whereas the biting rate of older animals leveled off after only 20 days. Other research has demonstrated that the development of foraging skills is important for other herbivore and plant species (Flores et al., 1989a,b,c).

Why is this important in the grand scheme of foraging behavior? It is another example of how early experiences

Photo by F. D. Provenza

Photo 6. Herbivores must not only learn *what* to eat, but *how* to eat. Goats nearly doubled their bite rate as they gained experience browsing blackbrush.

dictate not only *what* animals eat, but *how* efficiently they eat, as well. Intake is the product of grazing time, bite size, and bite rate. As animals learn to increase their efficiency with bite rate and bite size, intake increases. As intake of nutritious foods increases, so does animal production (weight gains, lamb, calf, fawn crops, antler growth, etc.). Because younger animals learn foraging skills more efficiently than older ones, it may behoove managers to expose animals at an early age with their mothers to the forages they will encounter later in life.

Conclusion

Wild ancestors of domesticated animals learned to forage in variable environments long before the process of domestication began. From the examples cited in this paper, a few thousand years of domestication has not hindered the ability of today's domesticated animals to learn. Over evolutionary time, the kinds and amounts of foods that were available to prehistoric herbivores have no doubt changed compared to what is available to today's domesticated descendants. More to the point of learning in today's world, the kinds and amounts of foods that were available when an individual was born may be vastly different from what is presently available due to changing environmental conditions (e.g., drought, fire) and human management practices (e.g., relocation, pasture moves).

Because animals must eat to live they need a reliable hard-wired mechanism that affords maximum flexibility to make correct foraging decisions in a world where the only constant is change. Learning through consequences is that mechanism. Animals inherit the ability to learn. For example, human infants do not have to be "taught" how to learn. They come into the world fully equipped to learn from their parents and from their environment at an astonishing rate. Likewise, young rangeland herbivores quickly learn which foods to eat (and which to avoid) from their mothers. After weaning, recurrent experiences with flavor-feedback associations, along with interactions with the social and physical environment, iteratively shape and reshape dietary preferences of individuals. Rangeland animals must continue to learn to forage in various contexts throughout their lifetime in order to survive. For example, the general principles of "learning via consequences" used in finer scale diet selection processes (discussed in this paper) also pertain to coarser scale habitat selection processes (see Edwards et al., 1994; Scott and Provenza, 2000; Launchbaugh and Howery, 2005; Villalba and Provenza, 2005).

By emphasizing the importance of learning in this paper, we do not discount the importance of genetics. The genome is the collective memory of a species which has evolved over the millennia in response to natural selection processes and pressures. Animals and genes both learn from the environment but on different time scales. Each individual is a unique composite of its genome (i.e., learning by a species over the millennia) and its experience (i.e., learning by an individual over its lifetime). The animal's physical and social environments continually interact with the genome during the growth and development of the species, which induces adaptive behavioral responses by individuals. Individuals that do not make adaptive choices are culled via natural selection processes or via human management practices. Thus, feedback pressures from both nature and humans interact to influence the individual, the social and physical environment, and ultimately, the genome.

Management Implications

Diet selection processes are dynamic and cannot be properly understood by examining snapshot events in time. For example, rangeland herbivores can and do withstand wide departures from National Research Council (NRC) "requirements" and they do not need to maximize consumption of any particular nutrient on a daily basis. Rather, animals respond to excesses, deficits, and imbalances in their diets. Animals remedy dietary maladies by cautiously sampling new foods and by making careful adjustments in their food intake in accord with flavor-feedback associations from the gut to the brain that holistically ripple through cells and organs, converging in the palate. Past dietary choices cause physiological, morphological, and neurological changes inside the animal, which, in turn, strongly influence future dietary choices. Individual animals vary in their acceptance or rejection of certain foods as a consequence of their past foraging experiences and their current physiological condition.

The issue isn't whether individual animals adapt to ongoing changes in social and physical environments; they must do so every day of their lives in order to survive (Provenza, 2003). The question is whether managers want to become more involved in the process. Understanding that animal behavior can be shaped over an animal's lifetime to improve animal production or to improve foraging environments provides managers with a "new" tool (that has been around for centuries) with which to manage rangeland landscapes and animals. Once mastered, behavioral principles and practices provide an array of solutions for rangeland managers to improve the sustainability of the land and to make a living from the land.

Here are a few things that managers should ponder when evaluating the question, "why would an animal eat that?"

- When and where were calves born on the ranch and what foods (plants) were they exposed to early in life? How might these things influence their current dietary choices?
- After weaning, what foods were animals exposed to? How might peers influence past and current dietary choices?
- How might experiences with a variety of environmental conditions (e.g., drought vs. wet conditions, poisonous plants, pasture diversity) influence current dietary choices?
- What is the current physiological condition of the animal (pregnant, lactating, parasite load)? How might these issues influence current dietary choices?
- How might changing nutrient and toxin content of plants influence their current dietary choices?

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