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# 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.

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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-

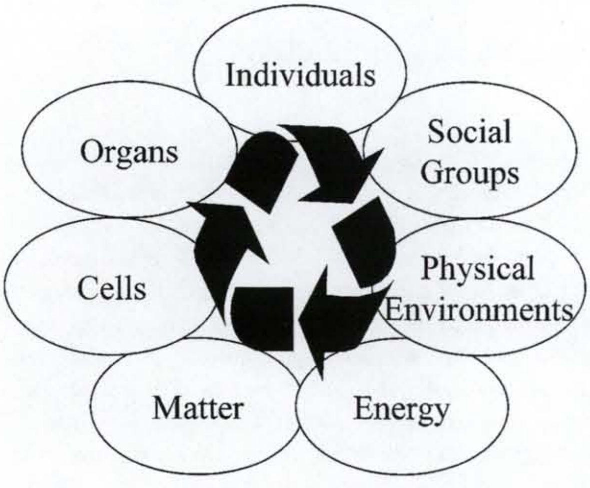

**Figure 1.** Life is interconnected and dynamic. Changes at any level in the environment lead to changes in behavior at all other levels. For instance, for responses (behavior) of a cell, independent environmental variables emerge from cellular, organ, individual, social, and physical processes, and 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 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 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 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.

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# Making Sense of Animal Conditioning

**Frances K. McSweeney**

## Abstract

**Operant and classical conditioning provide powerful techniques for understanding and controlling animal behavior. In classical conditioning, behavior changes when an arbitrary stimulus predicts the occurrence of an important stimulus. The animal's behavior towards the arbitrary stimulus changes as a result. In operant conditioning, the frequency of a response is changed by consequences that follow that response. This chapter briefly summarizes some of the characteristics of behavior undergoing conditioning. Topics include: the basic conditioning procedures, sign-tracking, classical conditioning with drug stimuli, the definition of a reinforcer, shaping, differences between reinforcement and punishment, schedules of reinforcement, acquisition, extinction, generalization, discrimination, higher order conditioning, and schedule-induced behavior.**

## Introduction

Classical and operant conditioning provide two powerful techniques for understanding and controlling animal behavior. In classical conditioning, behavior towards an arbitrary stimulus changes when that stimulus predicts that an important stimulus will occur. In operant conditioning, a response is followed by a consequence (e.g., a reinforcer or punisher) and the response increases or decreases in frequency as a result. This chapter briefly examines the basic conditioning procedures and some of the characteristics of behavior undergoing conditioning.

## Classical Conditioning

The discovery of classical conditioning is usually attributed to Ivan Pavlov (1927). Pavlov briefly turned on a metronome and then presented food to a dog. After a few pairings of the metronome with food, the dog salivated when the metronome was presented alone. This procedure is often described by stating that when an arbitrary stimulus (the metronome, called a "conditioned stimulus" or CS) is followed by an important stimulus (food, called an "unconditioned stimulus" or US), a part of the response that is elicited by the US (e.g., salivation, called the "unconditioned response" or UR) is evoked by the CS. The response that occurs when the CS is presented alone (e.g., salivation) is called the "conditioned response" or CR (Figure 1).

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Classical conditioning as studied by Pavlov is of some practical interest. For example, fears or phobias may be learned when a stimulus (e.g., a snake) precedes a frightening event (e.g., someone screams; Watson and Rayner 1920). Classical conditioning may facilitate digestion because stimuli that predict food may help to prepare the body for digestion of that food (Woods and Strubbe 1994). Classical conditioning is also thought to play a role in the development of learned preferences for and aversions to foods (Garcia and Koelling 1966). In the case of flavor aversions (Launchbaugh et al. this volume) the flavor of the plant is the CS and plant allelochemical(s) is the US which elicits illness (the UR) resulting in the future avoidance of the plant (CR). Therefore, it may play a role in understanding the feeding patterns of livestock and wildlife.

However, other aspects of Pavlov's procedure reduce the practical usefulness of classical conditioning. For example, Pavlov studied reflexive responses (e.g., salivation) while you may be more interested in "voluntary" behaviors (e.g., coming when called). He also studied salivation while his animals were immobilized by suspending them in a hammock; a practice of little relevance to understanding the behavior of free-ranging animals. In Pavlov's experiment, the same response served as the CR and the UR. That is, dogs salivated when food was presented (the UR) and they learned to salivate to the metronome that predicted food (the CR). If the CR must be identical to the UR, then the domain of classical conditioning is limited. For example, you could only use classical conditioning to train a response if you could find a US that automatically elicited that response. In many cases, this may be impossible. Luckily, these assumptions about classical conditioning are incorrect. In fact, classical conditioning probably plays a larger role in the behavior of free-ranging animals than is commonly assumed. (For more information, see Rescorla 1988).

## Classical Conditioning

CS ------> US
metronome food
\ /
CR UR
salivation salivation

**Figure 1.** The basic classical conditioning procedure. A conditioned stimulus (CS) is followed by an unconditioned stimulus (US) and the CS acquires the ability to evoke the response (CR) that was formerly emitted to the US alone (UR).

### Sign-tracking

Hearst and Jenkins (1974) formulated a principle that they called "sign-tracking". Sign-tracking states that, "Animals approach and contact the best predictor of reinforcers and they withdraw from stimuli that signal the absence of reinforcement." Notice that sign-tracking and the understanding of classical conditioning given earlier both describe how behavior changes when an arbitrary stimulus predicts an important stimulus. However, the two formulations differ in several ways.

According to Hearst and Jenkins, the behavior that is learned is movement in the environment (approach or withdrawal), not a reflexive response (e.g., salivation). The biologically important stimulus (US) is identified as a reinforcer, a term that will be defined later. Behavior also changes when the arbitrary stimulus (CS) predicts the reinforcer, not when the CS is followed by the reinforcer. To date, no generally-accepted definition of "predict" has been offered. However, you will understand Hearst and Jenkin's argument if you understand that prediction is a looser relation between the CS and US than temporal following. For example, the sight of clouds may predict rain even though you rarely get rained on immediately after you see a cloud. These differences make sign-tracking more useful in practice than the traditional view of classical conditioning. For example, I almost paid a heavy price once for underestimating the power of sign-tracking. I was visiting a wildlife park in Australia where a vending machine sold kangaroo chow. Unfortunately, the machine made a loud noise when it operated and that sound (CS) predicted the availability of food (US). As sign-tracking would predict, the kangaroos ran towards the food machine as soon as they heard it operating, an undesirable event for those standing by the machine.

### Drugs as USs

Although Pavlov measured the same response as his CR and UR, we now know that these responses need not be identical. Sign-tracking provides one example of the CR (approach) differing from the UR (whatever is evoked by the US, e.g., salivation). The study of drugs as USs provides another example. In this case, the CR may be the opposite of the UR. To give one example, Siegel (1977) used morphine as a US. He showed that an arbitrary stimulus (e.g., a light or tone) that was followed by a morphine injection eventually evoked a CR that was opposite to the UR evoked by the morphine itself. For example, morphine is a pain killer (the UR). In contrast, animals become hypersensitive to pain during a CS that predicts morphine (the CR).

Siegel went on to argue that classical conditioning may contribute to the build up of tolerance for drugs and to the withdrawal symptoms that are observed when drugs are not delivered. This can be more easily understood if we describe the UR to morphine as a "high" (a pleasant state) and the CR to morphine as a "low" (an unpleasant state). As will be discussed (see Acquisition ), classically conditioned responses gradually become stronger with each successive pairing of the CS and US. If a conditioned "low" becomes stronger with each successive morphine injection, then more and more of the drug will be required to overcome this "low" and produce the desired high. This is known as developing tolerance. If the CSs that accompany a drug injection (e.g., time of day, sight of the needle) occur without the drug, then the animal will experience only the CR (ie., a low) without the high produced by the US. This low will contribute to withdrawal symptoms.

These findings have several implications for people who deliver drugs to animals. First, if tolerance has developed to a drug, be careful not to give that drug unless the stimuli that usually predict a drug injection (e.g., time of day, method of injection) are also present. Those CSs help to prepare the animal's body to deal with the assault of the drug. That is, they send the body into a state opposite to that produced by the drug. As a result, the drug is less disruptive when it is delivered. Siegel showed that a dose of drug to which an animal has developed tolerance may kill the animal if it is delivered in the absence of the protection provided by its usual CSs.

This tolerance, attributed to stimuli that foreshadows the administration of a drug, may also be relevant to animals exposed to poisonous plants. The flavor, odor, or sight of the toxic plant may serve as CS's that activate detoxification systems or signal metabolic tolerance mechanisms in the animal. This may in part explain why animals can often increase consumption of toxic plants without apparent deleterious effects.

## Operant Conditioning

Operant conditioning refers to the fact that behavior changes as a result of its consequences (Figure 2). B. F. Skinner is the most famous student of operant conditioning (Skinner 1938). Because of the power of operant techniques, they form the basis for a multimillion dollar business devoted to training animals for performances in movies, at fairs, etc. Operant techniques are also used to correct animal behavior problems (e.g., for pets or farm animals). Finally, the techniques are used to answer questions of importance to those interested in animal welfare (Foster et al. 1997). For example, they can help to determine what animals "like" and "dislike".

### Positive reinforcement

The principle of positive reinforcement states that a response that is followed by a reinforcer will increase in frequency (Figure 2). Notice that you cannot reinforce a response unless you can identify a reinforcer. Over the years, many definitions for the term "reinforcer" have been tried and all have failed. For example, reinforcers have been defined as substances that are physiologically needed (e.g., food, water), but there are many reinforcers that are not physiologically needed (e.g., watching television, going to the movies). Reinforcers have been defined as stimuli that reduce tension (e.g., sexual behavior), but in many cases, stimuli that increase tension also serve as reinforcers (e.g., watching a scary movie, riding a roller coaster).

Because of these failures, a reinforcer is technically defined as any stimulus that increases the frequency of a response that it follows. This is an undesirable definition because it makes the principle of positive reinforcement circular. That is, the principle now reads, a response that is followed by any stimulus that increases the frequency of a response that it follows will increase in frequency. We can live with this definition because we can identify a stimulus as a reinforcer in one situation (e.g., by showing that it increases the frequency of one response that it follows) and then test the principal of positive reinforcement in another situation (e.g., ask whether that reinforcer will also increase the frequency of other responses).

Operant Conditioning

- Reinforcement
  S : R ----> Reinforcer ; R increases
- Punishment
  S: R ----> Punisher ; R decreases

**Figure 2.** Basic attributes of the operant conditioning procedure, a particular stimulus (S) response (R) pair, the frequency of the response will either increase or decrease depending on whether the events or condition following the response are positve (reinforcer) or negative (punisher).

In practice, many stimuli will serve as reinforcers for nonhuman animals (e.g., food, water, petting, access to conspecifics for herd animals). Others will be useful with humans (praise, money, the opportunity to watch television). If you are having difficulty identifying a reinforcer, try the Premack Principle (e.g., Premack, 1959). Premack argued that the opportunity to perform any high probability response would reinforce any low probability response. The probability of a response was measured by examining what the animal would do when it had free time. Therefore, you can find a reinforcer by observing what an animal does often and using access to that behavior as a reinforcer. According to Premack, if a child reads more than he watches television, then reading will serve as a reinforcer for television watching if, for some reason, you wanted him to watch more TV.

### Shaping

You may have noticed that you cannot reinforce a response until that response occurs. Shaping by successive approximations is a procedure that can be used to produce a response so that you can reinforce it. During shaping, you reinforce closer and closer approximations to the desired response. For example, if you want to teach your dog to sit up, you could begin by following any movement by a reinforcer. Then you might reinforce only movements that involved some transfer of the dog's weight to its back paws. Then you might reinforce only movements that involved weight transfer to the back paws plus lifting the forepaws off the ground. By judiciously chosing which behaviors to reinforce and when to alter the reinforced response, you should quickly have your dog sitting up.

### The four basic conditioning procedures

You can use operant conditioning to either increase (reinforcement) or decrease (punishment) the frequency of a response. The frequency of a response may change when the response produces something (positive) or when it escapes or avoids something (negative). It is called "positive reinforcement" when a response increases in frequency because it produces something (e.g., sheep walk into the corral when called because they receive feed). Negative reinforcement occurs when a response increases because it escapes or avoids something (e.g., a flock of sheep move into the corral to avoid getting nipped by the sheep dog). Positive punishment occurs when a response decreases in frequency because it produces something (e.g., a cow stops touching the electric fence with her nose because she gets shocked). Negative punishment occurs when a response decreases in frequency because it prevents something that would otherwise occur (e.g., your horse stands still after a ride because moving about delays the removal of the saddle and bridle).

Large organizations (e.g., governments, armed services, universities) control your behavior largely through negative reinforcement. For example, you probably pay your income taxes on time to avoid a fine (negative reinforcement) rather than because you receive a thank you note from the President (positive reinforcement). Positive reinforcers often cost money, but negative reinforcers often do not. Nevertheless, I recommend that you use positive reinforcement and negative punishment to alter behavior whenever possible. The other alternatives, negative reinforcement and positive punishment, involve the delivery of an aversive stimulus. Delivering aversive stimuli can have undesirable consequences. For example, they may elicit aggression. In contrast, positive reinforcement and negative punishment involve the delivery or withdrawal of a positive stimulus which should elicit fewer undesirable behaviors. To give only one example, if an animal is attacking other animals in a herd, a better way to decrease the frequency of attack might be to isolate the animal for a while (negative punishment) rather than to follow attack by a shock from a cattle prod (positive punishment).

### Schedules of reinforcement

In a continuous reinforcement procedure (CRF), every occurrence of a response is followed by a reinforcer. CRF is rarely used because it is expensive if the reinforcer costs money. The frequent delivery of reinforcers also disrupts behavior. Therefore, CRF is used to initially teach a response but a schedule of partial reinforcement is used as the response becomes stronger.

In a partial reinforcement procedure (PRF), some instances of a response are not followed by a reinforcer. There are several schedules of PRF, but the most useful may be the fixed (FR) and variable (VR) ratio schedules. In an FR x schedule, a reinforcer is delivered after every x occurrences of a response. For example, in a piece work factory, you might be paid (a reinforcer is delivered) every time you complete 10 widgets. This would be an FR 10 schedule. In a VR x schedule, a reinforcer is delivered after every xth occurrence of the response on the average. For example, a pigeon foraging for grain does not find grain (the reinforcer) each time it pecks the ground (the response), but it does find grain after some variable number of pecks. FR and VR schedules control behavior somewhat differently. Responses occur at a high steady rate if they are reinforced on a VR schedule. In contrast, animals pause after receiving a reinforcer and then later respond at a relatively steady rate when responding on an FR schedule. The pause is longer the larger the number of responses required for reinforcement. In fact, if the ratio requirement becomes too large, the animal may stop making the response. This is called ratio strain. To avoid ratio strain, the number of responses required for a reinforcer should be increased gradually, rather than in large increments.

## Characteristics of Conditioned Behavior

### Acquisition

Operantly and classically conditioned responses do not appear full blown the first time they occur. Instead, they are gradually acquired as the response is repeatedly followed by the reinforcer or as the CS repeatedly predicts the US. The strength of a conditioned response usually increases as a negatively-accelerated function of experience with the CS-US or reinforcer- response relation (Figure 3).

### Extinction

Extinction means that a response that has been classically conditioned will return to its baseline frequency if the relation between the CS and US is broken. This may be done in either of two ways. The US may be removed entirely or the CS and US may be presented randomly with respect to each other. A response that has been operantly conditioned also returns to its baseline frequency if the relation between the response and the reinforcer is broken. Again, this relation may be

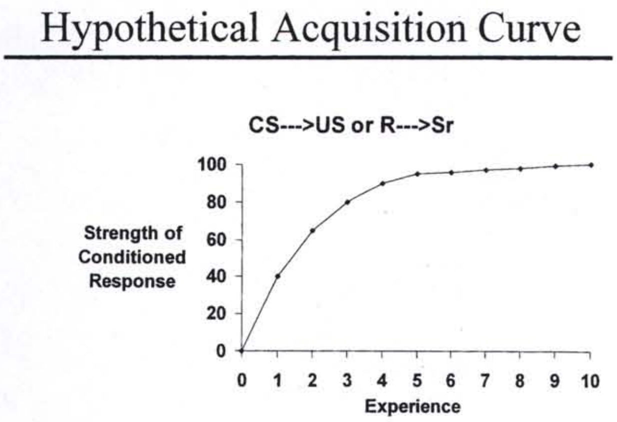

**Figure 3.** A hypothetical acquisition curve. The strength of a conditioned response increases as a negatively accelerated function of experience with the CS-US or response-reinforcer relation.

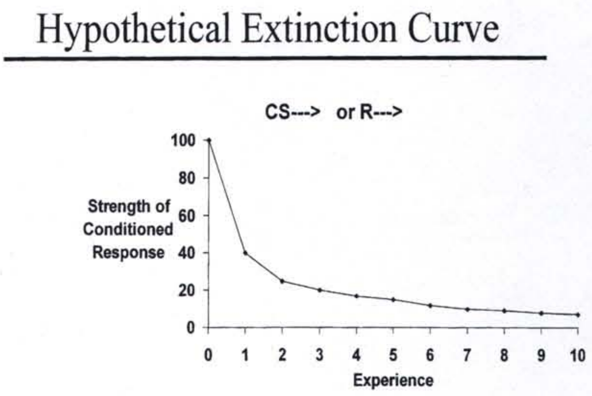

**Figure 4.** A hypothetical extinction curve. The strength of a conditioned response decreases with experience that the CS no longer predicts the US or the response no longer produces the reinforcer.

broken by removing the reinforcer entirely or by presenting the reinforcer randomly with respect to the response. For example, a deer may return to a specific location in its home range to eat a relished plant (reinforcer). However, the deer will return to this place less often if the plant is removed (the reinforcer was removed) or the plant begins to appear randomly throughout its home range (the reinforcer is presented randomly with respect to location).

A hypothetical extinction curve appears in Figure 4. Theoretically extinction, as punishment, can be used to decrease the frequency of an undesirable response. However, its use in practice may be limited. You can only extinguish behavior that has been conditioned. You can only use extinction if you can identify all of the reinforcers that support the undesirable behavior and can control delivery of those reinforcers. Most behaviors are partially rather than continuously reinforced and extinction is slower for partially than for continuously reinforced behavior. Responses undergoing extinction may also increase in frequency for a brief time at the start of extinction, an undesirable consequence if you're trying to eliminate the response.

## Generalization

Generalization refers to the fact that a CR that occurs to one CS will also occur to other stimuli that resemble the CS that was originally paired with the US. The greater the resemblance between the new stimulus and the original CS, the stronger the conditioned response to the new stimulus. For example, if you're stung (US) by a bee (CS), you may learn to fear (CR) other flying insects and your fear will be stronger the more closely the insect resembles a bee. A hypothetical generalization gradient appears in Figure 5.

A response that has been reinforced in the presence of one stimulus will also occur in the presence of other stimuli that resemble the original stimulus. Again, the stronger the resemblance between the new stimulus and the original one, the stronger the response to the new stimulus. For example, a deer may learn to limit intake of big sagebrush because it contains essential oils which have several deleterious digestive consequences. If the deer encounters a new species of sagebrush, such as three-tip sage, it may avoid eating it. The deer may generalize its avoidance of big sage to the newly encountered sage because they both contain similar essential oils which give them a similar odor and taste.

## Discrimination

During a classical conditioning discrimination procedure, a stimulus is followed by a US (CS+) and another stimulus is not followed by a US (CS-). The CR will occur to CS+ but not to CS-. During an operant discrimination procedure, a response is reinforced in the presence of one stimulus (S+) and not in the presence of another stimulus (S-). The response will occur in the presence of S+, but not in the presence of S-. For

Hypothetical Generalization Gradient

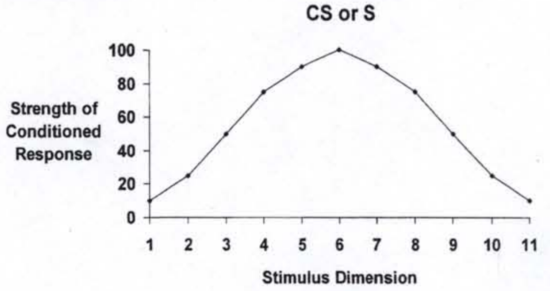

**Figure 5.** A hypothetical generalization gradient. The strength of a conditioned response decreases as stimuli become more dissimilar to the stimulus that was actually involved in classical or operant conditioning. The x-axis is a stimulus dimension (e.g., the brightness of a light, the loudness of a tone). The stimulus that was present during conditioning appears in position 6.

example, a herd of cows may learn that running to a vehicle (a response) results in getting feed (a reinforcer). They may further learn that feed only comes from the red feed truck when its horn is blaring (S+), but not from other pickups that drive through the pasture(S-).

Discrimination procedures provide a useful technique for asking questions of non-human animals or nonverbal people (e.g., infants). You may have heard that dogs do not "see colors". How do we know? Part of the answer comes from discrimination training. Suppose you reinforce sitting up by giving the dog a treat in the presence of anything red, but not in the presence of anything green. If the dog can see colors, then you will quickly have a dog that sits up when a red, but not a green, stimulus is presented. When this experiment is done properly, dogs do not develop a discrimination.

## Higher-order Conditioning

Some stimuli serve as USs or reinforcers from birth with no additional training. These stimuli are called primary reinforcers or USs. They include biologically important stimuli, such as food and water. Other stimuli acquire their ability to act as reinforcers or USs through experience. These stimuli are called secondary, or higher-order, reinforcers or USs. Money provides the most obvious example of a secondary reinforcer.

Stimuli acquire the ability to act as secondary reinforcers in many ways, two of which will be described. First, stimuli that can be exchanged for primary reinforcers will act as secondary reinforcers. Such stimuli are called "tokens". For example, money acquires the ability to act as a reinforcer because it can be exchanged for food, drink and other primary reinforcers. Second, classical conditioning pairing of a stimulus with primary USs or reinforcers will produce a secondary reinforcer or US. Therefore, a bell that is used to summon animals for feeding will gain the ability to act as a reinforcer itself.

The ability of these stimuli to act as secondary reinforcers or USs will extinguish if their relation to the primary reinforcer or US is broken. Therefore, money would gradually lose its ability to reinforce if it was no longer exchangeable for goods and the bell would lose its ability to reinforce if it was presented often without food.

## Schedule-induced Behavior

A final oddity of behavior undergoing reinforcement will be mentioned because you may sometimes encounter it. Falk (1971) gave hungry rats food (a reinforcer) when they pressed a lever (a response). In this experiment, food was delivered once every minute on average. When water was also available, Falk noticed that rats drank approximately 50% of their body weight in water over the course of a two hour experimental session. He called this behavior polydipsia (much drinking) and observed that it was counterproductive because the rat was wasting calories by heating a large amount of water to its body temperature and then excreting it.

Later studies showed that animals will perform many other behaviors in excess when reinforcers are spaced in time. These behaviors are called "adjunctive" or "schedule-induced". They include aggression, eating non-food substances (pica), running in a wheel, defecation, escape from the schedule of reinforcement and drug consumption.

Because adjunctive behaviors are excessive and often maladaptive, they have served as models for a variety of problematic behaviors. I cannot discuss these models in detail, but if you suspect that a problematic behavior is schedule-induced, one way of reducing that behavior is to identify the schedule of reinforcement that is maintaining the behavior and to change the interval between successive deliveries of the reinforcer. For example, I once received a telephone call from a woman whose dog was biting her when she fed it. One among many potential explanations for this behavior is that the bite was an aggressive response that occurred because food was spaced in time. In that case, the woman should change the interval between meals to reduce biting.

You can test yourself on the preceding material by explaining how biting could also be a classically or operantly conditioned response. What would you do to eliminate biting if you thought it was classically or operantly conditioned?

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# Grazers and Browsers: How Digestive Morphology Affects Diet Selection

**Lisa A. Shipley**

## Abstract

**Grasses (monocots), forbs and browse (dicots) differ in structure and chemistry. Grasses have a thicker cell wall containing potentially digestible structural carbohydrates, fewer secondary plant chemicals, and have a relatively low and homogenous growth relative to browses. Mammalian herbivores can be classified along a continuum according to which plant type they prefer. Diet choices correspond with morphological specialization within the gastro-intestinal tract, including the mouth and teeth, which may confer increased efficiency for extracting nutrients from grasses and browses. These differences are confounded with body size, and thus the full extent of the effects of morphology on digesting and harvesting foods is unclear. However, understanding the feeding niche of herbivores may help understand competitive interactions among herbivores and proper range management.**

## Introduction

An animal's anatomy and physiology clearly affect its food choices. Characteristics of food, in turn, are one of the primary forces that shape animal behavior, physiology and anatomy. The most basic difference among food choices is between meat and plants as food. Because these food resources differ in so many ways, carnivores and herbivores face completely different obstacles in satisfying their nutritional requirements (Table 1). Carnivores must spend much time and energy searching for and capturing their rare prey that have mastered hiding, fleeing, and fighting. In contrast, herbivores spend less time and energy finding and capturing bites of vegetation because plants are stationary and relatively abundant in the environment.

However, some key differences between plant and animal cells reduces the attractiveness of plants as food. Plant cells have a cell wall that acts as a fibrous "skeleton" for plants, whereas animal cells have only a cell membrane. The cell wall is made up of fibers consisting of structural carbohydrates (e.g., cellulose) and other compounds (e.g., lignin) that are not degradable by mammalian enzymes (Gibson 1978). Herbivores must rely on symbiotic microbes that can ferment these structural carbohydrates into energy-rich byproducts, primarily volatile fatty acids (VFA's) (Hungate 1966, Stevens 1988). Herbivores then use the VFA's as their primary energy source. Therefore, cell fibers make plants difficult and energetically costly to chew and digest. Plants typically are lower in protein (Bodmer 1990) and may contain toxic allelochemicals that further reduce their nutritional quality (Robbins et al. 1995). Because plant species, individual plants, and plant parts vary in allelochemicals and amount of cell wall composition, plants are low and variable in nutritional quality, whereas meat is high and uniform in nutritional quality. Because herbivores eat a low-quality diet, they must eat a greater quantity to meet energy requirements than do carnivores (Demment and Van Soest 1985). For example, herbivores search for and crop up to 10,000 bites of plants per day (Senft et al. 1987), whereas a carnivore may consume less than 1 to a few prey items per day. Harvesting thus becomes time-consuming for herbivores.

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## Differences Between Grasses and Browses

The variability in the morphology and chemistry of plants has led to numerous adaptations in anatomy and behavior within the herbivore community. Some fundamental differences exist between herbaceous forages consumed by herbivores, particularly between grasses (monocots) and browses (herbaceous and woody dicots such as forbs, shrub leaves and stems; Hofmann and Stewart 1972, Jarman 1974). These differences are seen in cell structure, plant chemistry, plant architecture, and plant dispersion (Table 2). First, grasses tend to have a thicker cell wall than browses, and their cell walls consist mainly of slowly-digestible plant fibers such as cellulose (Demment and Van Soest 1985). In contrast, forbs, leaves, and some woody stems have a thinner cell wall and more cell contents that contain completely digestible and rapidly fermentable compounds such as sugars, proteins, and lipids (Bodmer 1990, Gordon and Illius 1994, Owen-Smith 1997). Within the cell wall, however, browses usually contain more indigestible fibers such as

Table 1. A relative comparison of foraging between herbivores and carnivores.

| Characteristics | Herbivores | Carnivores |
|---|---|---|
| Food source | • Plants<br>• Stationary<br>• Abundant | • Animals<br>• Mobile (hide, fight, or flee)<br>• Rare |
| Capturing food source | • Little energy & time spent in search, pursuit, & capture<br>• High success of capture<br>• 10,000 bites per day<br>• High dry matter intake | • Much energy & time spent in search, pursuit, & capture<br>• Low success of capture<br>• 1 > prey/day to > 10<br>• Low dry matter intake |
| Quality of food source | • Low protein<br>• Low digestible energy<br>• High fiber in cell wall<br>• Quality varies among plants and plant parts | • High protein<br>• High digestible energy<br>• No cell wall/fiber<br>• Quality uniform among prey |
| Digesting food source | • Much chewing required<br>• Complex digestive tract<br>• Energy derived from microbial fermentation of plant fiber and cell contents in foregut and/or hindgut<br>• Protein derived from digesting rumen microbes<br>• Slow passage through system | • Little chewing required<br>• Simple digestive tract<br>• Energy and protein derived from breakdown of proteins, fats, and carbohydrates in stomach and intestines<br>• Plant fiber not digested<br>• Rapid passage through system |

Table 2. A relative comparison of chemical and structural differences between grasses (monocots) and browses (herbaceous and woody dicots).

| Characteristic | Grasses | Browses |
|---|---|---|
| Cell wall | • Thick<br>• Greater proportion is cellulose/hemicellulose | • Thin<br>• Greater proportion is lignin |
| Plant defense compounds | • Silica | • Phenolics – tannins<br>• Terpenes<br>• Alkaloids & other toxins |
| Plant architecture | • Fine-scaled heterogeneity in nutritional quality within a plant<br>• New growth added at base<br>• Low growth form<br>• 3-dimensional volume | • Coarse-scaled heterogeneity in nutritional quality within a plant<br>• New growth added at tips<br>• Low to high growth form<br>• Complex, diffuse, branching architecture |
| Dispersion | • Uniform | • Dispersed/discrete |

lignin. The amount of cell wall and lignin (and thus the nutritional value) changes more drastically among seasons and with age in grasses than in browses (Van Soest 1996). The thicker, more fibrous cell wall also makes grass more difficult and energy-expensive to fracture (bite and chew) than the more fragile leaves of browses (Choong et al.1992, Robbins 1993, Wright and Illius 1995). However, woody stems of dicots contain more lignin than almost any forage and are classified as "browse" (Van Soest 1996).

Second, the types of plant secondary chemicals that influence forage quality differs among grasses and browses. Grasses tend to have a higher silica concentration that can increase tooth wear (McNaughton and Georgiadis 1986) and reduces the ability of herbivores to digest fiber (Robbins 1993). In contrast, browses tend to have more phenolics, including tannins that reduce protein digestibility, terpenes that can reduce dry matter digestibility, and toxins such as alkaloids (Robbins 1993, Robbins et al. 1995).

Third, grasses and browses differ in architectural arrangement which creates unique challenges for herbivores when harvesting bites. Grasses consist of leaves, stem, sheath, and fruit that differ in quality and form over only a very fine-scale that cannot be differentiated easily by large mammalian herbivores while foraging (Jarman 1974). Grasses thus provide a relatively homogenous food source for larger herbivores (Jarman 1974). In contrast, browses tend to contain a more heterogeneous assembly of plant parts of various nutritional quality, including nutritious buds, mature leaves, and woody stems (Jarman 1974). The low growth form of grasses, in which new tillers are added at the base of the plant, creates a rather continuous 3-dimensional layer of vegetation with a relatively constant density (Jarman 1974). Moreover, grasses typically grow in continuous dispersion (i.e., the next nearest plant is likely a grass). In contrast, new plant tissue is added at the tips of browses, creating a branching geometry that is diffuse and irregular (Jarman 1974, deReffye and Houllier 1997). Many browse species also have spines, prickles, curved thorns or short, stubby branches that slow cropping and form an impenetrable mat (Cooper and Owen-Smith 1986, Belovsky et al. 1991). Finally, browses tend to be more discrete in dispersion, where their nearest neighbor is less likely to be a browse.

## Classification of Herbivores by Diet Choices

Ecologists have long-observed that many herbivores, even those from different taxonomic groups, tend to focus on either the grass or browse component of habitats. These observations have led to various classification schemes for mammalian herbivores, primarily ruminants (e.g., feeding niches: Bell 1970, 1971, Jarman 1974; herbivory rating: Langer 1988; browser-frugivore continuum: Bodmer 1990; selectivity axes: Van Soest 1996). However, the classification system of Hofmann and Stewart (1972) based on diet choices and related to specialized morphology of ruminants (and expanded by others to include non-ruminant herbivores) has been embraced by most herbivore ecologists, if only for its heuristic value (Robbins et al. 1995), as a key to understanding diet selection and community dynamics of herbivores. Hofmann and Stewart (1972) classified as: 1) Bulk and Roughage Feeders or Grazers that select diets containing < 25% browse; 2) Concentrate Selectors or Browsers that select diets containing at least 75% fruits, dicot foliage, and tree and shrub stems and foliage; or 3) Intermediate or Mixed Feeders that select both grasses and browses. Using this scheme to classify 65 ruminants on 4 continents, Hofmann (1989) found that 25% were grazers, 40% were browser/fruit-eaters, and 35% were mixed feeders. Many have argued that tree and shrub foliage and stems should not be considered "concentrates", because they are heavily defended by plant secondary compounds (Robbins et al. 1995) and lignin, and thus fruit selectors (true concentrates) and browsers should form separate categories (Bodmer 1990). Others suggest that these categories only reflect trends in body mass, because smaller herbivores tend to select concentrates whereas larger ones tend to choose roughage or grass (Gordon and Illius 1994, Robbins et al. 1995). For example, in tropical areas frugivores average 24 kg, browsers 394 kg, intermediate feeders 695 kg, and Grazers 670 Kg (Bodmer 1990).

Table 3. A relative comparison of digestive anatomy between grazers and browsers based on Hofmann (1989), Hoeck (1975), and Robbins et al. (1995).

| Characteristic | Grazers | Browsers |
|---|---|---|
| Foregut | • Large<br>• Subdivided<br>• Smaller opening between reticulum & omasum<br>• Sparser, more uneven papillae | • Small<br>• Simple<br>• Larger opening between reticulum & omasum<br>• Denser, more even papillae |
| True stomach (abomasum) | • Smaller | • Larger |
| Hindgut | • Smaller cecum and intestines | • Larger cecum and intestines |
| Salivary glands | • Smaller parotid salivary glands | • Larger parotid salivary glands |
| Liver | • Smaller | • Larger |
| Mouth | • Wider muzzle and incisor row<br>• Lower incisors of similar size<br>• Incisors project forward<br>• Smaller mouth opening and stiffer lips | • Narrower muzzle and incisor row<br>• Central incisors broader than outside ones<br>• Incisors more upright<br>• Wider mouth opening with longer tongue |
| Teeth | • Higher crowns in some species | • Lower crowns in some species |

## Differences in digestion between grazers and browsers

Differences between browsers and grazers extend beyond diet selection—they include specialization within the digestive tract that may allow grazing and browsing herbivores to better extract nutrients from their preferred forage class (Table 3). Grazers and browsers have measurable differences in the morphology of the foregut (rumen-reticulum-omasum), the hindgut, salivary glands, liver, mouth, teeth, and body mass that may influence their ability to digest and harvest grasses and browses. All herbivores have one or more enlarged portions of the gut used to house the microbes that ferment plant fiber (Langer 1988). All ruminants have a pouch (rumen/reticulum) that lies before the true (acid-pepsin) stomach (abomasum) in which the bulk of fermentation occurs. Plant fiber floats on the rumen liquid and is regurgitated and rechewed until particles are small enough to escape through the opening between the reticulum and omasum (Langer 1988, Van Soest 1994). The length of time food resides in this chamber depends on its size and the size of the opening. The longer plant fiber is retained in the rumen, the more complete the digestion of cellulose and other structural carbohydrates (Demment and Van Soest 1985). Nonruminant herbivores rely on enlarged portions of the lower intestinal tract or hind-gut where additional microbial fermentation occurs, including the cecum and parts of the large intestine (Langer 1988).

Hofmann (1989) characterized the anatomy of the foregut and hindgut of ruminants in detail and suggested how grazers and browsers should differ in rate and extent of digestion. Although differences in morphometrics are well-documented, the predicted effects of morphology on digestive physiology remain untested or unclear. Grazers tend to have larger, more muscular, subdivided rumen/reticulum, and a smaller opening between the reticulum and omasum than dobrowsers. This adaptation may serve to retard the passage of digesta to lower tract, giving more time for fermentation of plant fiber (cellulose). Because a greater proportion of grass cell is cellulose, this adaptation would presumably allow grazers to digest the cell wall more thoroughly and obtain more energy per unit of food. However, if food moves more slowly through the digestive tract, food intake may also decline. In contrast, most browses contain less cell wall and fibers within their cell wall are more lignified and indigestible, so the smaller rumen of browsing animals should allow indigestible food particles to flow more rapidly through the tract. This rapid flow should promote a higher food intake. Browsers tend to have extensive dense papillae in all parts of the rumen, enlarging the surface area by 22 times, which may allow efficient absorption of VFA's from the rapidly-fermenting cell contents of the browse plants. In contrast, grazers have fewer, uneven papillae that limits the absorptive capacity of the rumen. Browsers have a proportionately large abomasum, or true stomach, a larger hindgut (cecum and colon), and the ventricular groove in the rumen/reticulum may allow some cell contents to escape inefficient rumen fermentation in favor of direct digestion in the abomasum and lower digestive tract.

Besides differences in the structure of the gastrointestinal tract, grazers and browsers also differ in the relative size of the parotid salivary glands (which lie below the ear along the jaw line) and composition of saliva. Parotid salivary gland weight increases linearly with body mass in both grazers and browsers, but averages 4 times larger in browsers than in grazers (Robbins et al. 1995). Although Hofmann (1989) suggested that larger parotid salivary glands yield greater flow of liquids to the digestive tract and buffer fermentation, Robbins et al. (1995) did not find differences in the resting rate of saliva production between grazers and browsers. Cattle and sheep saliva is thin and watery compared to mule deer saliva which is viscous and gelatinous. These observations suggest that the larger parotid salivary glands of browsers produce tannin-binding salivary proteins that may prevent tannins in browses from greatly reducing protein digestibility (Austin et al. 1989, Robbins et al. 1995). Hofmann (1989) also noticed that browsers have up to 100% more liver tissue for their body size than grazers. Because allelochemicals present in browses may be detoxified in the liver (Foley et al.1995; Pfister, this volume), a large liver might be an additional adaptation to the chemicals in browses that do not commonly occur in grasses.

## Differences in harvesting skills between grazers and browsers

Besides differences in digestive morphology, grazers and browsers seem to possess different adaptations for harvesting grasses and browses (Table 3). To meet their metabolic needs on high fiber diets, herbivores must spend up to 10 hours a day foraging (Bunnell and Gillingham 1985). Adaptations that increase harvesting efficiency reduce foraging time and free up time for other activities that influence fitness, such as reproducing, thermoregulation, and avoiding predators. The rate at which an animal harvests food depends on how rapidly bites of food can be cropped (severed from the plant) and chewed, and the size of bite the animal takes (Spalinger and Hobbs 1992). Harvesting rate can increase up to 10 times simply by taking larger bites (Shipley and Spalinger 1992). Chewing, cropping, and harvesting differ depending on class of forage (grass or browse).

First, differences between browsers and grazers exist in the structure of molars, which would be expected to influence chewing rates and longevity of teeth. Herbivores in general tend to have ahigh level of hypsodonty – meaning that teeth have high crowns that allow for longer wear (Vaughan 1986). This adaptation is especially valuable for grazers that consume more fibrous and silica-laden grasses. Differences in molar structure in two species of hyraxes (small, nonruminant, African herbivores), seems to correspond with their preferred diets (Hoeck 1975, 1989). Molars and premolars of rock hyraxes (*Procavia johnsoni)*, which feed preferentially on grasses, are hypsodont, having high crowns and short roots. In contrast, yellow-spotted hyraxes (*Heterohyrax bruceii)*, a browsing species, have brachydont tooth structure with shorter crowns and longer roots. However, similar patterns in tooth structure are not found in ruminants.

Second, measurable differences in mouth structure among herbivores may influence cropping rates and bite size. Grazers tend to have wide muzzles, with lower incisors of similar size that project forward in a spatulate fashion (Janis and Ehrhardt 1988). The greater incisor width of grazers should serve to maximize bite size (and thus harvest rate) of herbivores when feeding on a continuous distribution of grasses (Illius and Gordon 1987, Janis and Ehrhart 1988). However, wider muzzles reduce the grazer's ability to select the smaller, more nutritious portion of grasses (Janis and Ehrhardt 1988). The rate of cropping grass depends on its toughness, a function of the age and diameter of grass (Wright and Illius 1995).

In contrast, browsers tend to have a narrower muzzle (Janis and Ehrhardt 1988) and a relatively larger mouth opening that permits sideways stripping of leaves. Some larger browsers, such as giraffes and black rhinos, have a longer tongue and prehensile lips (Hofmann 1989). The lower incisors are inserted in a more upright position with a cupped appearance, and the central incisors are broader than the lateral ones (Janis and Ehrhardt 1988). The smaller width of incisors and other adaptations allow for easier selection of specific plant parts that have less cell wall (Owen-Smith 1982). Structural defenses found on browses, such as thorns, slow harvesting by interfering with cropping (e.g., catching lips on thorns) and by separating leaves and reducing bite size available (Cooper and Owen-Smith 1986, Belovsky et al. 1991).

Finally, differences in the dispersion of grasses and browses may require different methods of searching and scales of food selection. Herbivores select food in a hierarchical fashion, making different decisions at different spatial scales ranging from the plant part or bite to the landscape and region (Jarman 1974, Senft et al. 1987). Because many grasses have a more continuous dispersion (Jarman 1974), they tend to be rather homogeneous except at very fine and large scales. Therefore, grazers are expected to choose diets based on the characteristics of the patch, pasture, or landscape, rather than individual plant or plant part. For example, grazers may select patches that provide the tallest, youngest, or most nutritious grasses (Lanvatn and Hanley 1993). In contrast, nutritional quality and bite size of browse varies greatly among plant parts, and thus browsers must choose bites carefully, selecting leaves over stem, or selecting the shrub with the larger leaves or thickest twigs (Shipley et al. 1998). Browsers, therefore, may make decisions on how to maximize nutrient intake more frequently than do grazers. Clearly experience and learning influence harvesting efficiency within limits set by herbivore morphology (Provenza, this volume).

### The influence of body size on grazing and browsing

Although Hofmann's (1989) predictions about digestion between grazers and browsers seems logical from differences observed in their anatomy, few have been tested quantitatively. Recent studies indicate that the characteristics of the food and the animal's body size, rather than anatomical adaptations for grazing and browsing, have greater significance for the nutritional ecology of the herbivore. For example, by developing a mechanistic model of the herbivore's digestive system, and by analyzing data contained in the literature for African ruminants, Gordon and Illius (1994, 1996) found that the mass of the digestive tract contents, rates of microbial fermentation, and the time food spent in the digestive tract were strongly related to body mass, but not on their classification as grazers or browsers. Likewise, Robbins et al. (1995) found that the liquid passage rates, extent of fiber digestion and the flow of saliva and rumen fluids did not differ between grazers and browsers, but were related strongly to body size.

Body size may obscure the effects of gut anatomy on digestion of grasses and browses. Larger animals, which tend to be grazers, have a proportionately larger gastrointestinal tract than do small animals, which tend to be browsers (Case 1979, Van Soest 1994). The larger rumen/reticulum of large animals promotes longer retention of food and thus greater nutrient extraction via microbial fermentation (Demment and Van Soest 1985). Small animals, which have less body mass to fuel, require less energy to survive, and thus need to obtain less food per day (Peters 1986). However, small animals require more energy per unit weight to fuel a higher mass-specific metabolism, and thus must obtain a high rate of energy return per gram of food ingested (Peters 1986). Therefore, large herbivores are better suited to extract energy from high-fiber grasses and small animals from the cell contents of browses (Demment and Van Soest 1985). Therefore, the influence of subtle morphological differences on digestion between grazers and browsers within a size class may be hard to detect.

Body size may also obscure any effects of mouth and tooth morphology on harvesting rate of grazers and browsers. Small animals naturally have smaller mouths that may help them to crop small bites of browse more efficiently, and limit the size of bite they can take on grass swards (Illius and Gordon 1987, Shipley et al. 1994). No definitive study has compared harvesting rates of browsing and grazing animals of the same size feeding on similar diets of grass and browse. Most evidence for the relationship between mouth structure and efficient harvesting is anecdotal and theoretical. For example, Shipley et al. (1994) found no noticeable patterns in maximum harvesting rate and chewing efficiency among 13 species of grazing, browsing, and intermediate herbivores feeding on alfalfa. However, the grazers tended to crop bites of alfalfa more efficiently than many of the intermediate and browsing species. Clarifying the independent roles of body size and morphological specialization on digestion, harvesting, and diet selection is difficult because relatively few browser-grazer "pairs" or "groups" of similar size exist that would allow a rigorous test of differences in harvesting and digestion among herbivores. In addition, virtually all studies comparing anatomy and physiology of browsers and grazers focus on ruminants, and thus fail to consider similar adaptations by other types of herbivores, such as hindgut-fermenters (e.g., rodents, rabbits, horses) and non-ruminant foregut-fermenters (e.g., kangaroos, sloths).

## Ecological and Management Implications of Grazing and Browsing

To better manage range livestock and habitats of free-ranging herbivores, ecologists and range managers often wish to estimate their forage intake rate. Morphological characteristics of grasses makes it easier to estimate the intake rate of grazers than that of browsers. Intake rate of grasses is predictable from estimates of pasture biomass, because bite size is directly related to grass biomass (Short 1985). Bite size on grasses is a function of incisor width (or diameter of tongue sweep) and grass height and density (Illius and Gordon 1987). Bite size, and thus intake rate, is reduced on shorter swards, and with successive grazing (Ungar et al. 1991, Ungar and Noy-Meir 1988). In contrast, intake rate cannot be predicted from the biomass of browse, because bite size is usually independent of browse biomass (Spalinger et al. 1988). The complex geometry and discontinuous arrangement of nutritious plant parts makes bite size difficult to estimate (Shipley et al. 1994).

Preference for grass or browse, regardless of body size and anatomy, seems to be an important feature of resource partitioning among herbivores (McNaughton and Georgiadis 1986). For example, the seasonal variation in patterns of habitat and forage use within ruminant and nonruminant herbivores in African savannas allow an astonishing array of wild herbivores to coexist (Jarman 1974). Sequential use of vegetation throughout the seasons and adaptations for different types of vegetation by one group of herbivore species can actually improve forage conditions for other groups of herbivores in an ecological relationship called "facilitation" (Bell 1970, 1971). Large grazers that require a large volume of food, but can efficiently digest fibrous food, may remove standing dead or mature grasses, promoting access to, and growth of, small forbs that may be used by small concentrate selectors (Bell 1970, 1971). However, when resources are scarce, particularly during the dry season or winter, more dietary overlap occurs among herbivores and interspecific competition is increased (Jenkins and Wright 1987). Within hyrax communities, for example, differences in diet between the grazing rock hyrax and the browsing yellow-spotted hyrax may reduce competition for food and allow these two species to coexist, frequently occupying the same rock outcrops, sharing burrows and raising their young in communal nurseries (Hoeck 1975, 1989). However, during droughts, rock hyraxes switch to browses. If poor forage conditions continue, yellow-spotted hyraxes may eventually disappear from the habitat (Hoeck 1975, 1989). Therefore, close coexistence of grazers and browsers and complex herbivore communities may only be possible when forage is relatively abundant.

Preference for browses or grasses may also play a role in effective range management. Often foraging by wild herbivores, which tend to be browsers or intermediate feeders in temperate ecosystems (e.g., deer, pronghorn, jackrabbits), has only a minimal influence on production of domestic livestock, which tend to be grazers (e.g., cattle, sheep, horses). However, foraging by intermediate or mixed feeders, such as elk, can occasionally reduce production of cattle (Hobbs et al. 1996a, b). Ranchers in Africa have taken advantage of the natural partitioning between browsing and grazing herbivores of different sizes in range management and meat production through game ranching. Game ranching is the husbandry of native animals in their natural habitat for the production of meat and other products (Bolen and Robinson 1999). Because some wild herbivores are grazers and others are browsers, nearly all forms of vegetation within a pasture are consumed (Western 1975, Taylor and Walker 1978). Likewise, a mix of domestic species (e.g., cattle, sheep, and goats) consisting of grazing and browsers to reflect the forage available is most productive and protects the plant resource in the same way as mixes of native ungulates (MacNab 1991).

The harvesting and digestion constraints of herbivores must also be considered when selecting animals for prescription grazing applications. The careful application of domestic livestock is currently being explored to accomplish agronomic, silvicultural, and ecological goals. For example, livestock grazing can be used to improve growth of trees in pine plantations (Doescher et al. 1987), for weed control on rangelands (Olson and Lacey 1994), and to improve wildlife habitat (Severson, 1990). In each of these prescriptions, understanding the herbivore's dietary constraints and opportunities can improve the manager's ability to alter the plant community and reach an ecological goal.

## Conclusion

Understanding the basis for diet selection by mammalian herbivores is clearly complex. The digestive system of most herbivores allows them to extract nutrients from a wide variety of vegetation. However, animals that are most efficient at obtaining required nutrients are those that will be most likely to survive, reproduce, and produce products such as meat and milk. Predicting diets selected by herbivores leads to better habitat and range management, and allows better understanding of interactions among wild and domestic herbivores. Therefore the relationship between "form" (morphology) and "function" (nutrient extraction and diet selection) in herbivores is a research priority for the next century.

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# Foraging Behavior: Experience or Inheritance?

### K.L. Launchbaugh, J.W. Walker and C.A. Taylor

## Abstract

**Selective grazing is a reciprocal process that, on one hand, determines the nutritional welfare of the herbivore, and on the other hand, alters the dynamics of the plant community. Therefore, it is important to understand how animals make dietary choices while grazing. Contemporary diet selection theories propose that food preferences and aversions are based on experiences within the life of the animal. The dietary likes and dislikes of grazing animals are certainly learned behaviors, but inherited morphological, physiological, and neurological characteristics can alter the nature and magnitude of digestive feedback. Therefore, diet preferences could be genetically passed from parents to offspring. Understanding the inheritance of diet selection could help managers improve the ecological sustainability of livestock grazing. The selection and breeding of animals with specific diet characteristic could also be used to create herds and flocks of livestock to control weeds or manage wildlife habitat with prescription grazing techniques. Therefore, selective breeding of diet characteristics could constitute a powerful new range management tool.**

## Is foraging behavior inherited?

Natural foraging environments are tremendously complex and at times inhospitable places for mammalian herbivores to make a living. They do contain nutritious plants, but there is immense variation in the nutritional value and toxic properties of these plants. To complicate matters further, nothing ever stays the same. The nutrients and toxins in plants vary from place to place and time to time. The herbivore's challenge is to acquire sufficient nutrients to evade starvation and produce viable offspring while avoiding the consumption of lethal doses of phytochemicals. The fact that herbivores generally succeed in walking this biological tightrope is credit to a highly sophisticated foraging process.

There is little doubt that mechanisms exist which allow animals to select nutritious diets and avoid toxins (Provenza 1995, Pfister this volume). Most scientists agree that a successful diet selection system gives animals the ability to relate plant flavor, appearance, or texture to digestive benefits or liabilities. However, there is significant disagreement over the mechanisms that accomplish this goal. On the surface, diet selection is simple; herbivores eat what they like and avoid what they don't like. The difficult challenge is to figure out how animals know what to eat or avoid. In the final analysis, animals must either be born knowing what to eat and avoid or learn appropriate dietary habits from conspecifics or through individual experiences.

Much has recently been written about how animals learn appropriate diets (Provenza 1995, Provenza and Launchbaugh this volume). Learned behaviors, as apposed to innate ones, usually evolve in situations where: 1) the behavior must be highly adaptive, for example, in dynamic environments; 2) detailed information about elements in the environment cannot be known before birth; 3) there is limited danger if the behavior is executed incorrectly; and, 4) information about dangers and opportunities can be socially transmitted between generations. It therefore makes sense that learning plays a major role in the foraging habits of livestock and wildlife.

On the other hand, heritable aspects of diet selection should be evident because natural selection favors animals that are good foragers. The success of grazing and browsing animals is based on how well they find, consume and assimilate nutritional resources. Because foraging efficiency influences reproductive success and survival, it contributes directly to "Darwinian" fitness. Therefore, many ecologists argue that foraging attributes are targets of natural selection and must therefore be inherited (Pulliam 1981).

It would be easy to get caught in a "nature or nurture" debate over whether diet selection is innate or learned. However, this is not the appropriate epistemo-

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logical approach to understanding foraging given the intertwined nature of learned and innate behaviors. A more constructive approach to deciphering diet selection is in terms of proximate and ultimate causes. It is generally agreed that post-ingestive consequences are a primary factor affecting diet selection. Thus, the pairing of pre-and post-ingestive stimuli are the proximate cause of learned foraging responses. However, these post-ingestive consequences are ultimately the result of morphological and physiological systems that control what is sensed both pre-and post-ingestively. Therefore, these genetically determined systems are ultimately responsible for learned diet selection. In other words, herbivores *inherit* their ability to *learn*. In this chapter we will examine the foraging behavior of mammalian herbivores, mostly domestic ruminants, to reveal the inheritance of diet selection.

## How Do Herbivores Inherit Their Diet Preferences?

Understanding which aspects of foraging are under genetic control and which are subject to animal experience, will reveal opportunities or limitations for managing herbivores. Several theories based have been advanced to explain diet choices.

### Inherited flavor preferences

The simplest explanation of diet preferences is that animals are born preferring foods that are nutritious and disliking foods that are toxic. Specifically, animals could have innate perceptions of palatability for either specific plants or for plant attributes such as sweetness, energy density, or texture (Owen 1992). This explanation, known as hedyphagia, is based on the idea that animals which prefer the flavor of nutritious foods will succeed and reproduce. Through natural selection, nutritious foods become "pleasing" and toxic or low quality foods become "offensive". An important consequence of this explanation is that diet preferences are inherited and not influenced by animal experience. Unfortunately, this behavior pattern is rarely observed in mammalian herbivores (Provenza and Launchbaugh, this volume).

An inherent preference for nutritious plants and avoidance of toxic plants would, however, contribute significantly to animal fitness (Provenza and Balph 1990). Plant sugars are presumably sweet, so animals that like sweet plants might enjoy an advantage by consuming plants high in non-structural carbohydrates. However, there is no evidence that grazing animals prefer sugary feeds (Hutson and van Mourik 1981). And, conditioned aversions can be easily created to highly nutritious plants (Burritt and Provenza 1989). The instinctive avoidance of bitter plants may have significant survival value because many plant toxins possess a bitter flavor (Garcia and Hankin 1975). Most herbivores initially avoid foods with flavors described as bitter to humans (Garcia and Hankins 1975, Pfister this volume). Herbivores are, however, generally not regularly deterred by bitter flavors (Nolte et al. 1994, Nolte this volume), and strong preferences can be formed to bitter-tasting foods when ingestion is followed by positive gastro-intestinal consequences (Molyneux and Ralphs 1992). We believe that inherited flavor preferences play only a minor role in diet selection of rangeland herbivores. As research uncovers details about diet selection, however, it may become apparent that some flavors are inherently pleasing or aversive or in some way less susceptible to modification through experience (Kalat and Rozin 1970).

### Specific hungers and nutritional wisdom

Richter (1943) proposed that animals select appropriate diets through inherited, specialized receptors that detect nutrients or toxins in foods and a system that monitors body status for specific nutrients or toxins. By this hypothesis, called euphagia, when animals become deficient in a nutrient they develop a "specific hunger" for that nutrient and consume plants with an abundance of the nutrient. A diet selection system based on specific hungers, is recognized for water and sodium (Rozin and Kalat 1971, Rozin 1976). To apply a pre-wired recognition system for each nutrient or toxin encountered by a generalist herbivore is nearly inconceivable. Nutritional wisdom through specific hungers would be easily passed to subsequent generations. The investment in neurologic machinery, however, to recognize all nutrients or potentially lethal phytotoxins in an herbivore's environment is simply too costly (Rozin 1976).

### Dietary preferences based on grazing experiences

Contemporary diet selection theories assert that food preferences and aversions are based on experiences within the life of the animal. Herbivores form dislikes for foods (called conditioned flavor aversions) when consumption is followed by negative gastro-intestinal consequences (e.g, nausea or malaise; Figure 1). Food aversion learning has been demonstrated in many herbivores including insects (Bernays and Lee 1988), monogastric mammals (Garcia 1989), and ruminant mammals (Provenza 1995). In a similar way, preferences are formed for foods when their consumption is followed by positive digestive feedback from protein or energy (Villalba and Provenza 1996, 1997) or cessation of illness (Green and Garcia 1971; Figure 1).

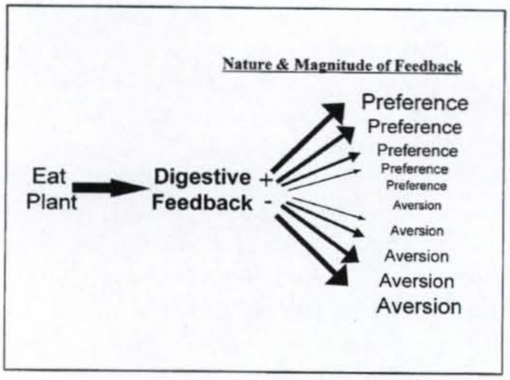

**Figure 1.** When herbivores eat a plant, they experience digestive feedback from energy and nutrient (positive feedback) or from plant allelochemicals (negative feedback). The nature and magnitude of this feedback determines the intensity of preferences or aversion formed to the plant.

The concepts of conditioned aversions and preferences have greatly advanced our ability to explain plant/herbivore interactions. Though preferences and aversions are certainly learned behaviors, we contend that the nature and magnitude of digestive feedback, which establishes and moderates plant palatability, is controlled primarily by inherited characteristics. In other words, herbivores learn to prefer plants that make them feel good (i.e., give positive digestive feedback) and avoid eating plants that make them feel ill (i.e, give negative digestive feedback). However, the amount of positive or negative feedback that animals "feel" upon digestion is determined by the physiology, morphology and physical abilities the animal inherited.

**Physiological attributes.** Much of the individual variation in diet preferences can be traced to inherited physiological characteristics. The inheritance of enzyme systems involved in digestion is well documented (Velázquez and Bourges 1984). This may explain why absorption of minerals (Green et al. 1989) and nutrients (Beaver et al. 1989) during digestion is related to animal breed. Enzyme systems necessary for detoxification of some drugs is also strongly inherited (e.g., hexobarbitol, Vessell 1968) and the same is undoubtedly true for enzymes that detoxify plant allelochemicals. For example, enzyme systems that detoxify flouroacetates in range plants are inherited and resistance to fluoroacetate poisoning has, in fact, been used as a genetic population marker in native Australian mammals (Oliver et al. 1979, Mead et al. 1985). The inheritance of systems to metabolize phytotoxins is probably widespread in herbivores.

An example of potentially inherited metabolic abilities is illustrated in the consumption of bitterweed (*Hymenozys odorata*) by sheep. The amount of bitterweed necessary to produce toxic signs of poisoning varies greatly among individual sheep (Witzel et al. 1977, Calhoun and Baldwin 1980, Calhoun et al. 1981). For example, as little as 500 g was adequate to kill some sheep, while at the other extreme, a sheep consumed 14,514 g of immature green bitterweed plants over a 50-day period without signs of poisoning (Hardy et al. 1931). Ranchers in Texas have commented that sheep raised in bitterweed country are much more resistant to bitterweed poisoning than sheep brought into bitterweed infested areas from areas free of bitterweed. Acquired tolerance following repeated exposure is partially responsible for individual variation, but variability has also been measured in sheep previously not exposed to bitterweed (Calhoun et al. 1981). We suspect that part of the variation between sheep for bitterweed toxicity is inherited.

**Morphological attributes.** Morphological characteristics are unquestionably inherited. Furthermore, digestive morphology affects diet selection, at least across species (Shipley, this volume). Therefore, it seems evident that inherited digestive morphology would affect diet selection. One line of evidence that relates to inherited digestive morphology is the observation that breeds of livestock differ in their ability to digest dry matter and energy from similar diets (Phillips 1961, Beaver et al. 1989). Another way that morphology could potentially affect diet selection is through differences in nutrient or energy demand. Body composition and size are strongly determined by genotype and the nutrient and energy demands of the herbivore influence diet quality (Owen 1992). Animals in a low nutrient state, which could result from high nutritional demands, can have a decreased ability to detoxify consumed allelochemicals (Freeland and Janzen 1974, Boyd and Campbell 1983). Likewise, animals in a high nutritional state will often be more selective and choose diets different from animals in a deficient nutrient state (Murden and Risenhoover 1993). Unfortunately, there is little direct evidence that inherited morphological characteristics affect diet selection.

**Skills and abilities.** Foraging skills also influence which plants are eaten (Ortega-Reyes and Provenza 1993, Provenza and Launchbaugh this volume). There is certainly a genetic basis for physical abilities (Marinier and Alexander 1991). Foraging abilities such as reach, physical dexterity, and strength can influence diet selection simply by providing access to desired species. However, as far as we know, this inheritance has not been documented.

**Sensory capabilities.** Herbivores also inherit their ability to taste, smell, see and feel the plants in their environment. For example, different species of livestock differ in their ability to taste and discriminate various purified compounds with sour, sweet, bitter, and salty flavors (Arnold and Dudzinski 1978, Church 1979). This research on domestic herbivores also revealed significant variation between individuals within a species. Such sensory capabilities undoubtedly have a genetic basis, though we do not believe this has been documented. It is plausible that the ability of herbivores to sense or tolerate digestive consequences is also inherited. Though very little is known about this topic, it is very likely that herbivores inherit their ability to taste, or otherwise detect, plants and relate the flavor of plants to post-ingestive characteristics.

### Magnitude of digestive feedback

How could differences in digestive feedback affect diet selection? Suppose the same plant species is eaten by several herbivores in the same amount. If some of these individuals extract more energy or nutrients from the plant than others, they will form a greater preference for the plant. This is because the greater the positive feedback the greater the preference for the food (Arnold and Dudzinski 1978).

The same is true for plants that contain allelochemicals which cause aversions. Herbivores with a superior ability to detoxify or tolerate a particular phytotoxin will experience less negative digestive feedback than lesser adapted animals when the toxin is consumed. The palatability of the consumed plant will therefore be greater for the tolerant animal because it experiences less digestive malaise (du Toit et al. 1991, Launchbaugh and Provenza 1994). Research by Pritz et al. (1997) examined the consumption of redberry juniper (*Juniperus pinchotii*) branches by Spanish and Angora goats naive to juniper. The first time goats received juniper branches, the breeds did not differ in the amount of juniper they consumed. However, on the second day of the trial, Spanish goats ate more juniper than Angora goats. Pritz and associates (1997) hypothesized that the Angora goats suffered greater internal malaise after consumption and therefore formed a greater dislike or aversion to juniper than Spanish goats. This contention was substantiated by blood serum enzyme analysis which indicated that Angora goats suffered greater liver damage from the consumption of juniper than Spanish goats. The learned preference or dislike for a plant could therefore be inherited because the digestive or detoxification abilities of herbivores are inherited.

Admittedly, there is a significant interaction between experiential and inherited aspects of digestive or detoxification abilities. Animals also often gain a superior ability to digest (Distel et al. 1994) and detoxify (Distel and Provenza 1991, Robbins et al. 1991) plants for which they have significant grazing experience. It is common for animals to increase their consumption of low quality foods as they become accustomed to them. This was observed with goats eating juniper (*Juniperus pinchotii*, Pritz 1995) and cattle eating mesquite (*Prosopis glandulosa,* Launchbaugh, unpublished) and sheep eating sagebrush (*Artemisia tridentata*, Banner 1999).

## Evidence for Inherited Diet Preferences

The most obvious example of how genetic background influences diet selection is found in comparisons between species for dietary preferences. When juniper consumption was compared for several rangeland herbivores in Texas, we found that consumption of juniper was as follows: deer>goats>sheep>cattle (Launchbaugh et al. 1997a). These differences between species are strongly held with little overlap between species. Similar species differences are often observed among wildlife herbivores. For example, whitetailed deer ate about 5 times more spotted knapweed (*Centaurea maculosa*) than elk when grazing on the same winter range (20% vs. 5%; Wright and Kelsey 1997).

An interesting comparison of learned and inherited diet selection attributes was examined in a cross fostering experiment with lambs and goat kids. It is well documented that goats have a higher preference for and consume more leafy spurge (*Euphorbia esula*) than sheep. To encourage leafy spurge eating behavior in sheep, Walker and associates (unpublished data) grafted lambs onto nanny goats so that each nanny raised one kid and one lamb. When the lambs and kids were grazed on spurge-infested range, the goats still ate more spurge than the lambs even though both species had similar grazing experiences.

Difference in diet selection between breeds is another way to document the genetic basis for diet preferences. Research on cattle (Herbel and Nelson 1966b, Winder et al. 1996), sheep (Warren et al. 1984), and goats (Warren et al. 1984, Pritz et al. 1997) has revealed that breeds differ in diet preferences indicating that diet selection is based on inherited somatic characteristics. Mariner and Alexander (1991) have shown that foraging behavior in horses is related to genetic lineage and some genetic lines appear more prone to plant poisoning than others. However, breeds do not always differ in the plants they prefer (Walker et al. 1981). Observed differences between breeds may depend on how similar the selective pressure or environmental conditions were during the development of the breeds (Launchbaugh et al. 1997b).

The most rigorous test for inherited diet preferences is half-sibling or sire analysis within a breed because dietary experience and social influences can be isolated from inherited attributes. Warren and associates (1983) studied the diet selection of 60 young male Spanish goats in Texas. These goats were raised in a common environment with no social influence from their sires. In a late summer trial, sire significantly affected diet composition. The influence of sire was observed in the proportions of 14 plants in the diet (of 33 plants examined). In other words, which sire a goat was conceived by recognizably affected which plants the goat selectively consumed. In a more recent study, Taylor and associates (1998, unpublished) examined the potential inheritance of juniper-eating behavior in 64 Spanish×boer cross goats in 2 trials. A consistent effect of sire on juniper consumption resulted. The heritability of juniper-eating behavior in free-ranging goats was calculated as .28; meaning that 28% of the variation in juniper consumption could be traced to variation due to sire. Winder et al. (1995) examined diet selection of brangus cattle in New Mexico and reported significant heritability for the consumption of several range plants with heritability estimates often exceeding 50%. Diet diversity (number of species in the diet) was also affected by sire in a fall trial (Winder et al. 1995).

## Other Inherited Attributes that Affect Diet Selection "In The Wild"

Foraging is a process by which herbivores find and consume the provisions of life. So far we have only discussed how animals make choices once they find food. However, foraging also requires a bit of rambling around the ecological neighborhood to find these provisions. Not surprisingly, the "rambling abilities" of herbivores are at least partially inherited. The ability of the herbivore to handle steep terrain, forage in areas without shade, or travel great distances from water has been shown to affect diet selection in domestic herbivores. On desert range in New Mexico, differences in diets selected by cattle were attributed in part to how far animals traveled from water (Herbel and Nelson 1966a, Winder et al. 1996). For example, Winder and associates (1996) noticed that dropseed grasses (*Sporobolus contractus* and *S. flexuosus*) grew more abundantly away from water sources (i.e., grass abundance was positively correlated with distance from water). Brangus cattle traveled greater distances from water than Hereford or Angus cattle in their study. Consequently, brangus cattle had a higher proportion of dropseed in their diet than the other breeds. This concept applies equally well to wildlife species. However, a genetic predisposition for home ranges or foraging sites is not well documented.

## Management Implications

Livestock managers have selected animals for desired characteristics and culled undesirable animals since the beginnings of livestock husbandry. Early selections gave us breeds of animals specifically designed to produce milk, meat, or fiber. Different breeds have resulted from selection of production characteristics, behavior, color, size, and resistance to disease, pests, or environmental extremes (Lasley 1987). However, to our knowledge, herbivores have not been selectively bred for their diet characteristics. Understanding inherited limitations of diet flexibility is important in designing interventions to boost animal populations or deal with nutrient stress even if selective breeding is not employed.

There are many ecological and livestock production goals for which it may be useful to assemble groups of livestock with specific dietary habits. Genetic selection for dietary habits could be used to improve the power of livestock as tools for wildlife habitat management, landscape watershed improvement, management of fuel for prescribed fire, and wildland weed control. Animals within a herd or flock that consume greater than average amounts of a specific plant could be identified and bred to create successive generations with exceptional preferences for the plant of concern. For example, groups of animals selected specifically for weed control could constitute a viable method for plant suppression and offer an alternative to chemical or mechanical control techniques. Or, grazing could be used in combinations with chemical, mechanical, or fire treatments to improve effectiveness (Lyme et al. 1997, Olson this volume).

Breeding animals with specific dietary characteristics represents a sustainable tool for rangeland management. Although it is recognized that individual variation (i.e., the basis for genetic selection) in diet selection exists (Dove 1935, Marten 1978, Arnold and Dudzinski 1978, Marinier and Alexander 1991), no attempt has been made to select for diet preferences in livestock. Genetic manipulation of grazing behavior has an advantage over learned manipulation of grazing behavior because once genetic change has been accomplished the changes are passed to succeeding generations with no additional input. Management-based alternatives must be reestablished with each cohort and reinforced throughout the life of the animal (Lush 1984).

The potential success of selecting animal behavior to meet human needs is demonstrated in domestic dogs

(Coppinger and Coppinger 1998). Stock dogs have been selected to bite either the head or heals of livestock (e.g., headers or healers; Fox 1978). Humans have taken advantage of this behavioral predisposition to manage livestock flocks and herds. Certainly a skilled trainer could teach a header to heal or vise versa, but a good stock dog handler would think it foolish to cross mother nature in this way (Butler this volume). The same could be said for harnessing foraging behavior of livestock; begin with a critter possessing the desired genetic predispositions. If you are looking for a browser, start with a browser; don't try to teach a grazer to browse.

Emerging technologies will greatly increase our ability to select for inherited grazing behaviors. One reason that diet selection has not been a basis for selective breeding is, in part, because it is difficult to measure. However, fecal analysis with near infrared reflectance spectroscopy (Walker et al. 1998) and laser-induced fluorescence (Anderson et al. 1996) are two technologies that make it possible to screen hundreds of animals for simple diet characteristics. Controlling the metabolic abilities of herbivores may likewise become increasingly viable as genetic engineering capabilities develop. Consider that the beef cattle genome project is currently being promoted as a way to ultimately control beef palatability. Would not another noble goal be to harness our knowledge of genetics to improve and restore ecosystems?

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# Manipulating Diet Selection to Control Weeds

Bret E. Olson

## Abstract

**Weeds continue to spread across western North America despite millions of dollars of public and private funds spent on herbicides and biocontrol. Herbicides and biocontrol address the symptom, not the cause, of the weed "problem". Grazing livestock on weeds has the potential to reduce the spread of weeds and control current infestations, assuming we can stimulate or increase the consumption of weeds by large and small herbivores. Stimulating or increasing consumption may be affected by inherent anatomical or morphological constraints, lack of experience with the weed, lack of an appropriate mentor, adjustment of rumen microbial populations, or potentially the use of anti-toxicants which adsorb or bind with plant allelochemicals present in many weeds. Increasing the use of weeds by domestic livestock, large and small, will begin to address one of the causes of weed infestations, an imbalance in the use of plant communities by single species grazing.**

## Introduction

Invasion by exotic species is one of the most significant ecological threats of our modern era. Exotic plant species reduce forage for livestock and wildlife, accelerate soil erosion, and lower biodiversity. Weeds continue to invade and spread in western North America despite the best efforts of researchers and land managers. Carefully managed grazing has the potential to control weeds where traditional methods (e.g., mechanical, cultural, biological, and chemical) are restricted or limited by environmental or economic concerns (Olson and Lacey 1994). Further, livestock grazing has a distinct advantage over other control methods. While controlling a noxious weed with livestock, income from their meat and fiber creates positive net returns (Walker 1994, Williams et al. 1996), compared with most herbicides which are out of pocket expenses that usually must be reapplied for adequate weed control.

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Like any tool, livestock grazing can be misapplied and cause harm. Overgrazing has been implicated in encouraging the spread of weeds. However, carefully managed grazing could be used as a tool to control weeds if we understood more about why animals select certain plants and avoid others. This would broaden our perspective from considering grazing solely for its ability to sustain wild and domestic animals to considering it a powerful tool to control weeds. Appropriate use of this tool will require information on plant and animal characteristics that influence which plants are preferred and which are avoided by different animal species.

Herbivores prefer certain plants that are inherently palatable or because the herbivore experienced positive postingestive consequences in the past (Provenza 1995, Provenza and Launchbaugh this volume). Herbivores avoid certain plants because they are unpalatable or because of negative postingestive consequences (Pfister this volume). Our dominant large herbivores in western North America, cattle and horses, usually avoid grazing weeds. If weeds were preferred by these large herbivores they would not be considered "weeds", and would only be a minor part of plant communities as they are in their countries of origin. These plants are usually not "invasive" in their countries of origin because they are kept in check by natural invertebrate enemies, pathogens, and herbivores. In their "home" countries, the dominant herbivores are often sheep and goats, not cattle and horses. In this review, I will describe why and how we might be able to stimulate or encourage the use of these plants by large and small herbivores alike.

## Selecting Weeds Is a Function of Plant Characteristics

Palatability is a collective term for the plant characteristics that influence whether an herbivore will prefer or avoid a plant. Plant palatability is affected by taste, smell, texture, tearing resistance, and moisture content. Many weeds have an acrid or bitter taste or have a "noxious" smell, at least to humans. Yet, mule deer savor "bitter" brush (*Purshia tridentata*), and sheep and goats readily consume the bitter-tasting spotted knapweed (*Centaurea maculosa*). Bitter tastes and noxious smells are often associated with significant quantities of secondary compounds. Although some weeds are high in structural components, imparting great tearing resistance and presumably reducing palatability, many are similar in structural components and digestibility to native grasses and forbs. Further, weeds as a group do not have any lower or higher moisture content than native species. In fact, many weeds, such as leafy spurge (*Euphorbia esula*), remain greener, more succulent, and more nutritious longer into summer than associated cool season plants (Fox et al. 1991, Olson et al. unpublished data).

In addition to reducing palatability, plant allelochemicals may cause negative digestive consequences when eaten. For example, plant allelochemicals (terpenoids) in essential oils from big sagebrush (*Artemisia tridentata*) inhibit *in vitro* growth of gram-positive and gram-negative rumen microorganisms collected from mule deer (Nagy et al. 1964). Monoterpene alcohols in Douglas fir (*Pseudotsuga menziesii*) inhibit rumen microbial activity of sheep and deer, reflected by sharp decreases in microbial activity (Oh et al. 1967). Leaves and inflorescences of spotted knapweed contain high concentrations of cnicin, a secondary compound (Locken and Kelsey 1987, Olson and Kelsey 1997). Although levels of crude protein and digestibility of leaves and inflorescences of spotted knapweed are higher than stems, rumen microbial activity is lower with leaves and inflorescences than stems, presumably because of the presence of cnicin (Olson and Kelsey 1997). Negative effects on microbial activity, resulting in negative postingestive feedback, may explain why some ruminants limit their consumption of certain weeds. In contrast to spotted knapweed, the high nutritive value of leafy spurge in early summer appears to counteract any negative effects associated with its plant allelochemicals (Roberts and Olson 1999).

Plant availability also influences which species are "preferred" by herbivores. Preferred species comprise a greater proportion of the diet than they represent in the plant community. Preferences for these species will change as the plant community is grazed. As preferred species become less available, the herbivore must switch to less preferred species, in some instances, weeds. This concept is implied when using the proper use factor. For example, in southwestern Montana the proper use factor for cattle grazing their preferred bluebunch wheatgrass (*Pseudoroegneria spicata*) may be 50%, but only 10% for spotted knapweed. This does not imply that spotted knapweed can only tolerate 10% use while bluebunch wheatgrass can tolerate 50% use. It simply indicates that if cattle are using spotted knapweed, a species they normally avoid, use on the preferred bluebunch wheatgrass would be excessive.

Availability of the weed may influence whether or not it is grazed. For example, when a particular weed is uncommon in the community, consumption may be relatively high. This is partly because animals are curious and seek diverse diets. If every animal in a pasture takes just a few bites of an uncommon plant, it may sustain rather high utilization. Plus, potential negative postingestive consequences from the weed are buffered because consuming large quantities of preferred forages may dilute the negative effects associated with the weed (Pfister this volume). On the other hand, with dense weed infestations the weed is no longer novel, the animal seeks other foods to provide diversity, and the full "negative" effects associated with consuming large quantities of the weed may surface. In these situations, the same herbivore may avoid the plant. In addition, animals avoid dense infestations of certain weeds because these infestations are a physical deterrent to animal movement (Lym and Kirby 1987).

## Selecting Weeds Is a Function of Animal Characteristics

Besides plant palatability and availability, whether an animal consumes a plant depends on the animal's capabilities and previous experience with the plant. Designing effective livestock grazing systems to control weeds will require selecting appropriate animals and preparing these animals with desired dietary experiences.

### Species of herbivore

Certain types of animals prefer certain types of plants. Cattle prefer grasses, sheep prefer forbs, and goats prefer shrubs. These inherent preferences partly reflect different morphologies and anatomies of these animal types, which influences their ability to prehend different plants and, or plant parts, and to detoxify plant allelochemicals. For example, goats have relatively large mouth openings and longer lips whereas cattle have relatively small mouth openings and shorter lips (Hofmann 1989). Tongues of goats are more dextrous than the heavily cornified tongues of cattle. These characteristics allow goats to strip leaves from stems or remove inflorescences from weeds, whereas the limited dexterity of a cow's mouth is ideal for tearing clumps of grass, not for stripping leaves or handling forbs.

Small ruminants evolved eating forbs and woody plants and have relatively large parotid salivary glands. Salivary excretions in small ruminants may counter the effects of plant allelochemicals (Hofmann 1989), which may explain why specialist grazers and browsers typically consume forages with high concentrations of plant allelochemicals. Sheep, goats and mule deer also produce high amounts of tannin-binding proline in their saliva, allowing them to use forages containing condensed tannins (Robbins et al. 1987, Austin et al. 1989, Mehanso et al. 1992). Cattle do not produce these salivary proteins (Jones and Mangan 1977, Austin et al. 1989). Browsing herbivores, such as goats, also have relatively large livers which may improve their ability to detoxify plant allelochemicals absorbed from the digestive tract (Pfister this volume). Salivary excretions and liver capacity may explain why specialist grazers and browsers typically consume forages with higher concentrations of plant allelochemicals than generalist grazers like cattle. Therefore, sheep and goats are more likely than cattle to consume and thus control weeds that contain significant amounts of plant allelochemicals. However, many weeds also become quite fibrous at maturity. Compared with small ruminants, cattle and horses are more able to digest fibrous materials, and would be more likely to trample or breakdown stiff stems that limit movement of smaller grazers and wildlife.

## How important is grazing experience?

In southwestern Montana, we assessed whether yearling sheep exposed to leafy spurge as lambs graze this weed more readily than yearlings that were not exposed to it as lambs (Olson et al. 1996). We also determined whether this difference, if present, persists through the grazing season. We found that experienced yearlings spent more than twice as much time grazing leafy spurge in early summer (late May-early June) compared with naive yearlings, but neither group actively selected the plant. This may reflect that the associated cool-season grasses were highly palatable and nutritious in early summer. In addition, these yearlings did not have mature role models to influence their diet selection, positively or negatively. By mid-summer, both groups were grazing leafy spurge, up to 45% of their diet. Our findings indicated that: 1) there would be a slight advantage to using experienced sheep on leafy spurge, but only in early summer, and 2) inherent dietary preferences for forbs such as leafy spurge is strong in sheep.

In a more recent study, we compared how sheep and goats, in adjacent small pastures, used five invasive weeds including leafy spurge, spotted knapweed, sulfur cinquefoil (*Potentilla recta*), dalmation toadflax (*Linaria dalmatica*), and oxeye daisy (*Chrysanthemum leucanthemum*). Neither the sheep or goats had any previous experience with these weed. They only had a two day "exposure" to these infested pastures before we observed their grazing behavior for three days in early summer and again in late summer. Even with only two days exposure, the sheep and goats grazed each of these weeds. Apparently, their innate preference for broad-leaved forbs, despite the presence of allelochemicals in most of these weeds, predominated over their lack of experience with these species. However, these were short term trials and other forage was available to buffer allelochemical effects. Potentially, the animals could have developed an aversion to one or more of these weeds if we had forced them to graze the weeds over a longer period.

With ruminants, whether the previous experience is positive or negative it reflects the response of two interdependent systems, the whole animal system and the rumen microbial ecosystem. If the plant tastes bad, causes nausea, or is directly toxic to the animal (e.g. toxins absorbed directly into the system) the animal will avoid the plant in the future. Alternatively, if a plant does not taste bad, does not cause nausea, or is not toxic to the whole animal, the animal ingests the plant, at least initially.

Once ingested, the plant material has passed the first line of defense, the decision making system. The plant may contain allelochemicals that affect the line of defense, the rumen microbial population. With rumen microbial populations, plant allelochemicals can affect species composition of the rumen bacteria, fungi, and protozoa, and/or the level of rumen microbial activity. If the compounds negatively affect rumen microbial species composition and thereby reduce microbial activity, forages will be digested at a slower rate. This will result in negative postingestive consequences, reducing subsequent intake, and presumably reducing subsequent preference for the plant. A change in diet is probably the most important factor influencing numbers and relative proportions of different microbial species in the rumen (Yokoyama and Johnson 1988), partly because ruminal bacteria vary widely in the nutrients they require (Russel 1984), and partly because they have different tolerances or abilities to metabolize plant allelochemicals.

If the appropriate microbial species composition is needed for a ruminant to ingest a weed, altering microbial composition could increase intake of the plant. Rumen fluid from sheep consuming leafy spurge was added to the rumen of cattle to see if this would increase their consumption of a novel food paired with leafy spurge (Kronberg et al. 1993b). Cattle, with and without sheep rumen inoculum, consumed similar amounts of the novel food, suggesting that either sheep rumen microorganisms cannot exist in cattle rumina, or that ruminal microbes in cattle may produce an aversive substance from leafy spurge; whereas, sheep do not produce an aversive substance. Simply inoculating an animal with the appropriate "weed adapted" rumen microbial composition from another animal is not usually the answer.

## What Can We Manipulate?
## Plant Characteristics

In limited areas, we may be able to improve the palatability of weeds to increase their use by small and large herbivores. Fertilizing with nitrogen (N) often increases crude protein levels of forage, but it can also stimulate excessive growth which may dilute nutrient concentrations in plant tissues (Kronberg and Walker 1999a). When fertilizing increases plant N concentrations, more N is available to the rumen microbial population which increases their activity and thereby increases forage digestibility. More importantly, fertilizing with N may lower concentrations of plant allelochemicals in weeds. By increasing the uptake of N, the increased synthesis of amino acids and proteins will reduce the amount of carbon available to synthesize carbon-based plant allelochemicals. On nutrient poor soils, nutrient uptake is limited so plants accumulate carbon-based plant allelochemicals (Bryant et al. 1983). For example, spotted knapweed plants from a fertile range site had lower cnicin concentrations than plants from an infertile, loamy sand site (1.8% versus 3.9%; Locken and Kelsey 1987, Olson and Kelsey 1997). In a 4-day trial, sheep consumed greater quantities of leafy spurge harvested from a fertilized site than from an adjacent unfertilized site (Kronberg and Walker 1999a). Although not quantified, I attributed this difference to the effect that fertilizing had on reducing concentrations of one or more carbon-based plant allelochemicals, because crude protein and fiber only differed slightly between leafy spurge from fertilized and unfertilized sites.

Palatability may be increased by spraying sweeteners, such as molasses, on weeds. Most herbivores have a "sweet tooth". Sweeteners may offset the bad taste or smell associated with plant allelochemicals. In addition, some sweeteners, such as molasses, are rich in sulfur (S). Sulfur is an important nutrient for rumen microbial activity in the synthesis of the S-bearing amino (e.g., acids, methionine and cysteine) and can improve detoxification in the liver (Launchbaugh 1996). On the Deseret Ranch in northern Utah, a dilute solution of molasses was sprayed on a patch of musk thistle (*Carduus nutans*; Greg Simonds, personal communication) to encourage cattle to use the spiny weed. The cattle readily consumed the musk thistle, and grazed the patch the following year even though it was not sprayed that year.

At times, spraying weeds with phenoxy herbicides can increase animal preference for them. This has been observed with 2,4-d and glyphosate. The actual mechanism is unknown, but these herbicides are essentially plant growth regulators, often accelerating growth rates. Accelerated growth rates may increase the amount of sucrose or salts, and possibly curtail the production of allelochemicals in the plant. In southwestern Montana, a patch of stinging nettle (*Urtica dioica*) was sprayed with glyphosate to eradicate the plant. Before spraying, the landowner's cashmere goats had avoided the stinging nettle but the goats grazed the stinging nettle avidly after it had been sprayed.

Why spray and graze a weed if spraying alone will control the plant? First, when weeds are sprayed late in their growth cycle, the stimulated growth rate may actually allow the plant to produce viable seed. Grazing this regrowth can reduce seed production; and degradation of consumed seed in the rumen can further degrade viability seed (Wallander et al. 1995, Olson et al. 1997a). Second, it would reduce the amount of standing dead material, decreasing a fire hazard, and opening the canopy for growth of desirable species. Third, many dense weed infestations, dead or alive, deter animal movement. Finally, the animals benefit by consuming a nutrient-rich resource when the weeds are sprayed early in the growing season. Arresting growth in early summer prevents the seasonal translocation of nutrients from aboveground leaves and stems to the root system. However, using herbicides to encourage consumption of weeds should be avoided where the grazing animals are producing milk or will soon be slaughtered for meat. It is important to follow label instructions of the herbicide.

## What Can We Manipulate?
## Animal Characteristics

Can we encourage livestock, especially large herbivores, to graze forages readily that they normally avoid? Avoidance related to morphological or anatomical constraints can only be addressed by selecting the appropriate species. Avoidance related to lack of experience can be addressed by exposing the herbivore to the weed at a young age or with appropriate mentors. Avoidance related to rumen microbial attributes, resulting in negative postingestive feedback, may be addressed by appropriate adjustment periods to the weed, or by using anti-toxicants. For most herbivores, avoidance is probably a function of not one, but a combination of these factors. Therefore, designing systems to use livestock to control weeds must begin by identifying the factors that cause avoidance.

### Manipulating stocking rate

The most common approach to getting livestock to eat weeds is to increase stocking rate to "force" the animals onto them. Altering plant availability by adjusting stocking rate will certainly affect the use of weeds by herbivores. At low stocking rates, herbivores may graze the weeds because they are seeking a varied diet (Provenza 1996), or because they will not ingest enough of a phytotoxin to cause a negative postingestive consequence. At high stocking rates, an animal's ability to avoid certain plants is compromised. All plants will be grazed. But even at high stocking rates, animals will graze preferred species to a greater degree than less preferred, weedy species, resulting in a competitive advantage for the weed.

Concentrating animals (e.g., high animal densities for short periods of time) to control palatable weeds can reduce weed populations. Intensive cattle grazing reduced the number of seedlings and rosettes of the invasive oxeye daisy *Chrysanthemum leucanthemum*, but the impact was attributed more to trampling than cattle actually consuming significant amounts of the forb (Olson et al. 1997b). Sheep or goats would have grazed this weed more readily than cattle (Howarth and Williams 1968). Concentrating animals limits their ability to select, which is intuitively appealing, but it does not always work. In southwestern Montana, sheep were concentrated on dense infestations of leafy spurge with a portable, power fence. Although sheep normally graze the highly nutritious leafy spurge, they went "off feed" after 10 days (personal observation). Either the sheep were bored with spurge and desired a more varied diet (Provenza 1996), or the whole animal or rumen microbial populations were affected by high levels of plant allelochemicals in their diet. Activity of sheep rumen microorganisms is reduced when leafy spurge exceeds 75% of their diet (Roberts and Olson 1999).

Animal preference can be neutralized by extremely high stocking rates. One producer in western Montana maintains 350 goats on 13 acres. His land is surrounded by spotted knapweed but he does not have any spotted knapweed on his land. However, he has to feed hay much of the year. Admittedly, in this example, a goat's ability to select preferred species is negated, but at the expense of the land resource.

## Choosing the best species for weed control

Another approach to getting animals to eat weeds is to manipulate animal selectivity or use the most appropriate animal species, one with a predilection for grazing the target weed. Given that cattle and horses actively avoid most weedy forbs, the common practice of single species grazing of these large herbivores in western North America exacerbates the tendency for weed populations to increase and spread. In contrast, multi-species grazing may help restore a balance to the plant community. In southcentral Montana, foothill rangelands infested with leafy spurge are grazed by sheep during the "yellow bract" stage (W. Pearson, personal communication). The sheep are herded quickly through the area, removing the tops of the leafy spurge plants. They consume the developing flowerheads which eliminates seed production, and allows sunlight to reach the grasses below. Then, cattle are "turned out" for the normal grazing season. When possible, the sheep are rotated through the area in August to graze the highly nutritious leafy spurge regrowth.

## Social influences on weed consumption

Exposing an herbivore to a weed at a young age can begin in the fetal stage. Many compounds pass from the mother through the placenta to the fetus (Keeler 1988). Mother's ingestion of a certain weed during pregnancy can reinforce food preferences in offspring, provided that it is not toxic to the fetus. If the mother avoids the weed, this may reinforce avoidance. Foods ingested by the mother also influence the flavor of her milk (Bassette et al. 1986) and can reinforce preferences. Finally, young herbivores learn which foods to eat and which foods to avoid from their mothers when they begin foraging (Mirza and Provenza 1990, Nolte et al. 1990). For mothers that avoid weeds because their mothers avoided weeds, etc., the challenge is to break these generational patterns by identifying ways to increase their consumption of weeds; which, could start a new pattern of preferred forages.

Providing appropriate mentors, such as peers or adult females, might be another way to increase consumption of weeds. This is most effective with young animals when they are relying less on their mother's milk and influence, and are highly influenced by their peers or other mentors (Mirza and Provenza 1990). An example of the possible influence of social models occurred in Montana where sheep are being used to control leafy spurge along streams and rivers. Along one river in southeastern Montana, a band of sheep was herded through areas infested with leafy spurge to control the plant, yet this particular band avoided leafy spurge for several years, even though this is a highly nutritious forb. One year, this band of sheep was inadvertently mixed with a band of leafy spurge-eating sheep. The "avoider" band then learned that leafy spurge was "OK" and subsequently grazed leafy spurge readily.

Grazing behaviors are readily socially transmitted among animals within the same species which normally ingest similar types of foods. Whether this learning occurs between species has received less attention. For example, goats, which readily consume leafy spurge, occasionally graze leafy spurge-infested pastures in the presence of cattle. Whether this increases cow or calf consumption of the weed has not been documented.

## Managing dietary experiences

Herbivores have been "taught" through aversive conditioning to avoid plant species that are poisonous or preferred (Provenza and Burritt 1991, Ralphs 1992). Whether herbivores can be "taught", via positive post-ingestive feedback, to increase their intake of a "less preferred" species, such as a noxious weed, has received little attention (Provenza 1992).

Previous dietary experience can influence which flavors animals prefer later in life (Nolte and Provenza 1991). They can also influence the ability of animals to digest (Distel et al. 1994), detoxify (Distel and Provenza 1991, Robbins et al. 1991) and harvest (Ortega-Reyes and Provenza 1993) certain plants. Further, experiences when animals are young, often have a longer lasting effect than experiences later in life (Distel et al. 1994). Thus, exposing young animals to weeds after weaning, with appropriate mentors, should encourage consumption of these weeds later in life.

## Manipulating rumen microbial populations

Avoidance could be related to effects of the weed on rumen microbial activity or composition, resulting in negative postingestive feedback. The composition of rumen microbial populations varies with diet, and these populations take time to adjust to dietary changes (Yokoyama and Johnson 1988). If, at one time, the animal rapidly consumed large quantities of the weed, the rumen microbial population may not have been able to adjust to the change or metabolize the plant allelochemicals, resulting in negative postingestive feedback and subsequent avoidance.

In a recent study with five invasive weed species, we increased the percentage of each weed in the diet of a sheep by 5% increments daily until the weed comprised 35% of its diet (adjusted sheep). Another sheep received only chopped grass hay (unadjusted sheep). We then collected rumen fluid from these two sheep, and fermented the fluid in flasks containing different proportions of the weed (weed:grass hay; 100:0, 50:50, 0:100) under conditions that simulated a rumen. With the 100:0 and 50:50 "diets", adjusted rumen microbial populations had greater microbial activity than unadjusted populations (Olson and Grindeland, unpublished data). This suggests that exposing animals to small populations of weeds, assuming the animals consume small quantities of the weed, will allow microbial populations to adjust to the weed. This may ensure greater consumption of the weed in the future.

## Offering nutrient resources to increase weed consumption

If increasing the consumption of weeds containing allelochemicals is desired, starving animals onto certain weeds may not be the answer. Nutrient deprivation often decreases the ability of the animal or rumen microbial populations to detoxify the compounds and thus increases an animal's toxic response (Boyd and Campbell 1983). Conversely, with some weeds, vitamins, minerals, amino acids and carbohydrates could be added to enhance the ability of herbivores to detoxify or tolerate plant toxins (Freeland and Janzen 1974, Conn 1979, Brattsten 1979, Boyd and Campbell 1983). Research and management opportunities exist to identify compounds that complex and inactivate allelochemicals in the diet (McNabb et al. 1993). A complete understanding of pathways that detoxify specific compounds can lead to supplementation programs that encourage, rather than coerce livestock into eating weeds containing allelochemicals.

## Offering anti-toxicants to increase weed consumption

Alternatively, if the avoidance is related to phytotoxic effects, anti-toxicants may be used to detoxify compounds in the weed. In concept, this is similar to "Bloat Guard" blocks for animals grazing alfalfa, but commercial "anti-toxicant" products have not yet been developed to increase the consumption of weeds. Polyethylene glycol increases the intake of foods with high concentrations of tannins, a secondary compound, but only if more nutritious alternatives are not available (Provenza, personal communication). Many weeds contain tannins. Activated charcoal, which adsorbs various plant allelochemicals such as terpenes, increases intake of sagebrush by sheep (Provenza, personal communication). Many weeds also contain various types of terpenes. Certain clays have the potential to bind with some toxicants (Smith 1992). Some organic compounds, or co-substrates including glucuronic acid, acetate, and sulfates, will conjugate with certain toxic compounds (Smith 1992). This increases the rate of excretion of the compound or renders it less toxic. Potentially, these co-substrates of detoxification could be added in feed, water, or a mineral block.

## Conclusions

The preceding examples illustrate how small ruminants with a predilection for consuming forbs have the potential to control weeds. Grazing weedy forbs and shrubs, particularly by small ruminants, help maintain a balance in the plant community. But, numbers of small ruminants continue to decline throughout western North America for various reasons. If we continue with single species grazing of large herbivores such as cattle or horses, a greater challenge is to find ways to encourage these large herbivores to consume weeds in greater quantities.

As resource managers, can we truly manipulate diet selection to stimulate the use of weeds by larger herbivores or to increase the use of weeds by small herbivores? Is there a magic answer with some yet-to-be-developed compound or genetically altered animal or rumen microbial population that will solve the "problem"? Yes, when fully developed these techniques may help us manage the problem, but we must remember the problem did not arrive overnight and it will not leave overnight. Further, most of our weed control techniques, including herbicides, biocontrol with insects or pathogens, revegetating with competitive desirable plant species, and altering diet selection, are aimed at addressing the "symptom" not the cause of the problem. Weed infestations are not "caused" by a lack of herbicides or by a lack of biocontrol agents. They are caused by a form of management that encourages their spread. Thus, we should identify ways to "manipulate" diet selection to control weeds, and simultaneously assess ways to "manipulate" our traditional management schemes to minimize the spread of weeds.

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# Behavioral Strategies for Coping with Poisonous Plants

James A. Pfister

## Abstract

**Poisonous plants are an integral component of most rangelands in the western U.S. Although domestic livestock losses can be severe, obviously most wild and domestic animals grazing on rangelands do not die of toxic plant ingestion. Grazing animals use several interrelated behavioral and physiological strategies to reduce the risk of poisoning: (1) avoid or reduce toxin intake through changes in diet selection; (2) select a mixed diet and dilute the toxin; (3) consume a toxin in a cyclic or intermittent fashion; (4) eject a toxin once eaten; (5) complex, degrade, detoxify, and (6) tolerate the toxin once eaten. A central tenet of the first 3 strategies includes postingestive consequences and aversive conditioning, whereby animals learn from the negative or positive consequences of eating particular forages. The last 3 strategies describe how animals handle toxins once consumed. When livestock reject toxic plants in favor of less toxic or nontoxic species, learning is usually involved. Domestic livestock losses attest that learning is not a perfect avoidance mechanism. Nonetheless, learning enables most livestock to survive grazing on ranges with poisonous plants. Domestic livestock are more often harmed by toxic plants than are wild ungulates, probably because many livestock losses result from human management errors that override coping strategies. Furthermore, wildlife survival is probably enhanced by increased capacity to tolerate or detoxify toxins relative to livestock.**

## Introduction

Poisonous plants have long been a topic for legends and scientific inquiry. The toxin is the plant compound responsible for the plant's effects, and the word is derived from the Greek word *toxikon*, or 'poison for arrows'. This paper is concerned, not with poisonous projectiles, but with plants poisonous to grazing animals. In the western United States, poisonous plants are ubiquitous on many rangelands, but domestic or wild ungulates grazing on rangelands do not usually succumb to poisonous plants. Although most survive, some obviously don't. Indeed, losses of domestic livestock to poisonous plants exceed $300 million per year (Nielsen et al. 1988), not including goats and horses. No figures are available for wildlife, but losses do occur (Fowler 1983). Economic impacts of toxic plants range from death and abortion to lost grazing opportunities (Table 1). Good range condition helps to reduce losses to some poisonous plants. Nevertheless, poisonous plants also kill or impair grazing animals on good condition rangelands because these plants are integral components of many rangeland communities, and at times are acceptable forages (e.g., larkspur, chokecherry, veratrum, water hemlock, oakbrush, pine needles, halogeton, greasewood). A partial list of important toxic plants is given in Table 2.

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Grazing animals use several behavioral and physiological strategies or adaptations to reduce the risk of poisoning. There are at least 6 strategies by which animals can avoid or reduce toxicity from plants: (1) avoid or reduce toxin intake through changes in diet selection; (2) select a mixed diet to dilute the effect of specific toxins; (3) consume a toxin in a cyclic or intermittent fashion to avoid permanent injury; (4) eject a toxin once eaten; (5) complex, degrade, or detoxify the toxin; and (6) tolerate the toxin once eaten. These categories are not mutually exclusive as there is substantial overlap. In general the first 3 strategies involve reducing or eliminating consumption of a toxin through behavioral changes, whereas the last 3 strategies deal primarily with how animals handle toxins internally when consumed. It is impossible to separate outward grazing behavior from the internal consequences of eating, because digestive consequences affect the animals' propensity to eat particular plants (Provenza et al. 1992, Forbes 1998). Most published work on grazing herbivores was conducted with domestic livestock, and this review will reflect that bias. Research on wildlife will also be discussed where information is available.

## Avoidance

It is clear that animals limit their consumption of poisonous plants at times (Table 3). How do animals

Table 1. Direct and indirect economic losses from poisonous plants related to production and off take from domestic livestock and wildlife

| ***Direct losses*** | ***Indirect losses*** |
|---|---|
| Death | Added fencing to restrict access |
| Wasting/reduced weight gains | Herding costs |
| Neurological incapacitation (horses) | Supplemental feeding |
| Abortions | Changes in grazing management |
| Weak/small offspring | Increased veterinary costs for treatment |
| Reduced fertility | Lack of immune response to vaccines |
| Birth defects | Lost opportunity to graze forage |
| Inability to sell/harvest animals | Lost nutrients in ungrazed forages |
| | Reduced land values |
| | Reduced value of grazing permits |
| | Herbicide costs for suppression |
| | Increased risk in overall enterprise |

Table 2. Major plant toxins, herbivores and body system(s) affected, and examples of plants containing the toxin.

| Toxins and subtypes | Animal Species Affected | Body System(s) Affected | Plants Containing Toxin | |
|---|---|---|---|---|
| | | | Common name | Scientific name |
| Alkaloids | | | | |
| Diterpene | Primarily cattle; wildlife unknown | Paralyzes muscles | larkspur | *Delphinium* species |
| Pyrrolizidine | Cattle, horses; deer | Liver toxin; photosensitization; wasting disease | groundsel | *Senecio* species |
| | | | houndstongue | *Cynoglossum officinale* |
| Steroidal (potato type) | Cattle, sheep, horses; wildlife unknown | CNS toxin; digestive tract | nightshades | *Solanum* species |
| Steroidal (veratrum type) | Sheep; mule deer unaffected | Birth defects; lung congestion | skunk cabbage | *Veratrum* species |
| | | | death camas | *Zigadenus* species |
| Piperidine | Cattle, sheep, horses; elk; presumably other wildlife also | CNS toxin; birth defects | poison hemlock | *Conium maculatum* |
| | | | lupine | *Lupinus* species |
| Quinolizidine | Sheep, cattle, horses; wildlife unknown | Respiratory paralysis; birth defects | lupine | *Lupinus* species |
| Indolizidine | Horses, cattle, sheep, elk, antelope, and possibly deer and other wildlife | Digestive, reproductive & CNS | locoweed | *Astragalus* and *Oxytropis* spp. |
| Glycosides | | | | |
| cyanide glycosides | Cattle, sheep; wildlife unknown | Inhibits cellular respiration | chokecherry | *Prunus* species |
| | | | forage sorghums | *Sorghum* species |
| | | | arrowgrass | *Triglochin* species |
| coumarin glycosides | Cattle; wildlife unknown | Vit. K deficiency | sweet clover | *Melilotus* species |
| cardiac glycosides | Cattle, sheep, horses; wildlife unknown | acute heart toxin | milkweed | *Asclepias* species |
| | | | foxglove | *Digitalis* species |
| saponin glycosides | Cattle, sheep; wildlife unknown | digestive system | cow cockle | *Vaccaria pyramidata* |
| | | | corn cockle | *Agrostemma githago* |
| nitropropanol | Cattle, sheep; wildlife unknown | Respiration; CNS damage | milkvetch | *Astragalus* species |
| Isoflavones | | | | |
| phytoestrogens | Sheep; quail, other wildlife unknown | Reproductive | clover | *Trifolium pratense* |
| | | | alfalfa | *Medicago sativa* |
| Oxalates | Sheep, cattle; wildlife unknown | Disrupts energy metabolism; possible hypocalcemia | halogeton | *Halogeton glomeratus* |
| | | | greasewood | *Sarcobatus vermiculatus* |
| | | | kochia | *Kochia scoparia* |
| Tannins | Cattle, horses, sheep; wildlife less affected | digestive system; kidney | oak | *Quercus* species |
| Terpenes | Cattle, sheep; bison also affected | CNS; reproductive system | ponderosa pine | *Pinus ponderosa* |
| | | | sagebrush | *Artemisia* species |
| | | | bitterweed | *Hymenoxys* species |
| | | | sneezeweed | *Helenium* species |
| Nitrates | Cattle, sheep; wildlife unknown | respiratory | pigweed | *Amaranthus* species |

Table 3. Examples from research studies in which animals have preferred less toxic or nontoxic plant species or populations compared to more toxic species or populations[1]

| Plant species | Toxin | Animal species |
|---|---|---|
| Sudangrass *Sorghum sudanense* | cyanide | cattle |
| Sorghum *Sorghum vulgare* | cyanide | sheep & cattle |
| Sericea *Lespedeza cuneata* | tannin | sheep |
| Reed canarygrass *Phalaris arundinacea* | alkaloid | sheep |
| Lupine *Lupinus angustifolius* | alkaloid | sheep |
| Crotalaria *Crotalaria spectabilis* | alkaloid | cattle |
| Sagebrush *Artemisia tridentata* | terpenes | sheep |
| Bracken Fern *Pteridium aquilinum* | cyanide[2] | sheep & deer |
| Blackbrush *Coleogyne ramosissima* | tannin | goats |
| Tall fescue *Festuca arundinacea* | alkaloid | cattle |

[1] Adapted in part from Laycock 1978; for references contact the author

[2] Bracken fern contains other toxic compounds, but the study involved cyanogenic glycosides

"know" which plants are poisonous? Grazing animals may innately detect and avoid plant toxins (i.e., genetic mechanisms). Alternately, herbivores may learn about plant toxicity through digestive consequences (Provenza et al. 1992).

## Innate avoidance

Herbivores use taste and odor to detect and avoid poisonous plants (Provenza et al. 1992). Sweet flavors in plants often indicate carbohydrates (i.e., calories), whereas bitter flavors hint that toxins are present (Garcia et al. 1974). Some argue that animals are genetically programed with knowledge about plant palatability, and for that reason animals are attracted to sweet flavors and repelled by bitter flavors (Owen 1992). This implies that even inexperienced grazing animals should avoid toxic plants (Fowler 1983) but, this does not appear to be the case for most interactions of herbivores with toxic plants. For example, naive animals are often most susceptible to poisoning (Provenza 1997). Grazing animals also eat some toxic plants with strong odors (e.g., pine needles) even when other forage is available (Pfister and Adams 1993). Furthermore, evidence of innate toxin recognition is lacking.

Many toxins supposedly taste bitter (e.g., alkaloids, saponins, cyanogenic glycosides), have offensive odors (e.g., terpenes) or provoke an astringent sensation when eaten (e.g., tannins). However, bitterness is not universally repellent (Glendinning 1994) and some toxins do not have a bitter taste (e.g., alkaloids; Molyneux and Ralphs 1992). Sheep (Arnold and Hill 1972), cattle (Pfister et al. 1996), and guinea pigs (Nolte et al. 1994) do not necessarily avoid bitter tastes, nor do sheep form stronger aversions to bitter than to sweet flavors (Launchbaugh et al. 1993). Furthermore, animals acquire preferences for bitter and sour flavors when consumption is followed by calorie enhancement even when these flavors were not initially preferred (Sclafani 1991). In fact, some foods, like coffee and chocolate, are highly desired by many humans precisely because of their bitter taste (Zellner 1991). It seems clear that animals are not, in the main, inherently deterred by the supposed bitterness or other detected quality of plant toxins.

## Learning through consequences

When grazing animals reject toxic plants in favor of less toxic alternatives (e.g., Table 3), learning is usually involved. Provenza (1995) recounted how goats introduced to blackbrush ranges initially ate current season's growth, yet within 4 hours goats shifted consumption to less nutritious older growth. Goats apparently avoided the more nutritious current season's growth because it contained a larger proportion of tannins that adversely affected the animals. If Provenza and colleagues had not observed the goats' initial diet selection, they would have continued to assume that goats never ate current season's growth.

Domestic livestock losses attest that learning is not a perfect avoidance mechanism (Provenza et al. 1992). However, learning is still a useful means by which most livestock survive grazing ranges with poisonous plants, as with larkspurs (Pfister et al. 1997). Wildlife survival, when interacting with toxic plants, is probably due primarily to other attributes such as tolerance or detoxification (Fowler 1983). Wild herbivores may not need to learn to avoid toxic plants if they usually suffer little harm (Nichol 1938).

How do animals learn which plants to eat and which to avoid? The answer lies in the concept of postingestive consequences (Provenza et al. 1992) and learned aversions (Garcia 1989) or preferences (Booth 1985). Provenza and colleagues have clearly shown the importance of aversive conditioning in diet selection (see Provenza, this volume), and these principles apply to the selection of toxic plants (Provenza et al. 1992, Provenza 1995, Howery et al. 1998). Four major types of learning are relevant to feeding strategies and toxic plants: (1) learning by offspring in the womb; (2) learning from mother; (3) social learning; and (4) trial-and-error learning.

**Aversive conditioning.** Postingestive consequences (or feedback) are signals from the gut to the brain telling the animal what effect the food is having; in the case of calories, the effect is positive; in the case of toxicity, the effect is negative (perhaps nausea or some other adverse feeling commonly termed malaise). Conditioned flavor aversions occur when negative feedback signals the animal that the ingested plant is having (or recently had) a negative (i.e., toxic) impact. When this occurs, the animal makes the unconscious association between plant flavor (taste and/or odor) and negative digestive feedback. In future encounters, the plant becomes less preferred by the animal (termed a hedonic shift) because of the past negative association. Flavor aversions occur subconsciously, but the sight and smell of the plant are inextricably linked with the negative feedback such that the plant is avoided in subsequent encounters. Thus, animals make diet choices that result from past experiences with the plant, both positive and negative. Positive feedback results in animals seeking out particular plants (e.g., "ice-cream plants"), whereas negative feedback causes animals to avoid specific plants (Provenza 1996).

Aversive conditioning has been shown with several plant toxins, including alkaloids, tannins, cyanogenic glycosides, terpenes, and glucosinolates (Provenza et al. 1992). Conditioned food aversions may be mild (i.e., temporary) or strong (i.e., permanent) depending on the toxin dose and when and how the toxin affects the gut and brain. The toxin must generally be sensed in the brain 4 to 12 hours after eating the plant for an aversion to occur, and stronger aversions are conditioned by a shorter delay between consumption and toxic effect. Therefore, aversions rarely develop if the toxin acts very slowly over days and weeks (e.g., pyrrolizidine alkaloids in senecio or indolizidine alkaloids in locoweed). Furthermore, the toxin must activate the emetic center in the brain that controls nausea and vomiting to condition an aversion. One cannot expect an aversion from toxins like strychnine that do not affect the emetic center. As will be discussed later, aversive conditioning may be employed to keep livestock from eating poisonous plants such as larkspur (Ralphs 1997) or locoweed (Ralphs et al. 1997).

**Learning in the womb.** Grazing animals may actually be born knowing something about which plants are "good" or "bad" because learning occurs while offspring are still in the womb. In humans (Mennalla and Beauchamp 1997), rats (Smotherman 1982a) and sheep (Nolte et al. 1992, Schaal and Orgeur 1992) *in utero* exposure to flavors in amniotic fluid may contribute to subsequent preferences for such flavors. Taste and odor aversions in young animals can also be conditioned *in utero* (Stickrod et al.1982, Smotherman 1982b). The impact of plant toxins eaten by pregnant animals may be very destructive to fetal development (Panter et al. 1992), but little is known about how toxins that pass the placental barrier influence subsequent diet selection in the offspring.

**Learning from mother: milk and model.** Learning from mother has a major influence in the selection of toxic plants, and can be indirect (through milk flavors) or direct (i.e., modeling). Mothers' influence can occur indirectly because of tastes passed through milk to nursing young. Experience with a strong flavor in milk predisposes lambs to eat more of a food with that flavor later in life (Nolte and Provenza 1992). Many toxins can be passed to the nursing young via milk (Panter and James 1990), but it may be difficult to avert suckling animals to mother's milk from toxin-induced illness because milk is usually a very safe food.

Young animals learn from their mother's example to eat preferred foods and avoid foods with toxins (Provenza et al. 1992). Using lithium chloride as an artificial toxin, Provenza and colleagues found that lambs learned to avoid novel foods that their mothers were conditioned to avoid (Mirza and Provenza 1990, Thorhallsdottir et al. 1990a, b). Conversely, animals learn what to eat by mimicking their mother, even if the plant is toxic. Nursing calves began to eat substantial quantities of locoweed (Pfister unpublished observations) and low larkspur (Pfister and Gardner 1999) on the same day as their grazing mothers, suggesting that calves mimicked their mothers' diet. Mother's influence does, however, have its limits. Young lambs avoided a plant paired with a toxin whether or not their mother ate the plant (Provenza et al. 1993). Calves that initially ate larkspur with their mothers sharply curtailed consumption a few days later (Pfister and Gardner 1999), perhaps because of adverse feedback (Pfister et al. 1997). Though mother is an important source of information for young animals, postingestive consequences are probably more important (Provenza et al. 1993).

**Others social influences.** Dietary social facilitation is the influence one grazing animal exerts on the diet selection of another. Domestic livestock, in particular, are social animals and they frequently observe one another and modify their diet selection based on what their grazing companions are eating (Thorhallsdottir et al. 1990a, Ralphs et al. 1994). Cattle eating locoweed (Ralphs et al. 1994) and larkspur (Lane et al. 1990) have influenced other animals to eat these toxic plants.

**Learning by trial-and-error.** Grazing animals learn about poisonous plants through cautious sampling of both familiar and novel foods (Provenza et al. 1992). As toxic plants grow and mature, they often change in nutritive composition and toxicity (Pfister et al. 1994). Because the quality and quantity of forage often varies both spatially and temporally, animals may be highly motivated to sample foods and monitor food resources (Wang and Provenza 1997, Day et al. 1998). Sampling is however an imprecise process and errors made while sampling toxic plants may be debilitating or lethal (Provenza et al. 1992). Trial-and-error learning is risky, but sampling usually involves eating only small amounts of a food, so the potential for toxicity is reduced.

One risk-reducing behavior analogous to cautious sampling is neophobia, in which animals are reluctant to eat much of novel foods (Burritt and Provenza 1989, 1991; Provenza et al. 1995). Animals may be particularly reluctant to eat novel foods with strong flavors (Augner et al. 1998). When grazing animals experience negative feedback from toxins or positive feedback from sampling foods, they usually associate such feelings with novel rather than familiar flavors (Burritt and Provenza 1989).

## Mixed Diets

Grazing animals usually select diets composed of many plant species. This may simply reflect the continuous sampling mode of herbivores (Day et al. 1998), or it may also reflect attempts to limit ingestion or impact of plant toxins (Provenza 1996, Launchbaugh 1996). A basic principle of toxicology is "the poison is in the dose"- in other words, many toxins exhibit a dose-response curve, where little or no toxicity is displayed at low doses and increasing doses produce more severe symptoms. Plants with toxins also contain varying kinds and amounts of nutrients. Thus, diet selection with toxic plants is always a tradeoff between nutrition and toxicity (Freeland and Janzen 1974, Freeland 1991, Provenza 1996). Freeland and associates demonstrated that animals can decrease the toxic effects of a single plant by eating a mixture of plants containing different toxins (Freeland et al. 1985, Freeland and Saladin 1989). Mule deer were able to eat about twice as much sagebrush and juniper together than when each was fed alone (Smith 1959), suggesting that the ruminal microflora in deer could handle plant secondary compounds from different sources better than from a single source. Besides positive feedback from nutrients, learning may be facilitated by a "medicine effect," wherein the negative effects of ingesting one plant may be ameliorated to some extent by eating another plant. Eating a mixed diet may therefore be the equivalent of self administration of antidotes (Freeland 1991).

Not only is the amount eaten important, but ingestion rate may also be important to allow sufficient time for detoxification to occur (Foley et al. 1995, Foley et al. 1999). Detoxification occurs through several pathways depending on the specific toxin and animal (Smith 1992). Thus, mixing foods in a nonrandom manner facilitates consumption of more food, including foods with toxins (Freeland 1991).

## Cyclic and Intermittent Consumption

Grazing animals can avoid toxicoses by limiting their consumption of a specific toxic plant each day. Alternatively, animals might vary toxic plant consumption from day-to-day to limit potential cumulative effects of specific toxins. Grazing studies with tall larkspur suggested that consumption above 25 to 30% of the diet for 1 or 2 days led to reduced consumption on subsequent days (Pfister et al. 1988). In pen studies, cattle responded to larkspur dosing with distinct cycles of food intake such that 1 to 3 days of higher consumption was followed by 1 to 3 days of reduced consumption (Pfister et al. 1997). We noted that larkspur had a dose-response threshold of 14 to 18 mg toxic alkaloid/kg body weight, and periods of reduced consumption below this threshold probably allowed animals time to recover from the larkspur-induced illness. Sheep adjusted intake of LiCl according to the toxin concentration in foods when the concentration varied greatly (Wang and Provenza 1996, Launchbaugh et al. 1993).

How might grazing animals become temporarily averse to a single plant and vary consumption of this plants? First, when illness follows a meal dominated by a toxic plant, grazing animals apparently can make the connection between the dominant food and the subsequent illness. Goats acquire an aversion to the food eaten in the greatest amount when poisoning follows a meal of novel foods (Provenza et al. 1994). In the case of larkspur, cattle eat large amounts during some grazing bouts (Pfister et al. 1988). Second, the strength of the plant flavor may be important (Augner et al. 1998). If a plant flavor is strongly correlated to the amount of toxin, grazing animals can regulate intake of the plant based on the strength of the flavor (Launchbaugh et al. 1993). Plus, re-experiencing the flavor during rumination may help the animal associate that flavor with illness that may last for several hours after ingestion. Third, previous experience with a plant, and certainly prior illness associated with eating a toxic plant, may signal animals to stop eating the plant. Lambs avoid the food that made them ill in the past when poisoning follows a meal of several foods (Burritt and Provenza 1991). Finally, limited intake of toxic plants may result from temporary aversions. Provenza (1996) has proposed that varied diets result from temporary aversions in which excesses of toxins and nutrients likely interact to partially regulate sampling and diet selection within a meal.

Why do animals return to eat a plant that has been aversive in the past? Animals begin sampling forages because ingestion of small amounts usually causes no or few negative effects. In addition, many toxic plants contain substantial nutritional value (larkspur: Pfister et al. 1989; locoweed: Ralphs and Molyneux 1989) and provide positive digestive feedback. Both locoweed and plains larkspur contain more than 20% crude protein early in the spring (Pfister unpublished observations). Eating some of a toxic plant provides needed nutrients with little toxicity, but increased consumption results in heightened adverse effects because of the dose-response characteristic of many toxins. Partial avoidance or partial preference (Day et al. 1998) for a toxic forage would likely result in a grazing animal eating variable but increasing quantities of the forage, until negative feedback (or alternatively excess of nutrients; Provenza 1996) became sufficiently strong to temporarily drive the animal "off" the feed (e.g., larkspur; Pfister et al. 1997). Each time a toxic forage is eaten without negative consequences, the aversion is weakened and will eventually vanish without additional negative feedback (Lane et al. 1990, Ralphs and Stegelmeier 1998).

## Eject the Toxin

Once a toxin is eaten, it is in the animals best interest to quickly get rid of it. This usually occurs through vomition or diarrhea (Kingsbury 1983). Although we don't normally think that ruminants or horses vomit, this reflex is common in mammals (except rodents). Sheep, goats, and cattle can and will vomit in response to eating toxins (Mullenax et al. 1966, Buck et al. 1966, Oehme and Barrett 1986). In livestock, vomition is problematic because animals can aspirate the gut contents into their lungs, which can be fatal. Vomiting in ruminants is apparently sensitive to dose, as some toxic plant doses resulted in vomiting, whereas higher doses produced severe retching (Mullenax et al. 1966). Horses probably do not vomit except when near death, but commonly experience diarrhea (Oehme and Barrett 1986). Diarrhea aids in rapid elimination of toxins from the gut before absorption. In some episodes of diarrhea, there is a decrease in intestinal motility, thus reducing the absorption of the toxin through reduced gut motility (e.g., cyanide).

## Complex, Degrade, or Detoxify

Much has been written about animals' abilities to detoxify substances in plants. For excellent reviews see Freeland and Janzen (1974), Allison (1978), McArthur et al.(1991), Smith (1992), Launchbaugh (1996), and Cheeke (1998). Animals may complex toxins in the mouth and/or the gut, degrade the toxin in the gut via microbial action, or absorbed toxins may be detoxified by various reactions in either the stomach wall or the liver. Without these detoxification systems operating effectively, animals would probably not be able to eat any plant toxins (Jason and Murray 1996).

## Complex in mouth or gut

Complexes formed in the mouth may provide protection from effects of plant toxins. Animals that have evolved eating tannin-rich shrubs secrete proline-rich proteins (PRPs) in their saliva which bind to tannins (Robbins et al. 1991). Interestingly, salivary proteins from generalist herbivores like bear and deer bind several tannins, whereas proteins from specialist feeders like moose and beaver bind only the tannin most commonly found in their diet (Hagerman and Robbins 1993). Tannin-containing diets did not induce PRP production in sheep (i.e., grazers), whereas deer (i.e., browsers) previously exposed to tannins produced saliva with PRPs when reexposed. The saliva-tannin complex essentially inactivates tannins and reduces absorption and toxic effects.

Other activity in the mouth and nose may facilitate survival when eating toxic plants. Cheeke (1998) speculated that detoxification activity in the mouth might allow animals to ingest some plants with very noxious odors, such as sagebrush. Many terpenes are lost through volatilization during chewing as when pygmy rabbits eat sagebrush (White et al. 1982). Increased chewing and ruminating has also been associated with increased sagebrush consumption in sheep (Fraker and Launchbaugh, abstract in this volume). Further, nasal tissue is capable of detoxifying some toxins through induction of the P450 enzyme system. Goats and sheep will eat pyrrolizidine alkaloid-containing plants such as tansy ragwort which is toxic to larger animals such as cattle. The inducible presence of a nasal detoxification system might facilitate the consumption of the noxious-smelling tansy ragwort by goats and sheep (Cheeke 1998).

Some plant toxins are bound (sequestered) with other eaten material to prevent toxic actions (Smith 1992). Geophagy (i.e., eating soil) is common among ungulates (Jones and Hanson 1985). Despite the widespread belief that mineral licks are sought by animals for their sodium content, it is more likely that other minerals (e.g., Ca) are more important (Jones and Hanson 1985). An early description of an Illinois mineral lick described it as "soft, salt[y] and sulphurous" (Jakle 1969). Detoxification using sulphur is metabolically expensive and sulphur is usually in short supply (Brattsten 1979, McArthur et al. 1991). Thus, animals might practice geophagy to enhance sulphur in the diet. Moreover, mineral licks are often high in various clays (Jones and Hanson 1985) and some clays naturally bind to various toxins (Smith 1992). Therefore, geophagy may help deactivate plant toxins.

## Gut degradation by rumen microbes

Ruminants may have a significant evolutionary advantage over nonruminants when dealing with plant toxins because of their large forestomach that dilutes and may degrade or detoxify certain plant toxins (Table 4; Oehme and Barrett 1986, Smith 1992). The nearly neutral pH of the rumen environment may modify the plant toxin, or by virtue of the large volume (60-70 gal) the toxin may be immediately diluted. Of great significance for ingestion of toxic plants is the massive numbers of microbes in the rumen, where millions of microbes may be found per milliliter of rumen contents. Certain microbes are capable of degrading or detoxifying some plant toxins. In some cases, however, rumen microbes can convert innocuous substances into toxic compounds (Table 4, Allison 1978). Generally for a rumen microbe to degrade a toxic plant compound, utilization of the compound must yield energy for the microbial population, and the microbial population must inhabit a particular rumen niche that allows it to survive when the toxin is not present, and expand the population rapidly when the toxin enters the rumen (Weimer 1998).

Once plant toxins are absorbed from the gut into the blood, they are often transported to the liver (hepatic tissue). All nonpolar foreign compounds are potentially toxic. Therefore, one of the first tasks for the body is to change these nonpolar (i.e., lipid-soluble) substances to polar compounds (i.e., water-soluble) so they can be excreted in urine. If left unchanged, they would ultimately poison the body. Therefore, the liver contains enzyme systems that metabolize (or alter) nonpolar compounds so that they can be excreted. Although most of the metabolic conversion of plant toxins occurs in the liver, cells in the kidney, intestinal mucosa, lungs and skin may also be involved (Zimmerman 1978). There are several advantages to liver detoxification vs. microbial degradation (Foley et al. 1999): (1) liver enzymes are under genetic control, so some protection can be passed to offspring; (2) there is much variability in enzyme system activity, so these enzymes can handle a variety of toxins; and (3) liver enzymes are rapidly inducible (i.e., can be jump started and the amount of enzyme elevated within hours if necessary).

The nutritional state of the animal and dietary nutrients are major factors in toxin intake, as detoxification requires nutrients and energy to alter toxins and maintain acid-base equilibrium (Jessop and Illius 1997, Foley et al. 1999). For example, low protein diets decrease detoxification activity in the liver (e.g., cytochrome P450 enzyme system; McLean and McLean 1969). In the case of tansy ragwort alkaloids, pretreatment of animals with the alkaloid jacobine results in elevated detoxification activity of pyyrolizidine alkaloids (Miranda et al. 1980). Antioxidants that promote detoxification also provide protection against bitterweed (Cheeke 1998).

## Tolerance

Some species or individuals are more tolerant to toxic plants than others. The enzymatic ability of the liver varies greatly between animal species. For example, sheep can tolerate more pyrrolizidine alkaloides (PAs) than cattle. Part of the detoxification occurs in the gut by microbes (Craig et al. 1992), but liver metabolism is more important (Cheeke 1994). It is also possible that differences in activity at receptor sites account for tolerance in some animals. Likewise, it took 5 times more tall larkspur to poison sheep compared to cattle (Olsen 1978), and the tolerance of sheep was thought to be due to differences in ruminal metabolism. Recent studies indicate, however, that sheep nicotinic acetylcholine (nAch) receptors bind the larkspur toxins much less avidly than do cattle nAch receptors, thus accounting for the species difference (Stegelmeier , unpublished data).

Microbial adaptations in the gut, detoxification in the gut wall or liver, and receptor site responses can be induced by consumption of plant toxins. Eating small quantities of some plant toxins may thus provide an opportunity for the animal's system to adapt to the toxin. Nonetheless, tolerance does not develop to all toxins. The effects of many toxins are cumulative (e.g., bracken fern, pyrrolizidine-alkaloid containing plants), and animals get progressively more poisoned as they continue to ingest the material.

Very little is known about tolerance of wildlife species for plant toxins (Table 5). Because of their experience and history, native wildlife on rangelands are

Table 4. Examples of ruminal or postruminal detoxification and toxification of plant secondary compounds

| Toxin | Plant Species | Degradation mechanism |
|---|---|---|
| **Detoxification: degradation of toxins by microbes and postruminally** | | |
| Oxalates | halogeton<br>greasewood | oxalic acid metabolized by *Oxalobacter formigenes*; ruminants can adapt to remarkably high concentrations |
| Cyanide | chokecherry<br>sorghum | cyanide oxidized by sulphur donors to yield thiocyanate |
| Pyrrolizidine alkaloids | senecios<br>houndstongue | Possibly ruminal degradation in sheep and goats, more likely high rate of pyrrole conjugation in liver. |
| Mimosine | *Leucaena* | mimosine converted to toxic DHP; the bacteria *Synergistes jonesii* metabolizes DHP to nontoxic compound |
| Estrogens | clover | cattle may metabolize estrogens more efficiently than sheep; or cattle may have different receptors than sheep |
| Miserotoxin | milkvetch | several ruminal bacteria degrade NPOH; diet dependent; reduced absorption of modified NPOH from gut |
| Essential oils | fir trees<br>sagebrush | ruminal degradation after adaptation |
| **Toxification: production of toxins by microbes or postruminally** | | |
| Pyrrolizidine alkaloids | senecios<br>houndstongue | alkaloids metabolized in liver to toxic pyrroles, especially in cattle; small ruminants much less affected (see above) |
| Nitrates | forage sorghum | nontoxic nitrates reduced to toxic nitrite in rumen; adaptation in the rumen can occur quickly and decrease nitrite toxicity |
| Miserotoxin | milkvetch | hydrolysis and release of NPOH, followed by enzymatic oxidation to very toxic NPA |
| Cyanide | serviceberry | hydrolysis of glycoside results in release of toxic cyanide |
| Estrogens | clover | sheep more susceptible; may have more sensitive receptors, may metabolize isoflavones to more toxic equol |

thought to be more tolerant of toxic plants than livestock introduced into pastures with poisonous plants (Arnold and Hill 1972, Laycock 1978). When offered various plants, deer avoid many, but not all, toxic plants (Nichol 1938, Longhurst et al. 1968, Jessop et al. 1986) and those that they do eat may do little harm (Nichol 1938).

## An Addictive Proposition

Addiction generally refers to an animal's craving for a particular plant or compound. Psychologists use the term "self-administration" to describe the behavior of animals seeking a particular plant or substance due to positive reinforcement (i.e., a chemically-enhanced sense of well being in the pharmacological sense, not the nutritive sense). Siegel (1979) identified 122 well-documented cases where mammals had self-administered a plant for CNS stimulation; most of the animals were herbivores (41% domestic and 59% feral). There have been numerous accounts of addiction in livestock grazing on range plants. Many alkaloid-containing plants have been regarded as addictive (Siegel 1979): buttercup, nightshade, laurel, rhododendron, and oak. Panter (personal communication) related that pigs fed fresh poison hemlock apparently became addicted to the flavor. The most famous of the "addictive" plants is locoweed (Lewin 1931). The German toxicologist Lewis Lewin (1931) described livestock addiction to locoweed by declaring that "animals refuse to take any other kind of food and greedily seek to procure their old fodder, like the morphinist his morphia." He also described animal addictions to the Australian plant *Swainsona*, long before it was known that *Swainsona* and locoweed contain the same toxin, swainsonine. Marsh (1909) also noted that locoweed was addicting to various animals, including mules, pigs and antelope.

Are addictions important in ingestion of toxic plants? It is likely that animals sometimes self-administer toxic plants for the pharmacological effects (Siegel 1979). Is locoweed addictive? Ralphs et al. (1990) reported that dried, ground locoweed was not addictive, but animals did habituate or become accustomed to eating the plant material. Many drugs (and all plant toxins are drugs) can have positive pharmacological effects but not cause addiction (Marinelli et al. 1998). Dose also is important, as drugs like methamphetamine can provide positive reward at low doses, and be aversive at higher doses (Cabib et al. 1996). Presently there are no clear answers about the addictive or rewarding capabilities of locoweed or other toxic plants. Positive reinforcement would increase the probability that animals continue to eat toxic plants under some circumstances.

Table 5. Examples of wildlife species in the U.S. where the animals apparently tolerated or detoxified the toxin once ingested, or alternatively, cases where intoxication resulted from ingesting a poisonous plant. In virtually all cases, the mechanism(s) is not known.

| Animal Species | Toxic plant | |
|---|---|---|
| | Scientific name | Common name |
| **Tolerate or Detoxify** | | |
| Mule deer | *Astragalus* spp. | locoweed |
| Mule deer | *Pteridium* spp. | bracken fern |
| Mule deer | *Psoralea* spp. | elk clover |
| Mule deer | *Artemisia* spp. | sagebrush |
| Black-tailed deer | *Pseudotsuga menziesii* | Douglas fir |
| Black-tailed deer | *Senecio jacobaea* | tansy ragwort |
| White-tailed deer | *Kalmia latifolia* | laurel |
| White-tailed deer | *Rhododendron maximum* | rhododendron |
| Pronghorn antelope | *Astragalus emoryanus* | peavine |
| Pronghorn antelope | *Senecio longilobus* | threadleaf grounsel |
| Pronghorn antelope | *Psilostrophe tagetina* | woolly paperflower |
| Pronghorn antelope | *Artemisia nova* | black sagebrush |
| Pronghorn antelope | *Artemisia tridentata* | big sagebrush |
| Elk | *Pinus ponderosa* | ponderosa pine |
| Moose | *Amelanchier* spp. | serviceberry |
| Moose | *Prunus* spp. | |
| **Intoxicate** | | |
| White-tailed deer | *Sorghum vulgare* | sorghum |
| White-tailed deer | *Crotalaria spectabilis* | crotalaria |
| Pronghorn antelope | *Fluorensia cernua* | tarbush |
| Pronghorn antelope | *Prunus* spp. | chokecherry |
| Pronghorn antelope | *Astragalus* spp. | locoweed |
| Sika deer | *Pinus banksiana* | jack pine |
| Elk | *Oxytropis sericea* | whitepoint locoweed |
| Elk | *Conium maculatum* | poison hemlock |
| Bison | *Pinus ponderosa* | ponderosa pine |
| Feral horses | *Oxytropis* spp. | locoweed |

## Management Implications

### Prospects for and problems with aversive conditioning

Many livestock producers are interested in using aversive conditioning to reduce domestic livestock losses to some poisonous plants (e.g., larkspur, locoweed, pine needles). As detailed by Ralphs and Provenza (1999), it is relatively easy to avert an animal to some poisonous plants using the emetic drug, lithium chloride (LiCl). Procedurally, livestock are placed into a corral in small groups, fasted for 12 to 48 hrs, offered freshly-harvested plant material, and observed to verify that they have eaten at least a few bites of the plant. As quickly as possible, the animals are given a dose of LiCl mixed with water (for cattle: 200 mg/kg; for sheep: 150 mg/kg) via a stomach tube. The LiCl acts quickly to make the animal nauseous. Thus, the animal will associate the taste of the plant with the illness and avoid the plant in future encounters. Averted cattle have avoided tall larkspur (Ralphs 1997), locoweed (Ralphs et al. 1997), and pine needles (Pfister 1999) in pen and field studies.

There are several potential pitfalls to using this technique (Ralphs and Provenza 1999). The most serious concern is that averted animals *must* be grazed separately from non-averted companions, or the aversion will be extinguished by the influence of social facilitation (Lane et al. 1990). The aversion is more persistent if animals are naive to the target plant; experienced animals can be averted, but it may take several pairings of taste and illness (Ralphs and Provenza 1999). An aversion conditioned to one plant species or form of the plant may not be generalized to another. For example, cattle averted to one species of larkspur did not avoid another species when the plants grew together (Ralphs, unpublished observations). Cattle averted to green pine needles extinguished the aversion after eating grass mixed with dried needles (Pfister 1999). Partial or temporary aversions will not be effective on rangelands (e.g., Houpt et al. 1990) as only complete avoidance will persist over a relevant time scale (i.e., months or years; Lane et al. 1990, Ralphs and Stegelmeier 1998, Pfister 1999).

Averting large numbers of animals requires extraordinary efforts by livestock producers (Ralphs and Provenza 1999). Producers may begin by averting only replacement heifers, but these animals will require special grazing management consideration thereafter. There is considerable stress placed on averted animals from the extensive fasting that may be required to induce initial consumption of a novel plant. Additional stress is placed on averted animals from the 2 to 3 day illness induced by LiCl, including profuse diarrhea and weight loss. Averting lactating cows may be problematic because of potential impacts on the calves. Overdosing or mishaps when dosing LiCl can be fatal to cattle. Nonetheless, producers with substantial and sustained losses, or those with small herds, should consider aversive conditioning as part of an overall solution to poisonous plants.

## Other implications of social facilitation

Social facilitation has important implications for management of grazing animals, even if livestock producers are not involved in aversive conditioning. Grazing animals eating toxic plants can influence either their calves or other companions to eat the plant. Young animals may be especially prone to follow their mother because of their close social proximity, tendency to mimic mother, and flavors experienced in the milk. Grazing animals with a proclivity to eat toxic plants should be identified and removed from the herd in some circumstances. Some producers in New Mexico with locoweed-infested pastures have systematically, over the several years, removed any cow from their herds seen eating locoweed, before she either becomes intoxicated or influences her calf or companions to eat locoweed. This "loco pull" strategy, combined with a recuperation period (if needed), has proven to be a better economic choice than doing nothing, or selling noticeably poisoned animals (Torell et al. 1999). Of course, this approach will not work with all toxic plants, but is worth considering for plants with chronic (i.e., slow) toxicity such as locoweeds, pine needles, groundsels, and snakeweed.

## Manipulating diet selection- for good or for ill

It is axiomatic that producers can sometimes reduce ingestion of poisonous plants by maintaining rangelands in good forage condition and avoid even temporary overutilization of ranges. Many toxic plants are not highly preferred when offered in a mix with other desirable forages (Taylor and Ralphs 1992). Even if animals eat small amounts of many poisonous plants, they will suffer few ill effects if other nontoxic forage makes up the majority of their diet. Taylor and Ralphs (1992) documented how proper grazing management, stocking rates, and mixed species grazing can decrease losses to poisonous plants in Texas. Even so, the more intensive the grazing management practices, the greater the likelihood for error, and management errors may contribute substantially to losses of domestic livestock. Producers in northern Utah graze cattle each summer on high elevation ranges in the Raft River Mountains. For many years, the producers used a rest rotation grazing system, wherein 3 pastures were grazed in sequence, and 1 pasture was rested each summer. Range condition improved yet annual losses to locoweed exceeded 20% (Ralphs et al. 1984). Based on observations that most consumption of locoweed occurred during August (i.e., after flowering), the grazing season was cut back from 71 to 47 days, while increasing cattle numbers, and the grazing system was altered to a Merrill 3-herd, 4- pasture system (Ralphs et al. 1984). These simple changes altered diet selection, as cattle were no longer forced to select locoweed, and shortened the exposure to locoweed when it was most palatable. As a result, yearly losses declined to about 3%.

Animal managers should be cautious about exposing naive animals to unfamiliar rangelands with toxic plants. Animals that are driven or trucked into a pasture may be hungrier or thirstier than normal, and may then accept toxic plants they would otherwise reject. As many as 1,200 sheep were lost at one time when hungry bands were released into halogeton-infested rangelands. Ironically, sheep can tolerate large amounts of the toxic oxalates if given time for ruminal adaptation. Naive animals placed in strange surroundings will probably reduce intake (i.e., neophobia) and increase exploratory behavior (Provenza 1997). Because most plants may be unfamiliar, grazing livestock are likely to increase their intake of toxic plants, and losses may be severe.

Nutritional stress may contribute to losses from poisonous plants. Animals that are not well nourished may be less able to detoxify plant toxins, thus the threshold for a lethal dose may decrease. Further, diet selection may expand to include some less palatable toxic plants when livestock are undernourished or hungry. Malnourished livestock may learn to eat less of a plant toxin if the adverse postingestive consequences are magnified by poor body condition and decreased detoxification abilities (Launchbaugh 1996). However, because an animal in poor body condition may have a lower threshold for a toxin, the initial exposure may kill the animal, before learning can occur.

Animals' perceptions of toxic plants differ when starved or deprived, as hungry deer eat some toxic plants that are rejected when forage is sufficient (Longhurst et al. 1968), and lambs are less discriminating when hungry (Wang and Provenza 1996). Nonetheless, pen-fed deer will starve before eating some toxic plants (Forbes and Bechdel 1931). Grazing livestock, when hungry, will also eat toxic plants that they reject in other circumstances (Merrill and Schuster 1978). As many poisonous plant researchers can attest, it is also common for pen-fed livestock to starve before eating some plants that are suspected of being toxic (Kingsbury 1983, Pfister personal observations). Hungry cattle ate progressively less larkspur as rumen fill decreased, suggesting that hunger *per se* provided little motivation to eat larkspur (Pfister et al. 1988). Further, poorly-fed animals may be more susceptible to some toxic effects (James et al. 1975).

## Supplementation

Strategic supplementation of limiting nutrients may alleviate some toxic plant problems. The supplement can provide nutrients (e.g., protein) that will change diet selection, and further provide nutrients to enhance detoxification capabilities. If livestock show a pattern of selecting a particular toxic plant during a portion of the grazing day, offering a supplement at that time of day can disrupt grazing behavior (Adams 1985) and possibly reduce toxin intake.

Several dietary additives can potentially ameliorate the adverse effects of tannins or terpenes, including polyethylene glycol (PEG), activated charcoal, and calcium hydroxide. PEG has a high binding affinity for tannins, and has been shown to increase intake of tannin-rich forage (Silanikove et al. 1994). Intake of tannin-rich foods is probably increased by PEG because binding the tannins with PEG may alleviate adverse postingestive consequences such as lesions in the gut. Activated charcoal has recently been shown to increase intake of terpene-rich bitterweed (Scott, unpublished). Further, activated charcoal fed to lambs increased intake of big sagebrush by 40% compared to control lambs (Banner et al. 1999). A supplemental ration containing 10 to 15% calcium hydroxide has been used with some success to reduce oak toxicity to ruminants (Dollahite et al. 1966).

## Conclusions

Most domestic or wild ungulates that graze on rangelands with poisonous plants do not succumb to these plants. Animals are able to cope with poisonous plants using both behavioral and physiological adaptations. Behavioral mechanisms converge on postingestive feedback and aversive conditioning, as animals learn which plants cause illness. Physiological mechanisms center on detoxifying plant compounds in the gut by rumen microbes or in the liver through enzymatic reactions that allow toxins to be excreted. Domestic livestock are more often made ill or killed by toxic plants than are wild ungulates, probably because wild animals have more developed avoidance or detoxifying capabilities than do livestock. Finally, some domestic livestock and many wildlife losses to poisonous plants result from human interventions that override coping strategies.

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# Behavioral Approaches For Limiting Depredation by Wild Ungulates

## Dale Nolte

## Abstract

**Wild ungulate foraging activities often negatively impact desirable resources, particularly where animal population densities are high. Agricultural crops suffer economic damage and natural ecosystems are altered. Various approaches to alter foraging behaviors are presented. Successful manipulation usually involves restricting ungulates access to a resource, encouraging animals to avoid an area, altering resource availability, or by reducing the desirability of the resource. Exclosures are probably the most effective means to reduce depredations. Ungulates also avoid areas that appear threatening. Habitat modification to reduce damage generally requires a reduction in resources to encourage animals to move out of an area, or an increase in resources to limit the use of the planted crop. Repellents are applied to plants to render the plant less attractive to foraging animals.**

## Why Manipulate Wild Ungulate Behavior

Wild ungulates (e.g., *Odocoileus* spp., *Cervus* spp.) occur across the United States and provide many desirable recreational and aesthetic opportunities. People generally enjoy watching these native species exhibiting their "natural" behaviors. Why then would anyone want to alter wild ungulate behaviors? Unfortunately, their foraging activities, particularly where population densities are high, often negatively impact desirable resources. These resources range from a homeowner's ornamental shrubs to valuable agricultural crops to native plant communities.

Deer and Elk damage a variety of grain crops, forage crops, vegetables, fruit trees, nursery trees, and ornamentals (Craven and Hygnstrom 1994). Beyond the immediate browsing damage, there are often residual damages, such as future yield reductions or growth deformities. Expanding ungulate populations are also a widespread detriment to reforestation efforts in the Pacific Northwest (Rochelle 1992). Ungulate browsing causes growth suppression and regeneration delays, as well as mortality among seedlings that are repeatedly browsed or pulled out of the ground (Crouch 1976, Tilghman 1989).

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Wild ungulates also thwart efforts to improve habitat quality. Considerable resources are currently being expended to establish native plants to increase forest diversity, improve riparian areas, re-vegetate disturbed sites, restore endangered or threatened plants, or to create wildlife habitat. Ungulates can be extremely detrimental to a project, particularly if animals make use of the plantings before the seedlings are well established or if use is severe. Interspersed western red-cedar (*Thuja plicata*) can add diversity to a forest stand or, when encountered by wildlife soon after planting, add diversity to an animal's diet. Habitat projects targeted to provide wildlife cover in ten years can be quickly converted to a meal supplement by a herd of migratory elk.

Natural ecosystems are being altered by high populations of ungulates (Stromayer and Warren 1997). Over browsing by herbivores can severely reduce seed production, plant establishment, and plant vigor and survival (Case and Kauffman 1997). Deer browsing has significantly impacted wildlife habitat in some northeastern forests by inhibiting the regeneration of stands or by altering tree species composition of regenerating stands (Curtis and Rushmore 1958, Brehand et al. 1970, Horsley and Marquis 1983). Under-story habitat changes have affected the presence of some bird species (DeGraaf et al. 1991). Wild ungulates have delayed the recovery of some riparian species following the removal of cattle (Case and Kaufman 1997). Ungulates also are reported to be responsible for changing forest regeneration in Europe (Motta 1996, Ammer 1996). There is an increasing concern regarding the impact of expanding deer populations on British woodland vegetation (Mitchell and Kirby 1990, Ratcliffe 1992, Kay 1993), and the concurrent indirect influences on invertebrates (Pollard and Cooke 1994). Habitat responses to grazing and browsing pressures also directly and indirectly affect other vertebrates and the future survival of ungulates themselves (Putman 1996).

Given these potential problems, resource managers may consider manipulating ungulate behavior to reduce depredation losses. Various approaches to alter behaviors are presented in this paper.

## Manipulating Behaviors

Problems induced by ungulates are invariably linked to foraging activities. Understanding "normal" activities, physical restrictions, and the ontogeny of dietary behaviors is beneficial when trying to alter problematic behaviors. The literature on wildlife is replete with observations of dietary activities and, to a lesser extent, the physical requirements and nutritional needs of wild animals. The ontogeny of dietary behaviors is reviewed by Provenza et al. (1998), Provenza and Launchbaugh (this volume) and others in this symposium.

Mechanisms governing the foraging behavior of wild ungulates are most likely similar to those of domestic ungulates. Deer acquire the anticipated responses when submitted to classical (Henke 1997) or operant (Pollard et al. 1994) conditioning (McSweeney this volume). Prior foraging experiences influence the food selection and searching behavior of deer (Gillingham and Bunnell 1989), and the initial dietary behavior of ungulate offspring can be learned from their mothers (Edwards 1976). Alternatively, Spalinger et al. (1997) suggest that food selection by white-tailed deer (*Odocoileus virginianus leucurus*) is largely an innate behavior, and that social learning would be maladaptive or detrimental to the animal. Instead of social learning, herbivores should rely on mechanisms that enhance gustatory or olfactory detection that permits an evaluation of forage quality (Spalinger et al. 1997). Regardless, wild ungulates have demonstrated a plasticity in their dietary behaviors which permits them to adapt to environmental conditions; a necessary requirement for behavior manipulation to be possible.

Training individual wild ungulates to avoid a particular food is rarely practical. Rather, the manipulation usually involves restricting ungulate access to a resource, encouraging the animal to avoid an area, altering resource availability, or by reducing the desirability of the resource. Operational success depends largely on selecting approaches which encourage behaviors within an individual's repertoire and which do not necessitate sacrifices that threaten survival. In other words, do not require the subject to fly unless it has wings, and do not set management objectives which require suicidal tendencies from animals.

## Excluding Ungulates

Exclosures are probably the most effective means to reduce depredation by ungulates (Palmer et al. 1985). Where ungulates are abundant or crops are particularly valuable, fencing may be the only way to effectively minimize damage (Craven and Hygnstrom 1994). Permanent structures are expensive and require maintenance (Caslick and Decker 1979). Temporary fences are less costly and can be moved as necessary, but they are generally less effective. Individual plant barriers are more economical and can be effective under the proper conditions.

Fences to keep out elk and deer should be a minimum of 8 feet and preferably 10 feet tall. Woven wires (Fig. 1a) are much more effective at deterring ungulates than are strands of smooth or barbed wire (Fig. 1b). Strands of wire installed immediately above woven wire provide additional height. An electrified fence is more effective than a similar non-electrified fence. Building a double or slanted fence adds depth making the fence more difficult for ungulates to jump over (Fig. 2a,b). Flagging should be attached to all wire fences to increase their visibility to animals.

Animal movements can be hampered by exclosures. When possible a series of small intermittent exclosures (30 x 30-feet) may be more effective than an extended barrier. The smaller exclosures do not block access to resources or impede the migratory movements of animals as severely as the large exclosures. Once the resource matures and becomes less vulnerable to damage, the small exclosures are then moved to adjacent areas.

Netting can be used to construct temporary exclosures. The light weight of netting does not require as durable or as strong a support as those needed for conventional fences. Netting strung between metal fence posts creates a barrier for deer and elk. Small plants or seed-beds can be protected by draping netting over supports to create tent-like structures. A series of inverted U's constructed out of plastic pipe also works well to support nets.

A baited electrified wire can encourage deer to avoid an area. Deer are enticed to lick peanut butter from the wire, and a shock is delivered on contact (Fig. 3). This method can be effective to protect small patches in areas with few animals. I have conditioned black-tailed deer (*Odocoileus hemionus columbianus*) to avoid flagging

**Figure 1.** Diagram depicting a (a) woven-wire fence and a (b) and a seven-wire vertical fence built to exclude ungulates (Craven and Hygnstrom 1994).

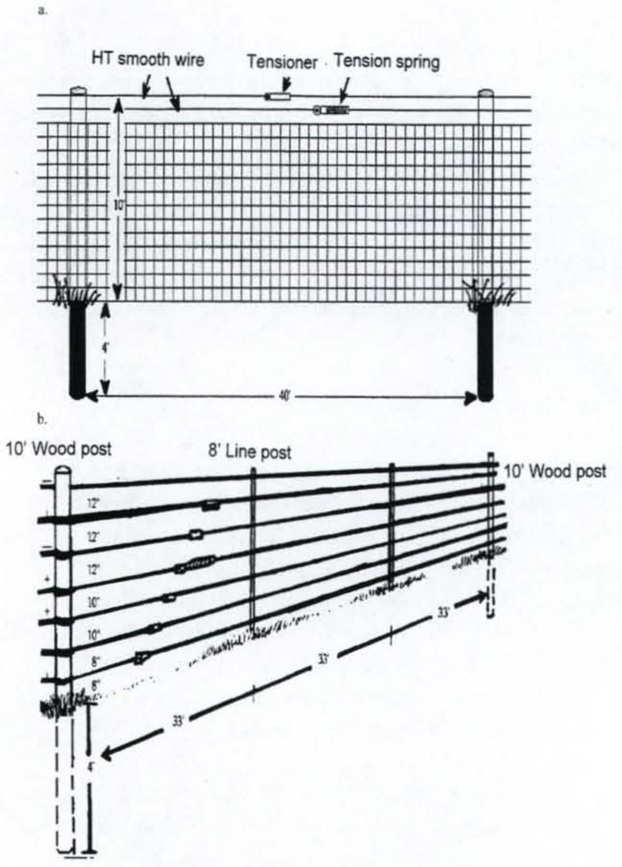
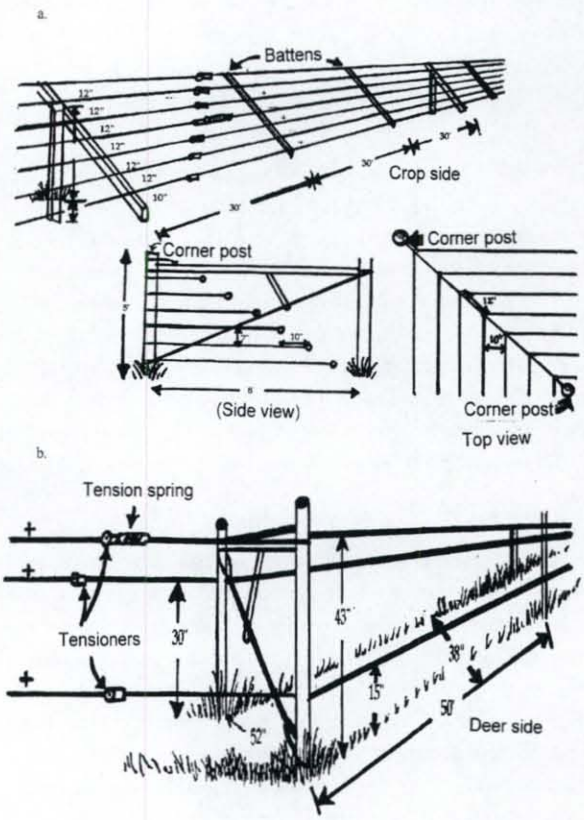


**Figure 2.** Diagram depicting a (a) slanted seven-wire deer fence and a (b) offset or double fence built to exclude ungulates (Craven and Hygnstrom 1994).



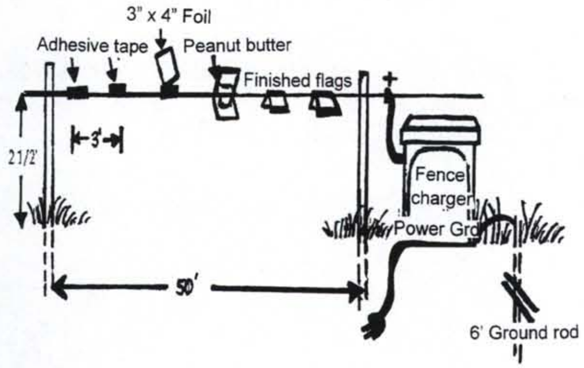
in a similar manner (unpublished data). During training, wires covered in flagging were hung around suspended apples. Other apples were suspended in wires without flagging. Deer then received a mild shock as they attempted to mouth apples associated with flagging. These animals soon avoided flag covered apples. The conditioning to avoid flags temporarily persisted in some animals and avoidance was generalized to other protected resources, such as flag draped seedlings.

Individual barriers also can be placed around seedlings or portions of their stems or foliage. Often tree seedlings will survive if their terminal bud is protected. A variety of products are commercially available or can be constructed from common materials (Marsh et al. 1990). When properly installed, individual barriers can protect most plants under moderate grazing pressure. They generally are not hazardous to wildlife and they do not impede wildlife access to other forage. Some barriers are relatively inexpensive and require minimum skill to apply, while others are quite expensive. Despite potential benefits, barriers come with a host of likely pitfalls. Increased humidity in some tubes may increase problems with foliar diseases. Improperly selected or poorly installed barriers can cause seedling deformities or increase seedling mortality. Brightly colored barriers also have been known to attract animals. Poorly staked barriers can be pushed over and though browsing is reduced the seedling is subsequently prevented from returning to an upright position. Conical protectors need to be removed as the seedlings grow or they will interfere with growth and cause deformities. Debris (e.g., branches) placed over seedlings can deter ungulates, but also provides protective cover for small mammals and may inadvertently increase damage by rodents.

## Encouraging Avoidance

Ungulates avoid areas that appear threatening. What constitutes a threat, however, depends largely on the experience of the animal. Wild ungulates in remote areas are rarely seen unless noise and movement is kept to

**Figure 3.** Diagram depicting a "peanut butter" fence. Deer receive a mild shock when they contact the fence to eat the peanut butter and learn to avoid the area. (Craven and Hygnstrom 1994).



a minimum, while urban deer may munch on roses adjacent to a house with an open window and kids playing inside. Regardless, visual displays or noises that do alarm the animal will discourage its presence. Humans screaming and chasing wildlife was most likely the first historical attempt at animal damage prevention. Modern noisemakers are still used to scare animals away from resources. Visual displays, such as scarecrows, also are traditional means to alleviate depredation in gardens or small fields.

Animals are generally wary of any unfamiliar sound or sight, but they become less wary with time unless the noise is paired with a negative reinforcer. Most frightening devices (e.g., artificial light, automatic exploders, pyrotechnics) rarely work for more than a few days or at most a week (Koehler et al. 1990). Familiarity of wildlife to devices can be minimized by installing or operating the devices only when resources are most susceptible to damage. Devices, however, need to be used immediately after the onset of damage. Established movements and behaviors are much more difficult to disrupt than are newly forming behavioral patterns. Efficacy of products can usually be increased by alternating techniques or use patterns. Sporadic displays or devices that are activated by an animal's presence are more effective than permanent or routine displays. Visual displays combined with noisemakers are generally more effective than either technique implemented alone. For example, sirens and strobe lights activated at irregular intervals are likely to be more effective than either a constant visual display or loud noises emitted at fixed intervals. Supplementing these techniques with occasional punitive measures also can increase their effectiveness. For example, elk on golf courses readily habituate to pyrotechnic devices, but when they are occasionally struck by rubber balls (scary but non-lethal) in conjunction with pyrotechnics, they quickly disperse from the fairways. Properly trained dogs confined within the boundaries of the resource to be protected also are very effective at deterring ungulates.

Most of the evidence that supports the use of frightening methods to reduce predation is anecdotal stories. Few devices have been well tested, particularly under field conditions. Ultrasonic, vibrating, and electromagnetic devices generally lack effectiveness and are of little practical value (Koehler et al. 1990, Shumake 1997). Warning whistles attached to vehicles have proven to be largely ineffective (Romin and Dalton 1992). Overall, frightening devices are most appropriate for use where a crop or situation needs protection for only a few days, such as just before harvest or from migratory elk (Koehler et al. 1990).

## Altering Resource Availability

Habitat modification to reduce damage generally requires a reduction in resources to encourage animals to move out of an area, or an increase in resources to limit the use of the planted crop. Over time, animal populations may decline with a reduction in favorable habitat. However, if the protected resource is reestablished too soon after habitat depletion it will likely be a limited, and thus valuable, resource and probably be consumed. Another consideration is the fate of the displaced animal. Resource depletion may work well if the animal is transitory and can readily locate suitable alternatives. Individuals with few options, however, are less likely to re-locate successfully. Abrupt habitat changes for these species probably becomes lethal, and more humane methods should be considered if population reduction is the objective.

Providing wildlife with viable alternative foraging options can alleviate foraging pressure. Desirable foods can be distributed across problem areas or on adjacent sites to encourage animals to move away from the protected resource. For example, alfalfa distributed along migratory trails may encourage ungulates to quickly travel past vulnerable seedlings. On succeeding days food should be placed at increasingly further intervals from the protected resource. Another approach is to plant or encourage the establishment of natural forages preferred by wildlife species (Campbell and Evans 1978). Food supplement can also be provided in semi-permanent structures strategically placed adjacent to or within sites that are vulnerable to damage. The efficacy of supplemental feeding, however, is variable and the results are commonly dependent on weather conditions (Doenier et al. 1997). Often animals continue to forage between bouts at the feed stations (Schmitz 1990). Supplemental feeding to deter ungulate damage may not be economically feasible. Food plots are generally more cost effective than feeders, but even they are not economical for most agronomic crops (McBryde 1995).

Before implementing a feeding program to reduce damage, the long-term consequences need to be considered. Alternative forages can increase or prolong the presence of wildlife on selected sites. Increased resources may encourage additional animals to frequent the area, or an improved nutritional status may enhance reproductive success. Further, resource-dependent territorial boundaries may shrink with improved resource availability, which in turn permits more individuals to exist within a given area. Big game herds may suspend or delay migratory movements. A feeding program, therefore, might actually increase wildlife pressure on resources if the program is not sustained or fails to meet the increasing demands. A successful program needs to be specific in targeting a problem. In addition, a way to continue the program indefinitely or plans to wean the supplemented animal from the program need to be identified before a feeding program begins. The potential for animals to later revert to protected resources also needs to be anticipated and avoided.

Damage to ornamental plants can be minimized by selecting landscape and garden plants that are less desirable to deer (Craven and Hygnstrom 1994). Lists providing the relative vulnerability of many ornamental plants are available (Cummings et al. 1980, Conover and Kania 1988, Fargione et al. 1991). Though a damage free guarantee can not be assumed, the likeliness of damage to a plant rated highly palatable is considerably greater than a plant listed as seldom eaten.

Environmental conditions can impact the chemical composition of a plant which in turn changes its relative preference for animal consumption. For example, the susceptibility of Sitka spruce (*Picea sitchensis*) trees to red deer (*Cervus elaphus*) browsing varies with monoterpene concentrations (Duncan et al. 1994). Kimball et al. (1998a) determined the role of chemical constituents in Douglas-fir (*Pseudotsuga menziesii*) on the foraging behavior of black bears (*Ursus americanus*). Basically, bears preferred trees high in carbohydrates and low in sugars. Subsequently, they predicted the relative vulnerability of timber stands based on how silvicultural practices affected these chemical constituents. Damage levels are expected to be higher in thinned stands, and in fertilized stands the year after urea application (Kimball et al. 1998c). Pruning reduced plant sugars, thus rendering trees less vulnerable to bear foraging (Kimball et al. 1998b). Similar efforts need to be made with ungulates to provide managers the ability to at least predict the impact agricultural practices have on damage vulnerability. Kimball et al. (1999) also rated select tree genotypes to damage vulnerability. Surprisingly, some genotypes with demonstrated higher growth potential ranked lower for anticipated bear preference than genotypes with low growth potential; indicating that it may be possible to select for genotypes less vulnerable to animal damage without sacrificing growth potential.

## Reducing Resource Desirability

An animal may select one food over another because it is attracted to the first or because it is avoiding the alternative (Galef 1985). Thus, the likelihood of a particular plant being eaten depends on its own palatability, and the availability and desirability of alternative foods. Repellents are applied to plants to make them less attractive to foraging animals. In theory, animals shift foraging to alternate plants or forage in areas that are not protected with repellents.

The avoidance of repellents by wildlife may be innate or acquired through a conditioned food aversion. Repellents that elicit initial avoidance are generally either irritants or those that evoke a "fear" response (Mason and Clark 1997). These stimuli require no prior encounters to cause avoidance behavior. Irritants stimulate trigeminal pain receptors in the mucous membranes of the eyes, mouth, nose and gut lining (Silver 1990). For mammals, including ungulates, strong irritants include capsaicin and capsicum oleo resins (Maga 1975), and volatile chemicals such as allyl isothiocyanate and ammonia (Budavari et al. 1989).

Fear-inducing repellents include sulfur compounds and volatile ammonium soaps of higher fatty acids (Milunas et al. 1994). Degrading animal waste products and most predator urine emit sulfurous odors. Several studies report BGR-P, active ingredient is fermented egg, to inhibit foraging by black-tailed deer (Melchoirs and Leslie 1985, Nolte et al. 1995, Nolte 1998), mule deer (*Odocoileus heminous*; Andelt et al. 1991, 1994), white-tailed deer (Dietz and Tigner 1968, Harris et al 1983, Palmer et al. 1983, Conover 1984, Swihart and Conover 1990, Milunas et al. 1994) and elk (*Cervus elaphus nelsoni*; Andelt et al. 1992). The aversive qualities of predator urine reflect the diet of the predator (Nolte et al. 1994a). Predator odors have been demonstrated to be avoided by several ungulates (Van Haaften 1963, Muller-Schwarze 1972, Melchoirs and Leslie 1985, Sullivan et al. 1985, Abbott et al. 1990, Swihart et al. 1991). Young black-tailed deer also spend less time foraging in areas contaminated with predator scats (Muller-Schwarze 1972).

Conditioned food aversions occur when ingestion of a novel food is paired with nausea or gastrointestinal distress (Garcia, 1989). Thus, any flavor paired with gastrointestinal distress can become an effective deterrent. Efficacy of repellents based on conditioned aversions, however, is generally limited because animals must be trained to avoid these materials. The use of conditioned-based repellents is especially problematic if the damage is inflicted by a transitory or migratory species (i.e., elk moving from summer to winter ranges). Further, the stimulus must be novel for animals to form a strong aversion. Damage inflicted to seedlings during training or subsequent sampling can be extensive.

Herbivores commonly ingest naturally occurring "bitter" compounds, and bitter substances that fail to induce gastrointestinal malaise are largely ineffective as repellents for herbivores (Nolte et al. 1994b). Several studies have reported bittering agents to be ineffective to deter browsing ungulates (Swihart and Conover 1990, Andelt et al. 1991, 1992, Nolte et al. 1995, Nolte 1998). An initial avoidance of these compounds probably reflects an unfamiliarity with the taste rather than an inherent aversion to the bitter taste. Animals commonly sample novel or unfamiliar foods cautiously (Rozin 1976). Herbivores, however, can detect bitter flavors and reliably acquire avoidance responses when these flavors are paired with gastrointestinal distress (Jacobs and Labows 1979). Red deer and roe deer (*Capreolus capreolus*) did differentiate between food altered with 1000 ppm denatonium benzoate and untreated food, and when offered a choice they restricted their intake of treated relative to untreated food (Wright and Milne 1996). These animals, however, did not restrict their daily intake when offered the treated food in a single-choice test.

A number of repellents are commercially available. Efficacy varies widely among them. Federal and State registrations certify that it is legal to use a product according to the conditions and restrictions stipulated on the approved label. At present, registration does not guarantee the availability or the efficacy of a product. A partial list of repellents marketed during 1998, and their respective active ingredient and delivery system is provided in Table 1. We recently tested a few of these to assess the efficacy to deter black-tailed deer browsing of western red-cedar (Table 2).

An effective program to reduce wildlife foraging through repellents depends on the relative desirability of the resource to be protected and the availability of alternative forage (Gillingham et al. 1987, Andelt et al. 1992). Preferred plants (e.g., western red-cedar) are more difficult to protect than less preferred plants, such as Douglas-fir (Nolte et al. 1995). An abundance of alternative forage permits animals to readily direct their consumptive behavior towards other plants. After treatment, an animal's foraging choices also depends on the size of the protected area relative to its territorial boundaries. Species with vague or extensive territories, such as deer, can more easily move to new areas to forage than can species with small and more rigid territorial boundaries (e.g., pocket gopher). Foraging pressure on protected plants also depends on the presence and densities of wildlife species. Competition among species may cause animals to be less selective. Likewise, high population densities may limit foraging alternatives, rendering repellents less effective.

## Summary

Ungulates can pose problems for resource managers. The intensity or severity of impacts caused by wildlife will reflect the density of animals present, along with the existing habitat. Whether these impacts create a problem depends on the goals of a manager and the resources available to achieve these objectives. Assessing the potential for a problem is simple if there is a history of similar operations in the area. Merely verifying past successes and reasons for failed projects ought to be adequate. Projects being established in new areas will require some knowledge of the species and habitat present, and how the proposed operation will alter the dynamics of the current plant and animal interactions.

The most appropriate approach to reduce animal foraging needs to reflect the overall objectives of the manager, as well as the conditions of the specific problem. All techniques are not feasible or appropriate for all situations. No action may be the appropriate action if the problem is relatively minor. A few preliminary considerations will increase the success of a program. Check the legal ramifications for any action selected, and ascertain that the action will not be potentially hazardous to non-target species, in particular to endangered or threatened species. Public attitudes also need to be considered when selecting an approach. Develop a strategy to implement the selected approach. Though it may require time and effort, implementing the program should be straightforward. Unanticipated problems or concerns, however, may require modified or alternative strategies. Monitoring a damage reduction program is a necessity. Determine whether the desired goals are being achieved and whether there are any unexpected negative consequences. Continue to evaluate the program until the resource is no longer vulnerable, or conditions warrant terminating the program.

Table 1. List of products marketed during 1998 to deter deer browsing[1,2].

| Product | Active Ingredient | Delivery System |
|---|---|---|
| Deer Away (BGR) | Egg | Topical spray |
| Deer Away (BGR-P) | Egg | Topical powder |
| Deer Off | Egg | Topical spray |
| Not Tonight Deer | Egg, Montok pepper | Topical spray |
| Mr. T's Deer Blocker | Egg, capsaicin, garlic | Topical spray |
| Deerbuster's Deer | Egg, capsaicin, garlic | Topical spray |
| Deerbuster's Deer | Egg, capsaicin, garlic | Topical powder |
| Deerbuster's Deer | Egg, capsaicin, garlic | Sachet |
| Dr. Deer | Garlic | Topical spray |
| Plant Pro-Tech | Garlic | Capsule |
| Hot Sauce | Capsaicin | Topical spray |
| Red Pepper Wax[3] | Capsaicin | Topical spray |
| Get Away | Capsaicin, allyl isothiocyanate | Topical spray |
| Green Shield | Capsaicin, allyl isothiocyanate | Topical spray |
| TKO Orange | d-limonene | Topical spray |
| C100 | Coyote urine | Scent darts |
| Deerbuster's Coyote Urine | Coyote urine | Sachet |
| Wolfin[4] | Di (N-alkyl) sulfide | Capsule |
| Hinder | Ammonium soaps/higher fatty acids | Topical spray |
| Deerbuster's Deer and Rabbit | Ammonium soaps/higher fatty acids | Topical spray |
| Bye Deer | Sodium salts/mixed fatty acids | Sachet |
| Deer No No[5] | Sodium salts/mixed fatty acids | Sachet |
| Plantskydd | Bloodmeal | Topical spray |
| Deer Stopper[6] | Thiram | Topical spray |
| Shot-gun | Thiram | Topical spray |
| Ropel | Denatonium benzoate/thyomol | Topical spray |
| Repel[7] | Denatonium benzoate/thyomol | Topical spray |
| This 1 Works | Denatonium benzoate | Topical spray |
| Tree Guard | Denatonium benzoate | Topical spray |

[1] Prepared by Kim Wagner.

[2] The use of trade names does not indicate endorsement of commercial products by the U.S. Department of Agriculture.

[3] Red Pepper Wax is advertised on the Internet as a deer repellent, but it is not labeled for use as a deer repellent.

[4] Wolfin is not currently registered for use in the United States.

[5] Deer Stopper was scheduled to be registered for use by the fall of 1998.

[6] Deer No No is advertised by the manufacturer on the Internet as containing specially formulated citrus scents, however, the label lists ammonium soaps of mixed fatty acids as the active ingredient.

[7] Repel also is advertised by Deerbuster's as a deer repellent, but this powder formula contains a different active ingredient and is not labelled as a foraging repellent.

Table 2. Average number of bites taken by black-tailed deer from western red-cedar seedlings at 2 and 12 weeks post treatment with select repellets[1] (unpublished data).

| Repellent | 2 Weeks | 12 Weeks |
|---|---|---|
| Untreated | 18.7 a[2] | 25.0[3]a |
| TKO Orange | 16.7 a | 23.8 a |
| Wolfin | 15.0 a,b | 23.6 a |
| Ropel | 14.9 a,b | 25.0 a |
| Deerbuster's Deer and Insect | 10.6 a,b,c | 25.0 a |
| Hinder | 10.4 a,b,c | 25.0 a |
| Plant Pro-Tech | 10.1 a,b,c | 23.6 a |
| Hot Sauce | 4.6 b,c | 20.6 a,b |
| Tree Guard | 3.8 b,c | 15.9 a,b,c |
| Detour | 3.4 b,c | 23.5 a |
| N.I.M.B.Y. | 1.7 c | 16.5 a,b,c |
| Deer Away (BGR) | 1.5 c | 9.3 a,b,c |
| Get Away | 1.4 c | 6.4 b,c |
| Bye Deer | 0.5 c | 1.5 c |
| Coyote Urine Sachets | 0.2 c | 10.6 a,b,c |
| Not Tonight Deer | 0.2 c | 8.8 a,b,c |
| Plantskydd | 0.1 c | 4.2 b,c |
| Deer Stopper | 0.1 c | 10.5 a,b,c |
| Mr. T's Deerblocker | 0.1 c | 16.0 a,b,c |
| Deerbuster's Sachet | 0.1 c | 1.2 c |
| Deer Away (BGR-P) | 0.02 c | 0.04 c |

[1] The use of trade names does not indicate endorsement of commercial products by the U.S. Department of Agriculture.

[2] Mean values within a column followed by the same letter are not significantly different $P > 0.05$.

[3] Completely defoliated seedlings were recorded as having had 25 bites.

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# Plant Attributes That Affect Livestock Selection and Intake

**Henry F. Mayland and Glenn E. Shewmaker**

## Abstract

**Grazing animals depend on a variety of physical and chemical cues when selecting which plants they will eat. The soluble energy in the plant may serve as a primary factor for selection. Management and plant breeding strategies should use soluble carbohydrate levels as likely indicators of animal grazing responses.**

## Introduction

Grazing animals eat an array of plants, but often prefer some and avoid others. These preferences or aversions are responses to certain physical and chemical senses of which touch, smell and taste are of greatest importance for ruminants (Arnold and Hill 1972, Bate-Smith 1972, Krueger, et al. 1974, Bazelly 1990). Food preference is seldom a response to a single factor, but rather a combined response to several stimuli. We will share our own experiences and limited review of other published literature on each subject. Additionally, we accept the theorem that chemical and some physical effects presented in our paper affect the postingestive feedback mechanism discussed by Provenza and Launchbaugh (this volume).

The intake of food is determined by the complex interaction of pre- and post-absorptive factors. Those factors operating before the food leaves the mouth can be collectively referred to as palatability while those operating after this stage are referred to as postingestive (Grovum and Chapman 1988).

We have completed cattle preference testing of eight, endophyte-free tall fescue cultivars (Shewmaker et al. 1997) and are relating preference scores to various physical and chemical components of the tall fescue that might serve as cues to grazing animals. We hope to analyze a series of chemical components including 1) volatiles, 2) amino acids, 3) organic acids, 4) carbohydrates, 5) minerals, and 6) fiber and agronomic quality characteristics. We also hope to analyze several physical components like 1) shear strength, 2) tensile breaking strength, 3) maceration scores and relate these to animal preference scores of tall fescues used in the grazing study (Shewmaker et al. 1997).

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Because of photosynthesis and respiration, total nonstructural carbohydrates (TNC) in plants increase during day and decrease during night. We have noted that cattle, sheep, and goats are able to differentiate between forages harvested in afternoon versus in morning (Fisher et al. 1999). Dairy cows produce more milk when fed a total mixed ration containing 40% alfalfa when that hay was cut at 4 in the afternoon rather than 6 in the morning (Kim 1995, Mayland et al. 1998).

## Physical Cues

### Color

It is generally accepted that ruminants see varying shades of gray, but are unable to distinguish between the primary colors. This is not to say that visual cues are not important in foraging (Howery et al. this volume).

### Plant texture

Grasses and especially forbs may have physical attributes that discourage grazing. Plants with pubescent leaves have greater resistance to some insect pests. These characteristics may have similar effects on ruminants. However, we (Rumbaugh et al. 1993) found that trichome density of globemallow (*Spaeralcea* spp.) leaves was positively related to accession preference by sheep. Thus other cues or factors were of greater importance in determining sheep preference.

### Sward structure

Ungar et al. (1991) summarized results from several studies indicating that sward heights below 4 inches are often related to significant depressions in intake by cattle. They reported significant (99%) reduction in number of bites and total dry matter intake by steers as the sward height was reduced below 4 inches. Laca et al. (1992) and

Distel et al. (1995) showed that cattle graze most efficiently and expend more time where forage density allowed the most rapid intake rate. That was not supported by Ganskopp et al.(1997) who found that steers did not seek out the highest density forages.

## Prehension

Prehension is the act of seizing or grasping forage with the tongue and then tearing it from the plant as might be done by ruminants. Energy expended in this action is quantified by measuring tensile breaking strength. Grazing behaviorists have not explored this factor as a potential grazing cue.

## Prehensile strengths

Prehensile strength is the energy required to bite or tear the forage from the plant. Herbivores, like horses that have incisors on top and bottom jaw impose a cutting or shearing action on forage. Ruminants use a combination of tear and shearing action. Energy requirements are characterized as either shear or tensile breaking forces.

The intrinsic shear strength is calculated as the force required to shear a leaf, divided by the length of the cutting blade in contact with the leaf material (Henry et al. 1997). Differences in these forces among forage cultivars has not been related to grazing preferences.

## Mastication

Mastication is the act of reducing particle size of ingested feed. For monogastrics there is one opportunity to do this whereas ruminants have a second chance because they regurgitate fiber boluses and chew the cud.

It is theorized that rate of mastication and particle size reduction by ruminants may affect consumption of forage. Troelsen and Bigsby (1964) reported that 88% of variability in hay intake by sheep was explained by similar variability in particle size indexes determined by combination of maceration and sieving. This idea has been pursued by others (Balch 1971, Chenost 1966) using more automated and quantitative methods. A proposed index of 'fibrousness' in ruminant diets would have units of minutes/pound of food. Values for the index increases as water content decreases and plant maturity increases.

## Water content

Some have speculated that livestock preferences are positively associated with moisture content of forages (Gesshe and Walton 1980). However, Ganskopp et al. (1997) did not support this hypothesis.

## Sight

**Observation.** Range-conditioned ewe sheep were used to evaluate palatability of various globemallow (Sphaeralcea) taxa (Rumbaugh et al. 1993) in a spaced-plant nursery. The plots in each of 4 pastures, contained 2400 spaced plants of which 85% were 'Hycrest' crested wheatgrass (Agropyron cristatum), 14% mallow, and 4% 'Spredor 2' alfalfa (Medicago sativa). Upon introduction to the test pasture, ewes would roam the area, investigating, and sampling available herbage. Within hours, ewes recognized the presence of highly sought alfalfa plants randomly scattered across a pasture area (44 x 44 yards). The sheep relished the alfalfa, and within hours, several of the lead ewes were observed stretching their necks and scanning for other alfalfa plants. Once sighted, the sheep walked and sometimes ran to eagerly graze the alfalfa plants.

# Chemical Cues

## Aroma

**Observation**. On 24 occasions of a grazing preference study, cattle were moved from one to another small pasture containing replicated plots (3x7m) of eight tall fescue (*Festuca arundinacea*) varieties (Shewmaker et al. 1997). Upon exploring the new pasture, animals would wander across different plots with their muzzles in the forage canopy, occasionally taking a bite. They were undoubtedly detecting various volatiles and sensing the forage canopy texture.

Aroma integrates the impact of volatile compounds released by plants upon the foraging animal's organoleptic sensory system. Scehovic (1985) and Scehovic et al. (1985) noted enhanced acceptability by cattle of a low-preference tall fescue when sprayed with juice expressed from a highly preferred Italian ryegrass (*Lolium multiflorum*). However, palatability of Italian ryegrass was reduced when it was sprayed with fescue juice. Individual compounds were not identified. Later, Tava et al. (1993) associated volatile constituents of tall fescue with suggested palatability groupings. There is little doubt that aromas were related to animal preference or palatability, but in neither study were specific aeromatic compounds quantitatively associated with palatability or preference.

In a much more detailed study, Mayland et al. (1997) identified 50 of 54 compounds emitted from fresh tall fescue cultivars representing a range in grazing preference. Preference scores were significantly ($R^2$ = 0.97) correlated with emissions of 6-methy-5-hepten-2-one, (Z)-3-hexenyl propionate, and acetic acid. These are simply correlations and their affect on grazing animals needs to be tested. This could be accomplished by spraying combinations of these three volatiles on a given forage and evaluating animal preference for the variously treated diets.

It is important to recognize that none of the five researchers involved in the preference study (Shewmaker et al. 1997) could detect any difference in aroma among the eight varieties. Humans have hundreds of different olfactory receptor genes that may be responsible for our ability to detect odorants. Yet, 72% of these genes may be dysfunctional (Rouquier et al. 1998) and we may be olfactory disadvantaged compared with ruminants.

## Flavor

Flavor or olfaction is a combination of taste and aroma. The stimulus for olfaction is chemical. For a compound to have olfactory characteristics the chemistry of the compound must be such that it will chemically bind to the organoleptic receptors on papillae of taste buds located front, back, and edge of tongue. Receptors or nerve endings are also located in nasal passage and phalanxes.

Goatcher and Church (1970) have made an extensive comparison between ruminant species. Sensitivity to chemical solutions based on the lowest concentration to be discriminated, was as follows:

Sweet: Cattle > Normal Goats > Pygmy Goats > Sheep
Salty: Cattle > Pygmy Goats > Normal Goats > Sheep
Sour: Cattle > Pygmy Goats = Sheep > Normal Goats
Bitter: Pygmy = Normal Goats > Sheep > Cattle

If some other threshold is taken, the results are different. For example, the molarities at which solutions are rejected (<40% total fluid intake) rank, over animal species, as follows:

Salty: Cattle > Sheep > Normal Goats > Pygmy Goats
Sour: Cattle > Sheep > Normal and Pygmy Goats
Bitter: Sheep = Cattle > Normal = Pygmy Goats
Sweet:: No rejection thresholds found

Assessing nerve responses to various chemical compounds dissolved in water have shown that chemoreceptors in the sheep's tongue are sensitive to salt, sweet, sour and bitter (Grovum and Chapman 1988). Krueger et al. (1974) had earlier reported that taste was the special sense most influential in directing forage preference of sheep grazing a mountain tall-forb community. The other senses appeared to supplement taste. Sheep preferred sour and sweet plants and generally rejected bitter plants. They reported that smell or odor was of minor importance in selection.

## Carbohydrates

We (Mayland et al. 1998), and others (Fisher et al. 1999), have observed a diurnal cycling of sucrose and other nonstructural carbohydrates (TNC) in forages (Orr et al. 1997). This class of compounds provides energy for animal metabolism. It contains very soluble and easily digestible to insoluble and very slowly or even indigestible compounds. Ruminants use the readily fermentable carbohydrates and may be able to cue on some of these compounds. Water soluble carbohydrates (WSC) have been high in cultivars considered highly palatable and WSC have been low in cultivars considered to have low palatability (Orr et al. 1997).

We have found that total nonstructural carbohydrates (TNC) are related ($r^2$ = 0.45) positively to animal preference for tall fescue (Mayland et al. Unpublished 1999).

## Organic acids

Differences in organic acids might affect animal preference and overall forage palatability (Mayland et al. 1999). Both malate and citrate increase salivary flow and intensify sweet flavors in diets of monogastric animals. Similar effects may occur in ruminants (Martin 1998). Malate content of the diet stimulates lactate utilization and propionate production by ruminal bacterium, *Selenomonas ruminantium* (Martin 1998). Mayland et al. (1999) found only weak correlations of grazing preference to concentrations of malate (r = 0.28), citrate (r = 0.35), or their sum (r = 0.44, P = 0.11).

## Amino acids

Provenza (1995) noted that deficits or imbalances of amino acids decrease intake and cause feed aversions in lambs. However, dietary amino acids, when consumed by the ruminant animal, are first metabolized by the rumen microflora, forming another set of amino acids whose profile may not resemble that of the diet. Such outcomes are difficult to predict. It is possible that amino acids in the forage eaten by animals or some metabolic product might have an immediate flavor effect. However, grazing preferences were not related to concentrations of any essential or non-essential amino acid quantified in these tall fescue cultivars representing the full range in preference (Mayland et al. 1999).

### Alkaloids

Alkaloids in grasses and legumes are sometimes of plant origin and sometimes produced by parasitic fungal endophytes growing in the plant stem and transmitted in the seed.

Marten et al. (1973) identified three alkaloids; gamine (3-dimethylaminomethyl-in-dole), N,N-dimethyltryptamine, and 5-methoxy-N,N-dimethyltryptaine in Reed canarygrass (Phalaris arundinacea L.). Total basic alkaloid concentrations of clones were highly correlated (r = 0.90)with each environments. Palatability ratings of clones grazed by sheep were highly correlated. Total alkaloid concentrations and palatability rating of clones were also highly correlated (r = 0.87 to 0.94).

## Summary

The reviewer may readily see the complex set of signals that plants may present to grazing animals. Knowing our responses to the odor of lilacs, the taste of ice cream, the texture of chopped nuts, and the flavor of cappuchino, we soon appreciate the potential array of cues awaiting the grazing herbivore. Nevertheless, they must and do make choices. These choices may be made on basis of odor, taste, feel, flavor etc., but these are ultimately linked to the post ingestive feedback mechanism built into the animals' system (Early and Provenza 1998). As we learn more about these relationships, we will be able to do a better job of forage and animal management.

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# Using Stockdogs For Low Stress Livestock Handling

**Wally Butler**

## Abstract

**Low stress livestock handling techniques have recently come to the forefront of western rangeland management. These techniques have been long used by some stock handlers, but only recently have gained widespread recognition. Stockdogs can be a very useful tool in accomplishing livestock production and rangeland resource management goals. To successfully apply low stress livestock handling, stockmen often need to rethink their methods and attitudes towards handling animals. Once handlers have mastered these techniques and trained livestock to be handled in a calm manner, a stockdog can be effectively used to allow one person to handle large numbers of animals. Dogs should be encouraged to work using their natural instincts and thinking ability rather than to be used in a robotic fashion with commands for every movement. Handlers who trust their dogs and give them sufficient experience will be amazed at how helpful stockdogs can be in a variety of situations.**

## Introduction

Stockdogs have long been used to facilitate the handling of domestic livestock throughout the world, and more recently on the farms and ranches of North America. Several breeds and working styles of stockdogs have evolved to fill various needs of livestock producers. These include livestock guard dogs, trial competition dogs, and feedlot working dogs. However, this discussion will be limited to the use of dogs for livestock herding, specifically, in western rangeland situations.

There are two working styles of stockdog currently in use on western livestock operations, commonly referred to as headers or heelers. Dogs described as headers have an inherent tendency to fetch stock to the handler. The term heeler describes a dog that has an inherent tendency to drive stock away from the handler. Some dogs will display both styles which can be very confusing to novice handlers and sometimes even to the dog. Both styles of work have a place in our livestock industry just as do various breeds of cattle and horses.

Most often when handling large herds of livestock, a dog's tendency to head or gather stock to the handler is more desired than is a driving dog's tendency. In the Northwest, large herds of livestock are frequently on rangelands that are steep and/or timbered. In these situations, animals are less difficult for the handler to drive away than to gather or move as a group.

## Breeds

There are about 60 recognized herding breeds of dogs worldwide (Wilcox and Walkowicz 1995). Four breeds dominate the stockdogs used by the western ranching industry: Australian shepherd, border collie, kelpie, and Queensland blue heeler. Various crosses of these and other breeds are common and have resulted in some locally recognized "strains" of stockdog. Each of these breeds has highly inherited working styles and attributes. Cross breeds have produced some fine working individuals, but a broadened gene pool can make it difficult to predict style inheritance.

Australian shepherds are the youngest of the four mentioned breeds and were developed, not in Australia but in the western United States within the last century. Their working style is not as fixed as the older breeds with some bloodlines being predominantly headers and others predominantly heelers. Inbreeding in the early years resulted in many dogs with blue or mixed eye coloration. Natural bobbed tails are common. The best working bloodlines are of medium bone, moderate size and are agile and very athletic. These dogs work from an upright stance with varying degrees of eye. "Eye" is a term that refers to a stare that results in a near hypnotic spell over livestock. They are highly social dogs that enjoy the company of their handler.

Border collies are one of the oldest breeds of stockdog in the world. They were developed in the British Isles centuries ago and consequently, breed very true for working style. Border collies have been selected solely for working ability with no emphasis on outward appearance. The dogs instinctively work "on balance" (opposite the handler) and fetch to the handler. They typically work from a crouch in a near creeping or down position with a great deal of eye.

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Kelpies or Australian sheepdogs are small to moderate sized dogs that have been imported from Australia in recent years. Kelpies are very quick and athletic, and are almost entirely fetch dogs. They are slick haired and prick eared. These dogs work with a great deal of eye and work from a crouch that resembles the stalking position seen in predator animals. The breed is heat tolerant, very social, and has gained rapid popularity in various parts of the West.

The Queensland blue heeler or Australian cattle dog was imported to the United States from Australia in the mid-twentieth century. They rapidly gained popularity but that popularity has diminished somewhat in recent years. The breed is almost entirely composed of drive dogs (heelers) making them of limited use in low stress livestock handling situations. They are excellent corral or feedlot dogs. They are very muscular, agile dogs with short hair and prick ears.

## Selection

When choosing a stock dog, first analyze your temperament and attitude toward livestock and decide on an appropriate breed or even on whether to use a stockdog. This paper is meant to aid stockmen who believe in low stress livestock handling techniques. A dog and handler can complement each other's efforts and abilities tremendously when properly implemented.

When selecting a breed and a puppy, it is important to deal with a reputable breeder with a known working bloodline. The recent acceptance of stockdog breeds by people with no need for stock handling has resulted in lines of dogs bred for companionship or conformation shows. With diminished emphasis on working ability, these breeds have been diluted to some degree. Begin by asking stockmen who work dogs in similar situations to yours, to refer you to a breeder or trainer. A good breeder is willing to guarantee the health and working instinct of his/her dogs. Environment and training is the major influence on the final ability of a stockdog, but you must begin with a healthy and willing dog.

When the time comes to select a pup, spend some time observing the litter. When the pups are first approached, there are two behaviors that I look for and avoid. The first is any puppy that hides or avoids contact and maintains a submissive posture. These pups either take a long time to develop and mature or never do mature. The second behavior is any puppy that unthinkingly charges right up to me running over other puppies in the process. Pups in this second group tend to act first and think later. An experienced trainer can usually make something of both pups, but the effort is normally greater than the outcome. These pups should be placed in companion homes and removed from lines of dogs bred for handling.

## Low Stress Techniques

The proper handling of livestock requires a deep understanding of behavior patterns. It is well documented that domestic livestock are prey species, and that fear plays a major role in their behavior (Grandin and Deesing 1998). With eyes at the sides of their heads, herd animals see in panoramic vision. They see primarily in shades of black and white and therefore, react strongly to movement and contrast (Doane's Agricultural Report 1979). Loud noises, abrupt noises, repetitive noises, and odors can also affect animal reactions.

A style of livestock handling called low stress livestock handling has recently come to the attention of the majority of stockmen. The most successful stockdog and horse trainers have been well aware of this style of handling livestock for many years. Stockdog trainers such as Allen (1979), Lithgow (1991), and Holmes (1992) have written excellent books about training dogs with an emphasis on efficient stock handling. Most modern day horse trainers also use quiet, gentle techniques that involve a great deal of animal psychology (Hunt 1985, Dorrance 1987, Lyons 1991, Roberts 1996). In my dog training clinics or when addressing stockdog trial contestants, I always emphasize that *the fastest way to move stock is slowly*. If the stock do not remain calm and controlled, the dog may create more work than it saves.

## Flight Zone

The flight zone of an animal is the distance within which a person may approach before the animal moves away. This circular zone around the animal may be equated to a balloon. When pressure is exerted on the balloon, it moves away and regains its circular shape. When a person enters the flight zone of an animal, it will move away. When a person retreats from the flight zone, the animal will normally turn to face the person and sometimes, move toward the person. The same principle applies to a dog entering or leaving the flight zone.

Several factors influence how the flight zone is used when herding animals. The first is the animals' previous experiences. For example, range cattle have a larger flight zone than dairy cattle that are constantly handled. Secondly, the speed and depth that the flight zone is invaded influences how fast an animal moves away. A dog rapidly penetrating the flight zone induces fear and a chase may result. Thirdly, the flight zone will often be a different diameter for the handler than for the dog. Be well aware of these factors when moving stock. I have often seen handlers incorrectly position themselves or ask their dog to exert pressure in the wrong spot, resulting in unexpected results that they should have anticipated. Remember, when moving stock with a dog, best results are achieved when the dog and handler work as a team and complement each other's actions.

## Rethink Methods and Attitude

In years gone by, horses and dogs were "broke" but thankfully, they are now "trained" in most good stockmen's minds. Calm, quiet methods prevail among successful stockhandlers. I have been in situations where I have lost my temper, as have most stockowners. Upon maturing as a stockhandler, you realize that force, vocal outbursts, and rage do not work. If you are sincere about proper livestock handling and proper use of a dog, begin by evaluating your methods and attitudes.

The following is a collection of analogies that should be commandments for the stockhandler. Some of these are my own, many are borrowed from other trainers and stockmen, and the remainder are collected from who knows where. They all readily apply to stockhandling.

-- If you always do what you always did, you will always have what you always had.
-- Make the wrong things difficult, and the right things easy.
-- The fastest way to move stock is slowly.
-- You can't teach experience.
-- There is no substitute for miles and wet saddle blankets.
-- Notice the smallest change and the slightest try and reward it.
-- Let your idea become the horse's idea.
-- Don't expect a pup to be born with a high school education.

## Starting a Pup

Once you have decided to use a dog in livestock handling, have adjusted your methods and attitudes, and, have selected a pup from a reputable breeder - you are ready to begin training a dog. First, teach yourself proper low stress livestock handling techniques. Secondly, train your livestock to respond to low stress livestock handling techniques. And lastly, practice, practice, practice.

Remember your pup was not born with a high school education and has no experience, just an inbred instinct to work stock. By the time he is old enough to start on stock, he should already know enough manners and verbal commands to be controllable. As a side note, most trial-trained dogs are nearly "robotic", in that they only do what they are commanded to do. The most useful dogs for ranch work, with properly trained livestock, will work with minimal commands purely on their natural instincts and experience.

Begin by working your dog in a small area, on young stock that have been properly handled and are responsive. A small corral or a round pen like horse trainers use is a good place to begin training. You can let the pup begin to get the feel of moving stock in the enclosed area; and then encourage the pup to circle the stock. Remember that you want to encourage calm movement of the animals. When the livestock are between you and the dog, encourage the dog to exert pressure and simultaneously release pressure on your side of the stock. The stock will move away from his pressure and into your release of pressure (Fig.1). By starting in a small area, you can block the dog's movement and push him away from you toward the other side of the stock. In short order, you will be able to move animals in any direction and at a steady pace. Next, move to an open area and begin working more animals over longer distances. Work with the flow of movement of the livestock. Larger herds of animals work with a collective flight zone and respond in the same manner as smaller herds. Once you have a smooth flow of movement, you can direct that movement to result in low stress handling of the livestock, even in large herds.

I like to use as few commands as possible and expect the dog to think for himself as much as possible. Given the opportunity, a dog will rapidly learn the edge of the flight zone and how to work in and out of that zone. That is commonly referred to as learning to "rate" stock. A young dog will often follow the edge of the flight zone to circle the stock. The result is animals that are frozen in one position and sometimes it is difficult to resume movement. The animals cannot be herded without movement, and the herding will be low stress only if the movement is calm and controlled.

There is no substitute for experience. Your experience as a stockhandler, the experience of your livestock, and the experience of your dog are important elements of success. Do not be afraid to seek the advice of experienced stockmen that handle their stock and dogs properly. Trust your dog to develop his instincts and to learn effective responses in different situations. You cannot correct a mistake until it happens. Corrections need to be well timed and generally, only verbal. If the dog is going around stock the wrong way, verbally correct him and push him in the correct direction by blocking his movement. Use the same single word command such as "no" or "hey" each time he goes a wrong

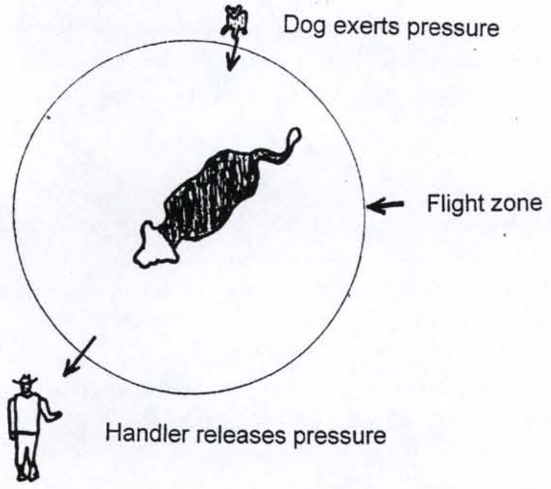

**Figure 1.** Stock will move away from pressure and toward a release of pressure.

direction. Say nothing when he goes the right direction to encourage him to "think on his own". Make the wrong things difficult, and the right things easy.

Dogs started in this fashion become "thinking dogs" rather than robots. They probably would not win a prestigious trial competition, but would do well and be invaluable on the ranch. In rangeland ranching situations, dogs need to think and react instinctively. Trust the dog and give him lots of experience. Have high expectations of yourself, your stock, and your dog and build on the experience. Remember to work as a team and to complement each other's actions.

## Conclusion

The principles of low stress livestock handling work well in modern range management applications. Stockdogs can be a useful tool in accomplishing the proper handling of livestock and the proper utilization of the rangeland resource. Many stock handlers need to rethink their methods and attitudes and should commit to a calmer approach. Once handlers have trained themselves, they can train their livestock to low stress handling techniques. Dogs can be introduced to stock and kept in a controlled situation to develop their instinct and encourage calm work. A dog should be advanced to larger herds in open areas as soon as possible and given as much experience as possible. Trust, high expectations, and timely corrections with appropriate rewards will result in a stockdog that will prove invaluable for many years.

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communication). Low stress livestock handling has the potential to be one of the most powerful, day-to-day range management tools ever used, when it is combined with sound range planning, training and dedicated effort. Control over the livestock gives control over the results.

Livestock producers can also expect some real benefits to their operation using the low stress livestock handling method. Potential benefits include: 1) time and manpower savings inhandling and moving livestock; 2) a need for fewer fences and handling facilities, thus reduced operating costs; 3) increased stocking rates through better distribution and better use of the total forage resource; 4) better herd health and nutrition, increased conception rates when breeding on the range, and increased weight gains; 5) reduced fly and predator problems; and 6) getting along better with your coworkers (including your spouse) when working livestock.

The benefits of low stress handling greatly outweigh the effort required to learn it. Grandin (1998) reviewed a number of scientific studies and trials that have documented the effects of stress on livestock, and the benefits of low stress handling. These studies show that it really does matter how livestock are handled, especially in those countries where nutritional requirements are at or close to an animals genetic potential to gain (Smith 1998). Handling can be the weak link in improving animal performance and reducing disease. The low stress handling method addresses the root of stress problems and it does not cost anything to use.

## Low Stress Handling Philosophy

The core of Bud Williams' philosophy is to create consistent and calm responses from livestock. Stress is a major contributor to livestock health problems and our lack of livestock control. Most of this stress is caused by humans. Low stress handling of livestock maximizes control and good herd health. Livestock quickly become conditioned to low stress handling and turn remarkable control over to the handler.

Creating consistent conditioned responses in livestock requires three basic steps. First, we need to stop forcing livestock to do what we want. This means we need to recognize what the animals perceive as force. Instead of using force, apply pressure that is patient and non-aggressive. In training animals, pressure is applied and released until the animals have had enough time and practice to understand they are not being trapped or forced into doing something. Secondly, we need to accommodate the emotional needs of the animals by abandoning practices that annoy or stress them. This helps create calmness and trust in the animals. Thirdly, use Bud Williams' low stress handling method when working livestock, to get a natural, predictable response from the animals. Practice the handling method until both you and the animals are familiar with it.

The biggest part of training cattle is simply letting them know we are not going to force them into doing something or do other things that stress them, and that our pressure has a release to it. When the livestock handler accomplishes these three skills, the livestock will change their behavior.

## Basic Principles of Livestock Training and Handling

Low stress principles, training guidelines and handling techniques create a herd that is conditioned to handling pressure. In handling livestock I know a conditioned response exists when animals react automatically and consistently to cues that I have practiced with them. Accomplishing a conditioned response in all my livestock is my goal in training; maintaining a conditioned response in my goal in handling. To create a conditioned response, there are three basic principles that are foremost in my mind every time I train or work livestock: 1) pressure/release; 2) end the lesson; and 3) do not start with your goal.

### Pressure/release

Livestock want to obtain relief from pressure first and foremost. Pressure without relief is stressful to the animals. Before animals will respond calmly and responsively to pressure, they must learn that pressure has a readily available release to it. To condition a desired response, I must make the "promise" to the animals that every time I ask them to do something and they respond correctly, I will reward them with relief from pressure. Pressure should be used to encourage certain movement of animals, not to force them to do what we want.

### Ending the lesson

Whenever I ask the animals to do something and they respond appropriately, I not only release the pressure, but I keep the pressure off for at least a short period of time; this is called "ending the lesson". This practice ensures that the animals clearly associate the release of pressure with what they just did.

### Start at the Beginning, Not at the End

Begin a training session with a plan and a goal, but do not try to reach your goal in one giant step. Organize

# Low Stress Livestock Handling

Steve Cote

## Abstract

**Ranchers grazing livestock on rangelands face difficulty and frustration trying to meet current riparian standards and cope with ever-increasing constraints. Low stress livestock handling, as promoted by Bud Williams, has been shown to be an effective range management tool for meeting riparian grazing standards. Low stress handling is based on accommodating innate mental and emotional characteristics of livestock to lower stress on the animals and increase control of them. It produces profound changes in livestock grazing and handling behavior. Using low stress handling to move cattle, it is possible to place and keep a herd together on the uplands, thus reducing grazing pressure on riparian areas without the use of fences. In addition to meeting riparian standards, benefits to producers using low stress handling techniques include healthier animals, greater weight gains and lower costs of operation. Success with low stress handling requires commitment to change from the handler, good training, practice and time to make it work.**

***This paper is a brief overview of the philosophy, basic principles and a few techniques of Bud Williams, of Lloydminster, Alberta, Canada. Handling information was obtained during training and personal communication with Bud Williams and his wife Eunice. For additional information, contact the author or Mr. Williams.***

## Introduction

A good understanding of how to modify the behavior of livestock and other herbivores (i.e., deer, elk, bison and reindeer) to achieve management objectives has existed for over 40 years. Recently, this subject has been the focus of increased interest and research. The ability to change the behavior of livestock is especially valuable today as range managers and ranchers face seemingly insurmountable challenges in meeting public rangeland and riparian grazing standards. Livestock numbers have been reduced and/or grazing seasons shortened in many casesin an attempt to achieve these new standards. However, in many situations the problem is not the number of animals but rather the time or duration of grazing and/or lack of control of animal distribution. Control of animal distribution requires high control over the grazing animals. Low stress livestock handling has proven to be a useful tool in managing livestock distribution.

Bud Williams is a livestock handler who has traveled the world to increase his experience with handling cattle under varied conditions. Through a lifetime of experience, Mr. Williams has distilled some of the most essential elements to handling livestock successfully. Mr. Williams' low stress handling method produces profound and lasting changes in the grazing and handling behavior of livestock. The method gives you the ability to keep livestock together as one herd, to place and keep them in uplands without fences, and to keep grazed areas completely clean of stock after a herd has been moved. Livestock will water in riparian areas and return to the herd on their own accord shortly after watering. Some grazing associations have changed their traditional grazing patterns from 70% in the riparian areas and 30% in uplands to 30% in the riparian areas and 70% in the uplands using lower stress handling techniques.

While riparian area protection is often the main concern on public rangelands, additional resource objectives can be attained when you have high control over livestock. More total forage can be removed from an area with lower use levels on individual plants. Range nutrition, palatability and productivity can be improved. Old, standing, dead plant material will be grazed and/or trampled into the soil surface, resulting in increased plant vigor and soil cover. Undesirable brush and wildfire fuel loads can be controlled just by using a herd of cattle. Crusted soils can be broken, improving air and water infiltration. Livestock can be herded around critical resource and recreation areas quite readily. Perhaps the greatest benefit is that plant diversity can be increased on over-rested portions of the range. Keeping a herd together and moving it frequently, with a rider getting around the herd once a day, has been reported to be effective in reducing wolf predation on cattle and reindeer in the Arctic and Canada (W. Holder 1998, personal

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your plan into a step by step approach, which creates a solid foundation in the animal of conditioned response to the pressure/release principle. For instance, if you need totrain a horse to load in a trailer, do not start the lesson by trying to load him in the trailer. First, train him to do the things he needs to do well to load calmly and consistently in a trailer. Almost all livestock require training to take pressure to do other things we want them to do. This does not mean you have to practice everything you will have the animals do, but it does mean that you need to be sure they will be responsive to the handling techniques you will be using. If you encounter a problem getting animals to do what you want, you can often solve the problem by stopping that activity and going back to practicing the basic pressure and release techniques.

### Additional training tips

For the fastest results, initially train livestock at a time and place that they will be most responsive. For example, initiating the training on a steep mountain range is difficult because the terrain makes it more problematic to be in the right position and work all the animals as you might like. Starting out with animals that are already stressed is also difficult. If an animal is real sensitive, put it with a group rather than trying to train it by itself. I also recommend the following three rules for both training and handling: 1) the activity must be safe for me; 2) it must be safe for the animal; and 3) the animals must be calmer and more responsive after the activity than they were before.

Let the animals respond naturally to your pressure and release. Repositioning yourself, apply pressure, release, reposition, etc. until the animals go the way you want them to. If you are out of position or move wrong, the animals will react by doing something other than what you want. Correct your position and always watch the animals. Your attitude in pressuring the animals should always be one of asking them if they would like to move, speed up, slow down, turn, etc.

Getting and keeping a herd together and placing it where you want it is not hard to do, but it is impossible to do if you try to use force. Our instinctive desire to use force and our mindset that we must make the animals do what we want now is very difficult for most of us to overcome. If you can overcome that mindset, you will find that livestock will give you exceptional control over them. If they see you as the predator or aggressor, then you sacrifice control.

These principles may appear complex in print, but they are really simple in practice. Cattle get the idea quickly, once you get it.

## Livestock Characteristics Related to Low Stress Handling

All livestock have behavioral characteristics that are important to keep in mind when you are handling them. Some of these characteristics are listed below.

1) All livestock have a flight zone. Roughly, if you are within this zone they will move; if you are outside of the zone they will not move. Work in and out of this zone to get the desired response.

2) Cattle respond very quickly to good handling and learn actions in a deliberate way, perhaps more so than horses.

3) Livestock feel less stressed if they have two or more directions to go when pressured. Always allow them this option when handling them.

4) Livestock want very much to see what or who is pressuring them. This is why they will go around you or weave if you pressure them from behind for any length of time. Avoid doing this.

5) Cattle prefer to go in the direction they are already facing or moving. Avoid spinning them around or jumping in front of them.

6) Livestock will follow others that are moving and they will follow the easiest route of movement. This is an important trait we should use to keep a herd moving.

7) Livestock sensitivity to pressure and handler position and movement will change as circumstances and situations change. Watch the animals to see the effects you are having on them during handling.

8) All stock respond to our direction (angle) of pressure. If we apply pressure into their sides, towards the head, they should go straight ahead. If we pressure the hip, the hip will move away from us.

9) Cattle are by nature herd animals and thus are more comfortable in a herd. Good handling allows them to want to stay as a herd. Stressful handling may make them leavethe herd.

10) Excessive pressure that causes bumping and crowding in a herd is one of the most stressful things we can do to the animals. Change whatever you are doing if this happens.

11) Fast moves, either our movements and/or the animals, heightens their stress level. Avoid running or fast moves.

12) Loud noise, such as shouting, also causes stress. Keep the noise down to a normal conversational tone.

Additional tips include: work as close as you can; be patient, at least a bit more than the animals; move earlier and slower, rather than later and faster; and always move in straight lines around the animals. Actions to avoid include: applying pressure from a head-on approach; applying pressure from too far away; walking or riding in arced lines up the sides of the animals; and working livestock when you are in a bad mood. Ninety percent of good handling is *not* doing the *wrong* things.

## Basic Handling Techniques

The following illustrations should help you get started in low stress handling of individual animals as well as a herd.

## Summary

The key to becoming a good livestock handler is to stop doing the things that stress or bother the animals and start using low stress handling techniques. Be sensitive to what constitutes force to the animals and abandon the idea of forcing them to do what you want. Work the animals with the low stress method until they are comfortable enough to respond consistently and naturally. In training, we are demonstrating that we are not aggressive. We do this by releasing pressure when they respond. Begin by training your livestock to appropriately handle pressure from theside, then to respond to pressure from towards the rear, and finally to go by you with ease.

Before you try to get your livestock to do what you want them to do (i.e., go through a gate, or load into a trailer), train them to do well the small tasks they need to accomplish the final feat. Then you can get them to do what you want. Patience is needed to be a good handler. The more we change the more the animals will change. It may take you 10 minutes or 10 hours, but you can get them to change if you do.

Start your lessons at the level of the livestock. They will tell you where that level is, how fast to progress and how it is working. If what you are doing is not working, change your technique or go back to a level where you can control the animals and build from there. Livestock, first and foremost, want relief from pressure. As they become more sure they can obtain relief, herds go from being afraid of us to responsive and relaxed to downright glad to be moving to a new place. Watch for these changes.

Low stress livestock handling has the potential to be one of the most effective range management tools we have, especially for protecting and/or enhancing riparian areas. The major obstacle in adopting low stress handling is that it requires a change in how producers and handlers think. I am convinced that without that change, grazing on public rangelands faces a grim future. Handling livestock with this technique requires patience and it takes time, both to learn the technique ourselves and to train the livestock to respond. Adopting the low stress method requires a commitment from the rancher, the livestock handlers or riders and the agency staff administering public rangelands. Grazing associations and agencies that have used collaborative planning and low stress handling, such as on the Morgan Creek Allotment at Challis, Idaho, have seen an improvement in riparian areas, lower costs in meeting grazing standards, and increased job satisfaction.

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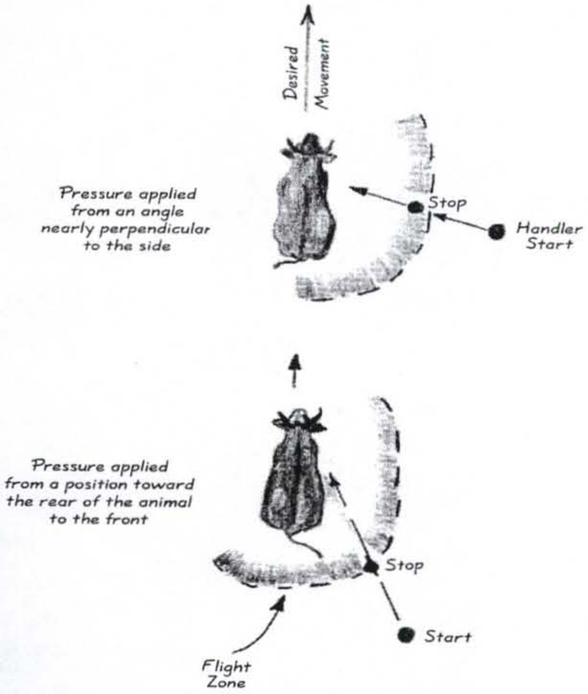
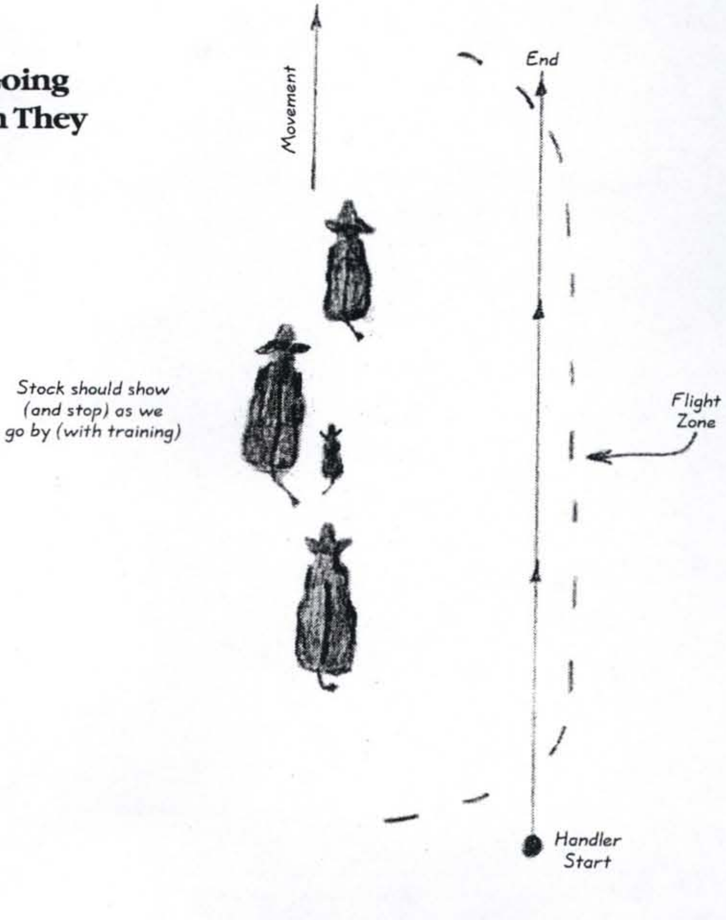
## Training Stock to Take Pressure From The Sides and The Back

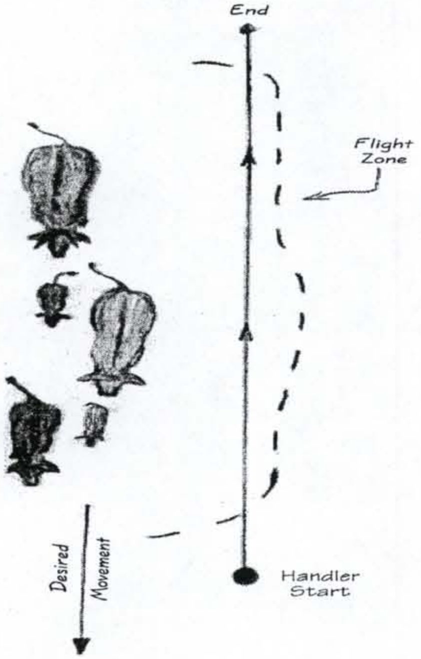
**Objective:** To move the animal forward and be comfortable with pressure applied into the side from different handler angles of approach.



## Letting Stock Slow Down By Going By Them In The Same Direction They Are Going

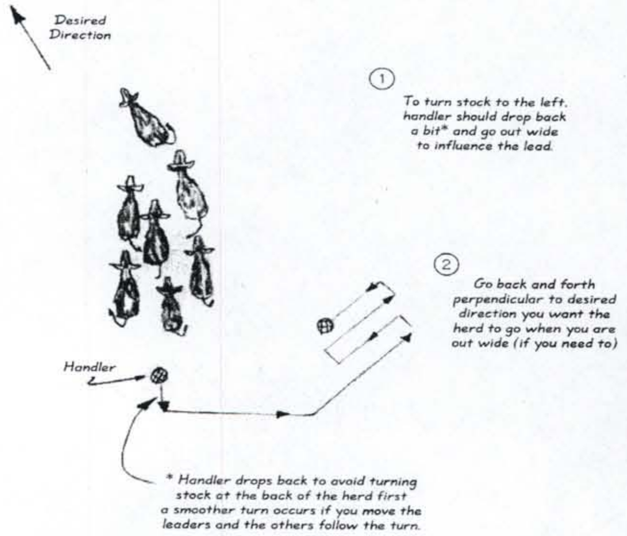


## Training Stock To Be Comfortable Going By Us And Move Ahead As We Go By (Speed Up)



Stock should speed up as we go by or walk straight away if they are standing still.

## Turning Stock By Moving Out To The Side



① To turn stock to the left, handler should drop back a bit* and go out wide to influence the lead.

② Go back and forth perpendicular to desired direction you want the herd to go when you are out wide (if you need to)

* Handler drops back to avoid turning stock at the back of the herd first a smoother turn occurs if you move the leaders and the others follow the turn.

# Some Basic Principles of Habitat Use

**Paul R. Krausman**

## Abstract

**The concept of habitat is a cornerstone in the management of wildlife. However, the understanding and management of habitat has been confused with loose terminology and flexible definitions that make communication difficult among biologists and with the public. My objective is to present some definitions related to habitat, summarize principles related to habitat use, and briefly discuss their implications to habitat management. I define habitat, habitat use, habitat selection, habitat preference, habitat availability, habitat quality, unused habitat, and critical habitat. Concepts related to habitat that biologists should be aware of include the concept that habitat has a specific meaning, habitat is species specific and scale dependent, and measurements matter. The management of habitat will be of little value unless biologists first determine an animal's habitat use patterns within a specific environment and then consider the evolutionary and human disturbances that influence it.**

## Introduction

In the simplest form, the habitat of an organism is the place where it lives (Odum 1971). This simple concept of habitat is informative, but one needs to go farther when discussing habitat in relation to wildlife management. Giles (1978) presents a wildlife-habitat-people triad that represents the three major aspects of wildlife management as equal and interactive. Thinking about any species is difficult without considering the species habitat or the human created influences, which so drastically influence them.

Most biologists would have a difficult time visualizing any organism without also visualizing its habitat. They go hand in hand. However, understanding habitats and managing them is not as simple even though there is an abundance of literature that addresses habitat (Verner et al. 1986, Hall et al. 1997). Leopold (1933) stated that "science had accumulated more knowledge of how to distinguish one species from another than of the habits, requirements, and inter-relationships of living populations." One of the earliest works examining the habitat of a species was Stoddards' (1931) study of bobwhite quail (*Colinus virginianus*). Since then, the field has advanced significantly. Leopold (1933) outlined the evolution of wildlife management as progressing through 5 stages: laws and regulations, predator control, reservation of land and refuges, artificial replenishment, and environmental controls. The last step could be expanded or a sixth step added: habitat management and control. However, as biologists' and land managers' understanding of habitat increases, the use of concepts and terms is not consistent. This distorts the communication among scientists in our disciplines, the lay person, and confuses the public because we give ambiguous, indefinite, and non-standardized responses to ecological inquiries in legal and public situations. All one has to do is quickly glance at the literature to see the different uses of terminology in relation to habitat (Hall et al. 1997). My objective is to summarize some of the basic definitions related to habitat, principles related to habitat, and briefly discuss the management of habitat.

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## Habitat Terminology

Hall et al. (1997) examined how recent (i.e., 1980-1994) authors used habitat-related terms by reviewing 50 papers from peer-reviewed journals and books in the wildlife and ecology fields that discussed wildlife-habitat relationships. In their review of each paper, Hall et al. (1997) noted if habitat terms were defined and evaluated the definition(s) against standard definitions presented by Morrison et al. (1992) and Block and Brennan (1993), which were derived from Grinnel (1917), Leopold (1933), Hutchinson (1957), Daubenmire (1968), and Odum (1971). Of the 50 articles reviewed, only 9 (18%) correctly defined and used terms related to habitat. The following terms and definitions ( Hall et al. 1997) are proposed as standard terminology.

### Habitat

Habitats are the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism. Habitat implies more than vegetation or vegetation structure. It is the sum of the specific resources that are needed by organisms

(Thomas 1979). These resources include food, cover, water, and special factors needed by a species for survival and reproductive success (Leopold 1933). Wherever an organism is provided with resources that allow it to survive, that is habitat. Thus, migration and dispersal corridors and the land that animals occupy during breeding and nonbreeding seasons are habitat.

### Habitat use

Habitat use is the way an animal uses the physical and biological resources in a habitat. Habitat may be used for foraging, cover, nesting, escape, denning, or other life history traits. These categories (e.g., foraging, escape) divide habitat but overlap occurs in some areas. One or more categories may exist within the same area, but not necessarily. An area used for foraging may be comprised of the same physical characteristics used for cover, denning, or both (Litvaitis et al. 1996).

The various activities of an animal require specific environmental components that may vary on a seasonal or yearly basis. A species may use one habitat in summer and another in winter. This same habitat may be used by another species in reverse order (Hutto 1985, Morrison et al. 1985).

### Habitat selection

Habitat selection is a hierarchical process involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment (Hutto 1985). Wecker's (1964) classical studies of habitat selection by deer mice (*Peromyscus maniculatus*) revealed that heredity and experience play a role in determining selection. Rosenwieg (1981) asserted that habitat selection was generated by foraging decisions. However, foraging is only one behavior driving habitat selection. Habitat may be selected for cover availability, forage quality and quantity, and resting or denning sites. Each of these may vary seasonally. If an individual or species demonstrates disproportional use for any factor, then selection is inferred for those criteria (Block and Breenan 1993). Hilden (1965) structured his ideas on habitat selection by categorizing the differences between proximate and ultimate factors. Proximate factors serve as cues an animal uses to determine the suitability of a site including the specific vegetation composition within a desired habitat. Reproductive success and survival of the species are the ultimate reasons that influence a species to select a habitat (Hilden 1965). The ability to persist is governed by ultimate factors such as forage availability, shelter, and avoiding predators (Litvaitis et al. 1996).

Several interacting factors have an influence on habitat selection for an individual (e.g., competition, cover, and predation). Competition is involved because each individual is involved in intraspecific and interspecific relationships that partition the available resources within an environment. Competition may result in a species failing to select a habitat suitable in all other resources (Block and Brennan 1993) or may determine spatial distribution within the habitat (Keen 1982).

Predation also complicates selection of habitat (Block and Brennan 1993). The existence of predators may prevent an individual from occupying an area. Survival of the species and its future reproductive success are the driving forces that presumably cause an individual to evaluate these biotic factors. With a high occurrence of competition and predators, an individual may choose a different site with less optimal resources. Once predators are removed, areas with necessary resources can then be inhabited (Rosenweig 1981).

Habitat selection is therefore an active behavioral process by an animal. Each species searches for features within an environment that are directly or indirectly associated with the resources that an animal would need to reproduce, survive, and persist. Habitat selection is a compilation of innate and learned behaviors that lie on a continuum of closed to open (i.e., learning) genetic programs (Wecker 1964). A genetic program gives an individual preadaptation to behave in a certain manner. Therefore, preadaptation to certain environmental cues plays an important role in habitat selection, but the potential for learning may exist in some species (Morrison et al. 1992).

### Habitat preference

Habitat preference is the consequence of habitat selection, resulting in the disproportional use of some resources over others. Habitat preferences are most strikingly observed when animals spend a high proportion of time in habitats that are not very abundant on the landscape.

### Habitat availability

Habitat availability is the accessibility and procurability of physical and biological components of a habitat by animals. Availability is in contrast to the abundance of resources, which refers only to their quantity in the habitat, irrespective of the organisms present (Wiens 1984). Theoretically, one should be able to measure the amounts and kinds of resources available to animals but in practice it is not always possible to assess resources availability from an animal's point of view (Litvaitis et al. 1994). For example, the abundance of a prey species for a particular predator could be measured, yet not all of the prey in the habitat is available to the predator because there may be factors, (e.g., ample cover) that restrict their accessibility. Similarly, Morrison et al. (1992) suggested that vegetation beyond the reach of an animal is not available as forage, even though the vegetation may be preferred. Measuring actual resource availability is important to understand wildlife habitat, but in practice it is seldom measured because of the difficulty of determining what is and what is not available (Wiens 1984). Consequently, quantification of availability usually consists of a priori or a posteriori measure of the abundance of resources in an area used by an animal, rather than true availability.

### Habitat quality

Habitat quality refers to the ability of the environment to provide conditions appropriate for individual and population persistence. Hall et al. (1997) suggest that habitat quality is a continuous variable, ranging from low (i.e., based on resources only available for survival), to median (i.e., based on resources available for reproduction), to high (i.e., based on resources available for population persistence). Habitat quality should be linked with demographics, not vegetative features, if it is to be a useful measure. For example, Ables and Ables (1987) evaluated habitat quality by comparing two groups of Rocky Mountain elk in Yellowstone National Park. Unused or unoccupied habitat are useful when biologists and managers are discussing threatened, endangered, or rare species that are reduced in number to the point they cannot use some areas of habitat. However, if their numbers were greater they would use the "unused" habitat.

### Critical habitat

Critical habitat is primarily used as a legal term describing the physical or biological features essential to the conservation of a species, which may require special management consideration or protection (U.S. Fish and Wildlife Service 1988). Because critical habitat can occur in areas within or outside the geographic range of a species (Shreiner 1976, U.S. Fish and Wildlife Service 1988) the definition is not ecologically specific enough to allow for easy and rapid delineation of critical areas for threatened and endangered organisms. Also, it is not definitive enough to satisfy many public interest groups concerned with U.S. Fish and Wildlife Service listing decisions. Critical habitat should be specifically linked with the concept of high quality hability; the ability of an area to provide resources for population persistence. This definition would make it an operational and ecological term and not political (Murphy and Noon 1991).

As exemplified by Hall et al. (1997) habitat terminology has been used in the literature vaguely and imprecisely. However, to be able to communicate effectively and obtain accurate information about habitats, land managers and biologists should be able to accurately measure all aspects of habitat.

## General Concepts Related to Habitat Use

Definitions only help understand how organisms interact with their habitat. To be even more meaningful there are basic concepts that have evolved with the importance of habitat: habitat has a specific meaning, is species specific, is scale dependent, and measurements matter. Some of these concepts are implied in the definitions provided but additional emphasis is warranted.

### Habitat Has A Specific Meaning

That biologists use the term habitat several ways is not useful, and is confusing to the public. Of course, habitats are variable but they all include the specific resources and conditions in an area that produce occupancy. This includes survival and reproduction. Habitat is frequently used to describe an area that supports a particular type of vegetation (Morrison et al. 1992). Vegetation is important but is only part of habitat that includes food, cover, water, temperature, precipitation, topography, other species (e.g., presence or absence of predators, prey, competitors), special factors (e.g., mineral licks, dusting areas), and other components in an area important to species that managers may not have identified. When habitat is viewed in this manner there are numerous components that are unique to the organism in question.

### Habitat Is Species Specific

When I hear someone state "This is great wildlife habitat", it is like walking into a brick wall and I can only guess what they mean. All the components necessary for reproduction and survival are not the same for all species and "great wildlife habitat" for one species may not even come close to serving as appropriate habitat for others. This has and will continue to be a problem because manipulations of the landscape will favor the habitats of some species but be detrimental to the habitats of others. A lot of effort has been placed on ecosystem management (Czech and Krausman 1997) in the 1990s, but when considering specific organisms the manager needs to consider their unique array of requirements for survival. With a knowledge of habitat requirements for the species of interest, the manager can make informed decisions as to how landscape alterations will influence plant and animal communities.

## Habitat Is Scale Dependent

Macrohabitat and microhabitat are common terms but actually relate more to the landscape level at which a study is being conducted for a specific animal than to a type of habitat. Generally, macrohabitat refers to landscape-scale features such as seral stages or zones of specific vegetation associations (Block and Brennan 1993). Microhabitat usually refers to finer scaled habitat features. Johnson (1980) recognized this hierarchical nature of habitat use where a selection process will be of higher order than another if it is conditional upon the latter. He summarized four natural ordering habitat selection processes (Johnson 1980).

First-order selection. This is essentially the selection of the physical or geographical range of a species.

Second-order selection. The second-order selection is the home range of an individual or social group within their geographical range.

Third-order selection. This relates to how the habitat components within the home range are used (i.e., areas used for foraging).

Fourth-order selection. This order of habitat selection relates to how components of a habitat are used. If third-order selection determines a foraging site, the fourth-order would be the actual procurement of food items from those available at that site.

Based on these criteria, macrohabitat is first-order of habitat selection and microhabitat is similar to the second, third, and fourth levels in Johnson's (1980) hierarchy. Understanding these levels can have profound influences on the management of a species. For example, Etchberger and Krausman (in press) found that the desert bighorn sheep (*Ovis canadensis mexicana*) used most portions of the Little Harquahala Mountains in western Arizona (second-order selection) throughout the year but individual females used specific individual sites for lambing. In addition, site fidelity was strong for each site used by each female. Understanding the importance of these smaller areas at specific times to the population would influence the way the population is managed. This example also demonstrates that habitat use is temporal.

## Measurements Matter

Habitat is not ambiguous and to understand how it interacts with a species one must ask the correct questions: What component is being measured? When is it being measured? And, how many samples are necessary for meaningful results? Obviously, to even pose these questions, one has to have knowledge of an animal's total life history strategy. Without it, measurements of habitat could be meaningless or erroneous. This is not always easy, even with well-studied species such as elk (*Cervus elaphus*). For example, for years many biologists accepted the concept that weather-sheltering effects of dense forest cover or thermal cover reduced energy expenditure and enhanced survival and reproduction. As a result, providing thermal cover for elk was a key habitat objective on elk ranges in the West. Cook et al. (1998), however, demonstrated that energetic status and reproductive success were not enhanced with thermal cover, and suggested that habitat management based on the perceived value of thermal cover should be reevaluated. The majority of the empirical support for the thermal cover hypothesis was derived from observational studies of habitat selection. Peek et al. (1982) and Cook et al. (1998) discussed and demonstrated the difficulty associated with determining habitat requirements from empirical observations of habitat use. They also demonstrated the need for scientific studies within a clear conceptual framework with adequate sampling rigor.

## Implications to Habitat Management

Obviously, a discussion of managing habitat is not possible within the context of this manuscript. The reader should consult Morrison et al. (1992, 1998) or Pain and Bryant (1994) for a detailed treatment of contemporary management. However, much of what is addressed in this paper has implications to habitat management. Leopold (1933) developed the basic tenants of habitat management: that organisms require the essentials of food, water, cover, and special factors for survival. Giles (1978) and others built on this concept and developed the wildlife- habitat-human triad that is so critical to management today. The triad forces one to examine wildlife in the context of its evolutionary origin and see how wildlife is affected by human disturbances. There are numerous models and techniques biologists can use to manage habitats (that are readily available in the literature), but for them to directly benefit wildlife, biologists must first consider the animal and its habitat use within the environment (Morrison et al. 1998).

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# Impact of Spatial Memory on Habitat Use

## Larry D. Howery, Derek W. Bailey, and Emilio A. Laca

## Abstract

**Spatial memory allows animals to remember where they have foraged and use that information to determine where they will travel and forage. Spatial abilities likely evolved as a survival mechanism to allow herbivores to forage more efficiently and safely. Spatial memory can be inferred when behavior can be predicted from an animal's prior experiences. Maze and arena studies have been used to demonstrate spatial memory in various livestock species. Anecdotal observations suggest that spatial memory plays an important role in grazing distributions of both wild and domestic ungulates. By examining how animals remember areas with abundant and scarce resources, researchers are discovering more about the behavioral mechanisms that determine grazing distribution patterns of large herbivores. The challenge is to use knowledge about spatial memory to predict grazing patterns and to manipulate grazing distribution through management. In this paper we review basic concepts and evidence for spatial memory in ungulates and other species, discuss working hypotheses regarding how land managers and livestock producers might manipulate grazing distribution and behavior using our current knowledge of spatial memory, and identify gaps in our understanding of spatial memory and propose hypotheses to address these gaps.**

## Introduction

The key to developing innovative management practices to solve animal distribution problems is to understand the behavioral processes that animals invoke during grazing (Bailey et al. 1996). Recent studies of spatial memory in large herbivores have improved our understanding of grazing distribution (Bailey et al. 1996, Edwards et al. 1996, 1997, Laca 1998). Other research and modeling efforts that incorporate spatial memory and other cognitive processes have also improved our understanding of grazing processes (Coughenour 1991).

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In a grazing behavior context, spatial memory is the ability of an animal to remember where it has foraged and use that information to determine where it will travel and forage. Spatial memory, the memory of locations in space, can be inferred when behavior can be predicted from an animal's prior experiences (Domjan and Burkhard 1982). By examining how animals remember areas with abundant and scarce resources, researchers are discovering more about the behavioral mechanisms that determine grazing distribution patterns of large herbivores. The challenge is to use knowledge about spatial memory to predict grazing patterns or to manipulate grazing distribution through management. The objectives of this paper are to: 1) describe basic concepts of and evidence for spatial memory in ungulates and other species, 2) discuss working hypotheses regarding how land managers and livestock producers might manipulate grazing distribution and behavior of large ungulates using our current knowledge of spatial memory, and 3) identify gaps in our understanding of spatial memory and propose approaches to address these gaps.

## Basic Concepts

### Working and reference memory

Spatial memory has been represented as a two-part code, working (short-term) memory and reference (long-term) memory (Honig 1978, Olton 1978, Staddon 1983). *Working memory* is retained only long enough to complete a particular task, after which the information is discarded because it is no longer needed, or because it may interfere with the successful completion of the next task. In contrast, *reference memory* is retained for longer periods because it is needed to complete successive tasks. Working and reference memory have been evaluated in mazes for a number of species where the animal's "objective" is to retrieve food without reentering any arms of the maze. Working memory is used *within* trials to remember which arms have been visited, whereas reference memory is used *between* trials to store the maze's spatial configuration and food availability and quality.

### The importance of scale

Senft et al. (1987) and Bailey et al. (1996) identified discretionary spatial hierarchies to describe grazing behavior. For grazing herbivores, temporal and spatial scales of forage and habitat availability probably determine the functional value of working and reference memory (Laca and Ortega 1996). Knowledge of how working and reference memory interact across hierarchical levels is incomplete, but the following discussion provides a framework for our current level of understanding.

A *bite* is defined by a sequence of prehension, jaw and tongue movements, and severance by head movement (Laca et al. 1994). Diet selection of individual plants and plant parts is determined by animal decisions made at this level. Because livestock consume thousands of bites a day, it is unlikely that spatial memory plays a significant role at this level.

A *feeding station* is defined as an array of plants available to an animal for grazing without moving its front feet (Novellie 1978). Working memory may affect behaviors at this hierarchical level as animals may remember and avoid recently grazed areas.

A *patch* is a cluster of feeding stations separated from others by a break in the foraging sequence when animals reorient to a new location (Jiang and Hudson 1993). Working memory operates at the patch level *within* grazing bouts (i.e., grazing periods that are separated by non-grazing activities such as resting or ruminating) so that animals avoid depleted or poor areas and stay within preferred and ungrazed patches. Reference memory may also be used at the patch level *between* grazing bouts because patches vary in levels of nutrients and may be routinely visited or avoided on a daily basis (Bailey 1995, Ruyle and Rice 1996).

A *feeding site* is a collection of patches in a contiguous foraging area that animals use within a grazing bout. Animals may use working memory to return to or avoid feeding sites that were visited during the preceding grazing bout. Animals may also use reference memory to remember important abiotic and biotic characteristics of feeding sites from one day to the next.

A *camp* is a set of feeding sites with a common focus where animals drink, rest, or seek cover between grazing bouts within their home range area. Reference memory is probably used at this level to store the location(s) of water, cover, and the relative value of feeding sites within a camp. This information may be stored for periods of weeks to months.

Finally, *home range areas* are collections of camps defined by fences, natural barriers, and extent of migration or transhumance. Reference memory is used to remember the relative value of several camps within a home range area for months, even years.

### Incorporating spatial memory into other grazing behavior models

Although many foraging models ignore the cognitive abilities of animals, we submit that paradigms that disregard spatial memory (e.g., random search) may fail to accurately predict grazing distribution patterns of large herbivores because they do not recognize that animals can learn, retain, and react to previous foraging experiences. Livestock can remember areas that produce high quality forage and seek them out (Howery et al. 1996), and conversely, remember and avoid areas with low quality forage (Bailey 1995). Bailey et al. (1996) developed a conceptual model that incorporates spatial memory (Fig. 1). Their model predicts that selection of foraging areas is based on previous experience and that feeding sites are selected based on both abiotic and forage characteristics.

## Evidence of Spatial Memory in Livestock

Researchers have only recently begun to investigate spatial memory in livestock. Spatial memory has been studied in cattle (Bailey et al. 1989a,b, Laca 1998) and sheep (Edwards et al. 1996, Dumont and Petit 1998), as well as in a number of non-livestock species (Dyer et al. 1993, Healy and Krebs 1992, Langley 1994, MacDonald and Wilkie 1990, Noda et al. 1994, Olton and Samuelson 1976). When evaluating each piece of evidence, it is important to understand that other mechanisms can produce behaviors that appear to come from spatial memory. Laca (1998) discusses several mechanisms that can influence animal distribution and suggests experimental procedures to partition them from spatial memory. The anecdotal observations and experimental studies that follow are examples of how spatial memory can help explain many foraging behaviors.

### Observational and anecdotal evidence

Rangeland and livestock managers have observed that when animals are moved from a "home" pasture to a new pasture they congregate in and explore areas that are in the direction of the pasture they were moved from. This has been observed in cases where many miles of rough terrain separate the pastures. Spatial memory may also assist livestock that are familiar with a pasture to relocate preferred watering and feeding points (Howery et al. 1996).

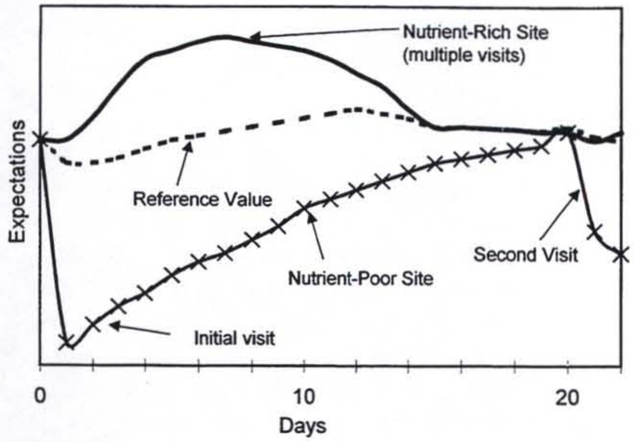

**Figure 1.** Hypothetical simulation of expectations from nutrient-rich and nutrient-poor sites. Initially, an animal has no expectations and selects the poor site. However, because the perceived value is greater than the poor site, the nutrient-rich site is selected for 20 days. Repeated encounters with the nutrient-rich site causes its expectation to exceed the perceived site value for the first few days. The standard of comparison (reference value) increases and approaches the nutrient-rich site's expectation level in a few days because it is a moving average of perceived site values from encounters during the last 4 days. Repeated encounters with undesirable foraging sites occur rarely and are not reinforced. Within 20 days, however, memory of the encounter with the poor site decays to a level where the expectation for the poor site is approximately equal to the reference value, and the poor site is selected again (Modified from Bailey et al. 1996).

Some species of domestic and wild ungulates exhibit predictable distribution patterns that repeat year after year (Gruell and Papez 1963, Geist 1971, Festa-Bianchet 1986a,b, 1988, Cederlund and Okarma 1988, Cederlund et al. 1987). Sheep (Lynch 1974, Gluesing and Balph 1980, El Aich and Rittenhouse 1988), cattle (Hodder and Low 1978), goats (Biquand and Biquand-Guyot 1992), deer (Gillingham and Bunnell 1989), and moose (Andersen 1991) may walk long distances searching for preferred plants or habitats, often passing areas with abundant forage along the way. One explanation for this seemingly enigmatic behavior is that "long-term spatial memory" of an apparent safe home range area is passed from older to younger animals (Andersen 1991, Provenza and Cincotta 1993). For example, Geist (1977) suggested that bighorn sheep were unable to expand their established home ranges because young animals rigidly conformed to the range use patterns of their predecessors. Archaeological evidence along migration routes revealed that moose in Norway continued the same migration patterns for 5000 years despite deterioration of their range (Andersen 1991).

## Maze studies

Maze studies (i.e., radial- and parallel-arm) have clearly demonstrated spatial memory in birds and small mammals (Lanke et al. 1993, Olton and Samuelson 1976, Olton et al. 1977, 1978, 1981, Kovalcik and Kovalcik 1986), and have been recently used to study the same phenomenon in livestock (Bailey et al. 1989a). Cattle were as capable as other species (rats and pigeons) tested in 8-arm radial mazes. Cattle performed much better than expected by chance, evincing an accurate working memory (Bailey et al. 1989a). For example, cattle revisited a maze arm < 0.4 times in the first 8 arm choices. Pigeons and rats reentered arms at a similar frequency (Beatty and Shavalia 1980, Roberts and Van Veldhuizen 1985). Working memory in cattle persists for at least 8 hours. Bailey et al. (1989a) removed cattle from a radial maze after they had consumed food in 4 or 8 arms and then returned the animals after a delay interval. Cattle were able to remember where they had foraged after delays of up to 8 hours but performed poorly, equivalent to chance levels, after delays of 12 hours. This decline in performance may have been an artifact of the experimental design. Trials were completed on successive days, 24 hours apart. After a 12-hour delay, cattle may not have distinguished between the delay interval within a trial (e.g., 0700 to 1900) and the 12-hour interval between trials (1900 to 0700). Rather than a failure of working memory, cattle in this study may have "reset" their working memory in anticipation of a new trial.

If food quantity or quality at a foraging location is consistent, this information also becomes an important component of reference memory. Cattle in a parallel arm maze were able to associate a location with the *quantity* of food found there and avoided locations with less food until areas with more food were exploited (Bailey et al. 1989b). Cattle are also capable of associating a location with the *quality* of food found there. Animals avoided radial arm locations with low quality food and selected locations with higher quality food first (Bailey and Sims 1998). The strength of association between food quality and spatial locations appeared to decline after 30 days because animals more frequently visited low-quality sites. Although this observation could have reflected a decay in reference memory, cattle may have been revisiting the low-quality sites to update their assessment of those locations. This behavior would be adaptive in natural environments where forage quality periodically changes across space and time (see Fig. 1).

## Arena studies

Arena studies can be characterized as a "bridge" between maze and field studies because they attempt to quantify spatial memory in a controlled environment that approximates an open field (i.e., landscape level studies). Ksiksi and Laca (1995) found that steers were able to remember 4 food locations (from 64 potential locations) in an 0.62-acre arena for up to 45 days. In a much more difficult test involving 20 food sites (64 potential locations), steers maintained an accurate spatial memory for at least 15 days after being exposed to the arena 28 times (Laca 1998).

Arena experiments have also been instrumental in elucidating the role of vision as a critical component for the development of spatial memory. Arnold (1966a,b) was probably the first researcher to experimentally evaluate the relative importance of the senses (i.e., sight, smell, taste, and touch) in grazing behavior. Arnold's tests were primarily restricted to the bite and patch levels. He concluded that "preventing sheep from seeing what they ate had remarkably little effect on their total food intake and productivity", and that the sense of sight is important mainly in orientation of the animal in space. More recent studies (Bazely and Ensor 1989, Edwards et al. 1997, Howery et al. 1999a,b, Kidunda and Rittenhouse 1992, Ortega and Laca 1997, Renken et al. 1998) indicate that animals that learn to associate forages with visual cues forage more efficiently than without cues. For example, Howery et al. (1999a) found that steers searching for fixed or variable forage locations in a 1.58-acre arena with artificial visual cues spent more time feeding and less time in non-foraging activities than without cues (i.e., animals relying on spatial memory or random search). Animals exposed to fixed and variable forage arrangements with cues also located feed more efficiently and had higher intakes than without cues.

## Managing Animal Distribution

Experimental and anecdotal evidence strongly suggests that rangeland herbivores have well-developed spatial memories. This is not surprising because of the apparent adaptive value that a cognitive process like spatial memory affords free-ranging animals. Yet, more extensive tests in realistic grazing situations are necessary before grazing distribution can be reliably managed using our knowledge of spatial memory. With that caveat in mind, we offer some working hypotheses about ways to achieve desirable animal distribution patterns by applying the current understanding of spatial memory.

Management of animal distribution using spatial memory principles can be classified based on whether the manipulation is focused upon the animal or the environment. Manipulations of animals may be invasive (e.g., hormones, emetics, electric shock), moderately invasive (e.g., herding), or noninvasive (e.g., selection for behavioral traits within or among breeds). On the other hand, environmental manipulations are those that are completely external to the animal; such manipulations (e.g., reward schedules, pasture configurations, visual cues) are intended to modify an animal's experience with the environment to alter their use of a particular location or habitat.

### Manipulating the animal

**Invasive techniques.** Hormones influence the spatial abilities of birds and mammals (Gaulin and Fitzgerald 1986, Hess and Birecree 1978). Males generally have better spatial memory than females, although there are notable exceptions depending on the adaptive value of spatial performance between the sexes (e.g., female brown-headed cow birds have better spatial memories than their male counterparts apparently because nest parasitism is a spatial task). Female rats given masculinizing hormones performed as well as males (Williams et al. 1990 op cit by Sherry 1998). Conversely, male rats gonadectomized shortly after birth perform about the same as females in radial mazes. Castration of livestock may produce a similar outcome, however, we know of no experiments that have compared the spatial capacities of cows, steers, and bulls. The potential for using these treatments in livestock management is remote but experimentation could be considered.

Animals have evolved 2 fundamentally different systems to protect them from hazards in their environment (Garcia and Holder 1985, Garcia et al. 1985). The gut-defense system protects animals from hazards to their internal environment (e.g., toxins in foods), whereas the skin-defense system protects animals from hazards in their external environment (e.g., predators). These 2 systems are stimulated by different events with different behavioral outcomes. For example, rats more easily associate taste stimuli with gastro-intestinal illness and audio-visual stimuli with shock (Garcia and Koelling 1966). Herbivores are no different from rats in this regard because they readily learn to avoid foods paired with emetics (see Provenza and Launchbaugh this volume) and places associated with electric shock. For example, steers were trained to avoid a designated "aversion area" in less than 2 days by using remotely controlled audio-electrical stimulation (Quigley et al. 1990). The audio signal alone was sufficient to keep steers out of the area after 4 days. Heifers that were shocked after entering an aversion area avoided it for 7 days, whereas heifers that were prevented from entering the aversion area with electric fence readily entered the area when the fence was removed (Markus et al. 1998). Goats wearing shock-collars learned within 30 minutes to remain within a designated area (Fay et al. 1989). Non-collared goats remained close to collared goats and thus also remained in the designated area.

**Moderately invasive techniques.** Herding or drifting has been used for many years by rangeland managers to promote desirable distribution patterns in domestic livestock, typically sheep (Skovlin 1957). More recently, herding has been employed on public rangelands to decrease the amount of time that cattle spend in riparian habitats. In order for herding to be effective, the new area that animals are herded to must have adequate forage, cover, and water so they do not immediately return to their previous location. Moreover, initial efforts may need to be exercised daily to effectively modify a pleasurable spatial memory that ostensibly causes the distribution problem. For example, cattle on Idaho summer range were drifted from gentle to more rugged terrain in an attempt to achieve more uniform distribution across the grazing unit (Howery 1993). Although more forage, water, and shade were present in the rugged area, about half of the herded animals returned to the gentler terrain within 24 to 48 hours of being moved. A favorable memory of the gentle area apparently overrode any desire to remain in the rugged area. On the other hand, persistent herding over a series of years has proven effective in training cattle to use upland areas more and riparian areas less in mountainous terrain (Butler 1998). Animals eventually learn to associate a negative event (e.g., aggressive herding using horses and dogs) with the area they previously found attractive.

Another approach that has potential to enhance animal dispersion involves introducing animals to underused areas within a grazing unit the first day of the grazing season. Roath and Krueger (1982a) suggested that heavy cattle use of riparian areas might be reduced by changing the turn-in point so that animals are not initially exposed to a high resource location (i.e., riparian area). In a later paper, Roath and Krueger (1982b) recommended introducing naive animals to underused areas within grazing units so they would become "behaviorally bonded" to those areas. Naive animals would theoretically not be predisposed to overuse high resource areas because they would have no spatial memory or expectations of concentrated food rewards in specific locations on the grazing unit (Bailey et al. 1996, Laca 1998). However, naive animals may also exhibit lower productivity because of lower intake levels (Provenza and Launchbaugh this volume). This problem needs to be resolved before this approach can be considered practical to livestock managers.

**Non-invasive techniques.** Changes in grazing patterns and behavior can be accomplished by changing animal species, breed, and perhaps individual animals (Bailey this volume). Grazing patterns differ among animal species and cattle breeds with some being more willing to use slopes and travel further from water. Grazing patterns also differ greatly among individual animals. These differences in grazing behavior may be related to the animal's spatial memory capabilities and temperament. In the future, managers may be able to select both within and between breeds to improve livestock grazing distribution.

Just as there may be genetic differences concerning forage or habitat selection within species or within livestock breeds, there may also be differences that are perpetuated socially (Mosley this volume). Ungulate offspring glean critical information from their mothers about the specific environment in which they are reared, such as the location of food, water, and cover resources. Thus, a young animal's spatial memory of a grazing unit is likely shaped early in life through exposure to a home range area with its mother. For example, replacement heifers returning to a grazing unit their second and third years of life tended to repeat their mother's or foster-mother's general location and habitat use patterns (Howery et al. 1996, 1998). Other researchers have also reported that offspring of both wild and domestic ungulates use the same general location they were exposed to by their mothers early in life (Hunter and Milner 1963, Geist 1971, Key and MacIver 1980, Festa-Bianchet 1986a,b, Cederlund and Okarma 1988, Lawrence and Wood-Gush 1988, Nixon et al. 1988, 1991). These studies suggest that ungulate herbivores apparently remember and respond to certain biotic and abiotic factors within their camps or home range areas. Thus, it would seem that waiting for animals to forget such information by moving them to another pasture is not a promising method to modify animal distribution. However, these findings do suggest an additional opportunity for managers to manipulate animal foraging and distribution patterns through animal selection. A herd's "spatial memory" of a pasture might be molded over several years by selecting animals with desirable distribution patterns that would ostensibly be transmitted to young herd members.

## Manipulating the environment

**Associative learning and reward schedules.** Animals can learn to associate specific behaviors, such as searching or moving in certain directions, with the consequences of the action (Skinner 1981, McSweeney this volume). Thus, within the proper context, animals will perform actions in order to obtain rewards such as food, water, or cover. The intensity and rate of a behavior depend on the "schedule of reinforcement"

(McSweeney this volume). In the jargon of experimental psychology, a "fixed interval" schedule of reinforcement is one in which a reward (food pellet) results from an action (pressing lever) only after a fixed time has elapsed. Animals learn to respond (i.e., perform the action) intensively just prior to the expiration of the fixed time, and to completely cease responding immediately after the reward is delivered. A "variable-interval" schedule of reinforcement involves a random time interval between rewards which results in a more constant response by the animal over time.

Laca (1998) studied a spatial analogue of temporal schedules of reinforcement. Cattle were exposed for a few weeks to either fixed or variable food locations that were not identifiable by any proximate cue other than spatial location. Steers developed contrasting search patterns that reflected their experimental treatment. When food was always in the same locations, animals used the long-term strategy (reference memory) of returning to places where food was previously found. Search efficiency was very high and animals traversed only a fraction of the experimental arena. Conversely, when food locations were randomly changed before each trial (i.e., long-term spatial memory rendered useless), animals used the short-term strategy (working memory) to avoid places visited within a trial. Search efficiency was low because animals explored most of the available area to find foods. Thus, animals apparently used reference or working memory depending on the spatial arrangement of foods: return to locations that previously contained food (fixed treatment, use reference memory), or, systematically search until food is located, avoiding previously visited sites that contained no food (variable treatment, use working memory).

More information is needed to determine if distribution patterns can be made more uniform by manipulating spatial reinforcement "schedules". For example, managers might apply various spatial reinforcement schedules by manipulating fertilization or burning practices, or by strategic supplement placement. The configuration and timing of such treatments could be applied as fixed or variable reinforcement schedules depending on management objectives. However, the effect these practices might have on animal productivity must also be addressed (e.g., increased distance traveled and declining search efficiency).

**Spatial configuration of pastures.** Bailey and Rittenhouse (1989) asserted that the addition or removal of physical barriers are powerful tools to limit or vary forage and habitat choices of grazing animals. For example, choices can be limited by locating pasture fences to restrict cattle from critical habitats while providing access to gentle inclines that afford passage to more rugged, well-watered, but underused country. Choices can be varied by subdividing large pastures to attain more homogeneity among forage patches. The more homogeneous the forage choices are within a pasture, the less likely animals will concentrate in certain areas (Bailey 1995). Conversely, the more heterogeneous a grazing area is, the more likely animals will overuse more desirable patches and avoid undesirable ones. Integrating spatial configuration of pastures with other range management techniques (e.g., judicious water and salt placement, prescribed burning) provides managers with additional tools to manipulate grazing patterns.

**Visual cues.** As stated earlier, visual cues have recently been shown to enhance the foraging efficiency of grazing animals (Bazely and Ensor 1989, Edwards et al. 1997, Howery et al. 1999a, Kidunda and Rittenhouse 1992, Ortega and Laca 1997, Renken et al. 1998). Animals using visual cues were more efficient in tracking variable and constant forage environments in small arenas (Ortega and Laca 1997, Howery et al. 1999a,b). Additional research is needed to determine whether strategic placement of visual cues can be used under field conditions to alter undesirable distribution patterns across landscapes.

## What Should Be Studied Next?

We have argued that until the underlying behavioral mechanisms responsible for aggregate distribution patterns are better understood, grazing behavior models usually will be site-specific. Although grazing behavior is always site-specific to some degree, understanding how ungulate herbivores use spatial memory will improve our ability to predict and desirably manipulate animal distribution patterns.

Numerous gaps remain in understanding the cognitive abilities of herbivores during foraging. For example, the persistence of reference memory has only begun to be examined. Effects of social interactions on spatial memory must be thoroughly evaluated because actions of herd members can override the actions of an individual (Lane et al. 1990). Current research has not thoroughly evaluated the cognitive abilities among or within livestock breeds. The ability of cattle and other species to solve complex spatial tasks needs further study. More complex tasks should be developed to further test the extent of spatial memory in large ungulates and to determine if some individuals are more adept than others. If there are individual differences in spatial abilities, are such differences inherited, learned, or both?

Many of the research ideas recently tested under controlled conditions need further evaluation in the field (surgical and hormonal treatments, visual cues, shock collars, etc.). Recent advances in navigational technology will provide new and improved ways to accurately track animal movements and behavior. For example, global positioning system (GPS) receivers have been incorporated into collars and placed on cattle and other animals. This new system can track animals within 15 feet and record their position at intervals of minutes to hours for periods of weeks to months. Data collected from GPS units might be used to test how manipulations of animals and their environment affect grazing distribution patterns across landscapes (e.g., Bailey et al. 1996).

In conclusion, recent research demonstrates that ungulate herbivores have excellent spatial memories. These abilities likely evolved as a survival mechanism to allow herbivores to forage more efficiently and safely. Increased understanding of spatial memory presents new opportunities to better predict where animals forage and to develop new management strategies to improve grazing distribution. Continued research at both basic and applied levels is needed to advance current understanding.

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# Influence of Species, Breed and Type of Animal on Habitat Selection

## Derek W. Bailey

## Abstract

**Improving grazing distribution may improve resource conditions of many rangelands. Land managers and livestock producers may be able to modify grazing use by selecting livestock species or wildlife that are more adapted to rugged terrain. Economic and management considerations must be carefully evaluated when selecting which species will be used. Livestock breeds differ in their use of rugged topography. Ongoing research is investigating the potential of selecting and culling individual animals to improve livestock grazing distribution. Cows with calves are more reluctant to graze steep slopes or travel far from water than cows without calves or yearlings. Managers should consider selection among animal species, livestock breeds, ages, nursing status, and perhaps culling and breeding individual animals as tools to improve grazing distribution.**

## Introduction

Cattle often utilize grasslands unevenly by grazing some areas more than others, leading to localized heavy grazing (Coughenour 1991). Uneven grazing distribution can reduce the carrying capacity of grasslands and the efficiency of livestock production (Anderson 1967). In the upland areas of Europe, low grazing pressure leads to the creation of unexploited areas that are increasingly covered with shrubs (Bailey et al. 1998a). These areas are more sensitive to fires, and may potentially erode and change aspects of the landscape. In the western United States, livestock often congregate along riparian areas (Smith et al. 1992) where trampling may reduce streambank stability and increase erosion (Kauffman et al. 1983). Concentrated grazing on uplands can reduce litter and vegetative cover which may reduce water infiltration, increase active erosion and increase the sediment load of waterways (Vallentine 1990). Livestock producers and land managers must consider spatial variation in grazing to adequately evaluate the impact of grazing by livestock and other herbivores (Coughenour 1991), and to prescribe appropriate management actions needed to remedy grazing distribution problems.

Virtually all of the approaches currently used to improve livestock grazing distribution (water development, herding, salting and fencing) were described over 40 years ago (Skovlin 1957). Some of these management actions such as water development and fencing may require large capital inputs. Innovative and cost-effective techniques to improve livestock grazing distribution are needed. Choosing grazing animals that are more willing to graze further from water, graze steeper slopes and higher elevations may be an effective practice to reduce uneven grazing that is often observed in large, rugged pastures in extensive rangeland livestock operations. The objective of this paper is to discuss approaches that land managers and livestock producers can use, or may someday use, to select and produce animals whose grazing patterns achieve management objectives.

## Selection of Animal Species

Selecting which livestock species is to be used should be based primarily upon management objectives, marketing opportunities and economics (Vallentine 1990). Ungulate species often utilize different types of topography and vegetation types, but the choices are often limited for a given producer. In the western United States, livestock producers generally graze cattle, sheep, goats and horses. Sheep and goats are generally considered more suitable for steep, rugged mountainous terrain than cattle (Bell 1973). Areas grazed by cattle and sheep in mountain rangelands in Utah were usually separated by topography (Ruyle and Bowns 1985). This separation is at least partially a result of herding that encourages sheep to use steeper terrain. A recent study in Idaho (Butler 1998) suggests that consistent herding, similar to that traditionally used with sheep, can minimize cattle use of riparian areas and increase grazing on upland slopes.

Horses usually travel directly to and from water, often on the run. This grazing characteristic suggests that they will more readily utilize areas that are further from water (Bell 1973). When grazed in common pastures in Wyoming, both feral horses and cattle spent most of their

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time within 7 miles from water (Miller 1983). Salter and Hudson (1980) concluded that cattle and horses used different areas of the same pasture when both species were present.

Rangeland livestock producers may, in some situations, use other ungulate species such as bison, elk and deer to generate income from rangelands. Private game ranching and fee hunting have gained more attention and popularity. Anecdotal observations and some studies suggest that wild ungulate species utilize extensive rangeland areas more evenly than domestic livestock (Vallentine 1990).

Although ungulate species differ in their use of rangelands, only one or two species (usually livestock) can be practically or economically managed on a given parcel of rangeland. In the western United States, the focus has been on improving beef cattle grazing distribution (Vavra 1992, Walker 1995).

## Breed Selection

Differences in grazing patterns have been observed among cattle breeds, suggesting that selection for grazing distribution within livestock species may be effective. Brangus cattle travel further during grazing than Hereford-Angus cattle (Herbel and Nelson 1966). Havstad and Doornbos (1987) found differences in distance traveled between Simmental and Hereford or Angus cattle, but differences were not consistent from year to year. Tarentaise cattle used higher terrain and steeper slopes than Hereford cattle for two successive years (Table 1). In one pasture at the same location, Piedmontese- and Charolais-sired first-calf heifers traveled further from water (horizontally and vertically) than Angus-sired heifers. However, in another pasture, grazing use was similar among these Angus-, Charolais-, Piedmontese- and Salers-sired first-calf heifers. Meuse-Rhine-Yssel cattle spent more time grazing patches with shorter and less stemmy vegetation, which resulted in a higher quality diet than obtained by Herefords (WallisDeVries 1994).

Although more research is needed, livestock producers and land managers may be able to identify cattle breeds that are more willing to travel from water and use rougher terrain. For example, Tarentaise cattle originated in the French Alps and may be better adapted for grazing steeper, more rugged topography. In warmer climates, cattle with Brahman breeding appear more willing to travel from water, especially at higher temperatures. Using more adapted breeds in extensive and rugged rangeland pastures, may increase uniformity of grazing and minimize localized areas of heavy grazing.

## Selection of Individual Animals

Selecting livestock based on their grazing patterns has the potential for improving grazing distribution (Roath and Kruegar 1982). This suggestion was based on the observations that cattle formed social groups that grazed in different habitat types; these authors speculated that livestock grazing distribution could be improved if the social groups that preferred and remained in riparian areas were culled. Howery et al. (1996) found that cattle showed a high degree of fidelity to a home range, indicating that selective culling might change grazing distribution. Selective culling is a potentially cost-effective technique to improve grazing distribution if: 1) there is significant individual variation in the trait; 2) distribution behavior is heritable; 3) the trait can be readily identified, measured or predicted; and, 4) there are few adverse relationships between grazing distribution and animal performance.

## Selection Differential

Managers may be able to take advantage of the large variation observed in individual behavior (Bailey et al. 1998b). For a selection program to be effective, the selection differential must be large. Greater progress will be made if the cattle kept for breeding are more likely to use rugged topography than cattle that are culled, and thus higher levels of variation among individuals are desirable.

In a foothills pasture in northern Montana, grazing patterns of individual cattle were observed 2 or 3 times per week for at least 6 weeks in each pasture. Use of slopes and distance traveled to water (horizontally and vertically) varied greatly among individual cattle (Table 2). Some cattle spent most of their time on slopes over 20% and climbed over 60 m (200 feet) above water, while others used more gentle slopes (10% or less) and climbed less than 15 meters (160 feet) above water.

Global Positioning System (GPS) tracking system equipment (e.g., Lotek GPS 2000) can track cattle and other animals at intervals of minutes to days with an accuracy of within 7 meters (20 feet). Cattle that were observed more frequently on steep slopes and ridges (hill climbers) or more frequently on gentle slopes near water (bottom dwellers) were tracked the following year. The GPS tracking system clearly showed a distinction between the grazing patterns of cattle previously classified as hill climbers and bottom dwellers (Fig. 1 to 4). The hill climbers in this sample (Fig. 1 and 2) used opposite sides of a high ridge; whereas the bottom dwellers concentrated in different areas (Fig. 3 and 4) but tended to avoid steep slopes. Most importantly, these

Table 1. Differences in use of slopes and horizontal and vertical distance traveled to water by cattle of Hereford and Tarentaise breeding in two foothill pastures.

| | | Slope (%) | | Horizontal distance to water (m) | | Vertical distance to water (m) | |
|---|---|---|---|---|---|---|---|
| Breed | Year | Pasture 1 | Pasture 2 | Pasture 1 | Pasture 2 | Pasture 1 | Pasture 2 |
| Hereford | 1997 | 14.4 | $19.2^{ab}$ | $349^{a}$ | 440 | $31^{a}$ | $48^{a}$ |
| | 1998 | | $19.4^{a}$ | | 468 | | $53^{a}$ |
| ¾Hereford-¼Tarentaise | 1997 | 13.9 | $18.9^{a}$ | $365^{ab}$ | 460 | $34^{ab}$ | $53^{ab}$ |
| | 1998 | | $20.0^{ab}$ | | 492 | | $57^{ab}$ |
| ½Hereford-½Tarentaise | 1997 | 14.7 | $19.4^{ab}$ | $371^{ab}$ | 469 | $34^{ab}$ | $56^{ab}$ |
| | 1998 | | $21.0^{ab}$ | | 494 | | $61^{bc}$ |
| ¼Hereford-¾Tarentaise | 1997 | 14.2 | $21.3^{b}$ | $373^{ab}$ | 414 | $34^{ab}$ | $60^{b}$ |
| | 1998 | | $21.8^{b}$ | | 461 | | $63^{bc}$ |
| Tarentaise | 1997 | 15.0 | $20.1^{ab}$ | $382^{b}$ | 430 | $38^{b}$ | $59^{b}$ |
| | 1998 | | $21.6^{b}$ | | 475 | | $64^{c}$ |

Breeds with different superscripts for the same year and within the same column differ significantly (P<.05) for that trait.

Table was adapted from Bailey et al. (1998b).

Table 2. Variation in individual cattle use of slopes and horizontal and vertical distance to water in two foothill pastures.

| | Slope (%) | | Horizontal distance to water (m) | | Vertical distance to water (m) | |
|---|---|---|---|---|---|---|
| | Pasture 1 | Pasture 2 | Pasture 1 | Pasture 2 | Pasture 1 | Pasture 2 |
| Year 1997 | | | | | | |
| Maximum | 21.4 | 28.1 | 498 | 896 | 62 | 103 |
| Minimum | 7.7 | 10.1 | 210 | 236 | 11 | 15 |
| Std. Dev. | 2.7 | 3.6 | 52 | 120 | 11 | 17 |
| Year 1998 | | | | | | |
| Maximum | | 29.1 | | 834 | | 87 |
| Minimum | | 13.6 | | 297 | | 29 |
| Std. Dev. | | 3.1 | | 101 | | 12 |

Adapted from Bailey et al. (1998b).

data show that grazing patterns of individual animals can vary greatly in Montana foothills rangeland. Howery et al. (1996) also observed that individual grazing patterns of cattle differed in a mountainous Idaho pasture. The wide variation in individual grazing patterns suggests that sufficient selection differential is available for a grazing distribution selection program to be effective.

## Heritability

The differences in grazing patterns observed among cattle breeds mentioned above suggests that this behavior may be heritable. Grazing patterns of first-calf heifers were compared to the grazing patterns of their dams at our research center in Havre, Montana. The hypothesis of this study was that any observed relationships between cows and their female offspring would indicate that grazing patterns could be inherited, learned from their dam, or both. Dams and daughters were observed in the same foothills pastures during the same period. Preliminary analysis showed that in one of the two pastures there was a weak relationship (P<0.10) between a cow and her female offspring. In the other pasture, there was no relationship. Further observations and analyses are planned because younger cows tend to graze gentler slopes and lower elevations than older cows. In addition, younger animals are more influenced by their peers' use patterns than older animals (Howery et al. 1998). This age effect may confound any relationships between dams and their female offspring.

Other grazing behaviors appear to be heritable. Winder et al. (1995) suggested that diet selection may be highly heritable. Sires in their Brangus herd accounted for a significant amount of the variation in diet selection for certain forage species during certain times of the year. The corresponding heritability estimates were high (.51 to .87), but the standard errors for the estimates were also high (.49 to .52). Differences in diet selection in the Winder et al. (1995) study may be the result of variation in spatial grazing patterns. Cattle from some sire groups may have traveled further from water and selected a higher quality diet. Further studies are needed to determine if grazing distribution is heritable.

## Predicting Grazing Patterns

In order to cull animals with undesirable grazing patterns (e.g., concentrated grazing in bottoms or riparian areas) or to select animals with desirable grazing patterns (e.g., dispersed grazing of upland slopes), managers must be able to characterize individual animals. However, determining whether animals have desirable or undesirable behavior is difficult and time consuming, especially because of the diurnal and day-to-day variations in grazing patterns (Low et al. 1981, Bailey et al. 1990). Readily observable traits are needed to predict individual grazing patterns.

Behavior of cattle during trailing may be related to grazing distribution. Position of animals within the herd during trailing appears to be a reliable, consistent trait. Repeatability of this trait was estimated to be over 60% for cattle (Bailey and Hoffman 1998). Cattle found in front of the herd during trailing generally grazed in higher elevations than cattle found in the back of the herd (Bailey and Hoffman 1998).

Other behaviors may also be useful as predictors of cattle grazing patterns. Grazing distribution may be related to animal docility with more aggressive animals

**Figure 1.** Locations of cow 2036 (3/4 Tarentaise, 1/4 Hereford) observed with a GPS tracking system at 5-minute intervals from Sept. 1, 1998 to Sept. 9, 1998. Cow 2036 was identified as a hill climber (more frequent use of steep slopes and high elevations) during 1997 using data obtained from observers on horseback.

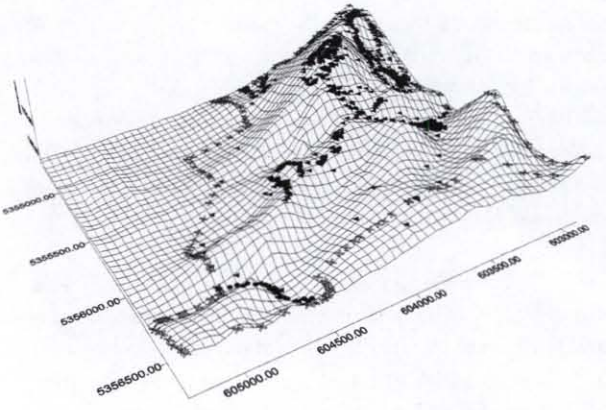


**Figure 2.** Locations of cow 3102 (3/4 Tarentaise, 1/4 Hereford) observed with a GPS tracking system at 10-minute intervals during the day and 20-minute intervals at night from Aug. 18, 1998 to Sept. 9, 1998. Cow 3102 was identified as a hill climber (more frequent use of steep slopes and high elevations) during 1997 using data obtained from observers on horseback.

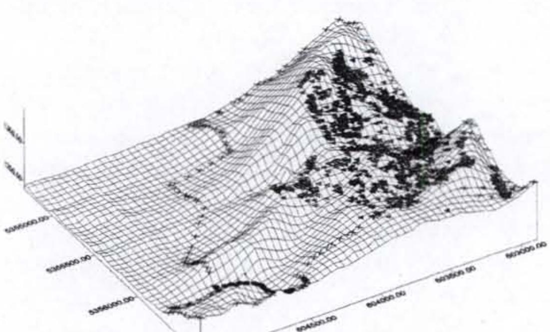


**Figure 3.** Locations of cow 3024 (1/4 Tarentaise, 3/4 Hereford) observed with a GPS tracking system at 10-minute intervals during the day and 20-minute intervals at night from Aug. 18, 1998 to Sept. 9, 1998. Cow 3024 was identified as a bottom dweller (more frequent use of gentle slopes and bottoms) during 1997 using data obtained from observers on horseback.

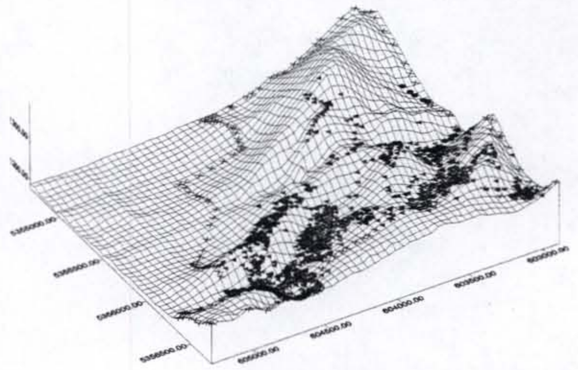
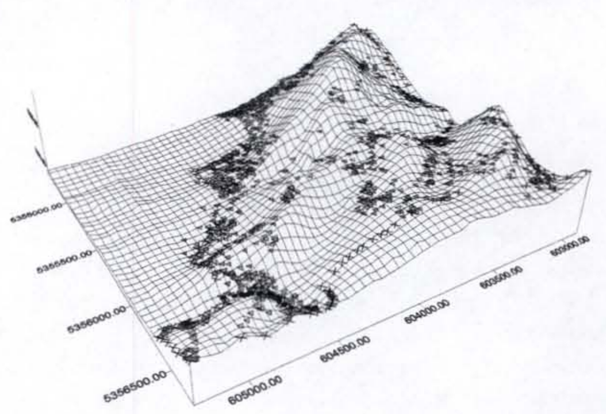


**Figure 4.** Locations of cow 3227 (1/4 Tarentaise, 3/4 Hereford) observed with a GPS tracking system at 10-minute intervals during the day and 20-minute intervals at night from Aug. 18, 1998 to Sept. 9, 1998. Cow 3227 was identified as a bottom dweller (more frequent use of gentle slopes and bottoms) during 1997 using data obtained from observers on horseback.



using rougher terrain than more docile animals. The order in which cattle tend to go through a working chute or scale may also be related to grazing distribution. Anecdotal observations at our research center suggest that cattle that tend to graze steeper slopes are usually the last cattle to go through a livestock handling facility. We plan to evaluate these and other behaviors and hope to find a readily identifiable behavior or trait that can be used to predict an animal's general grazing pattern.

## Relationship Between Grazing Distribution and Performance

If animals are selected for grazing distribution, managers must consider the effect this selection pressure would have on performance. Culling cattle that concentrate their grazing in bottoms or riparian areas would be expensive if those cattle performed better than others in the herd. In northern Montana foothills pastures (Bailey et al. 1998b), grazing distribution was not related to age-adjusted weaning weight of calves, milk production, cow height or cow body condition score (Tables 3 and 4). Correlations between use of slopes and distances traveled to water (horizontal and vertical) were very low. In contrast, cows with older calves and correspondingly higher actual weaning weights used higher elevations and steeper slopes than cows with younger calves. Perhaps cows with older calves can travel further because the calves are better able to keep up with their dam, or the dams are more willing to leave older calves behind. Studies are being conducted at our research center to investigate this question.

## Incorporating Social Interactions into a Selection Program for Distribution

Movements of domestic herbivores during grazing may be directed by a limited number of individual animals. Cattle have been classified as leaders, followers and independents with regards to movement of a social group during grazing (Sato 1982). High-ranking animals were usually leaders and low-ranking members were independent and did not always follow the group. Movement of the herd may be the cumulative result of high-ranking animals and independent movement of low-ranking animals. Small herds of cattle generally followed an animal that had special knowledge of locations containing highly palatable food (Greenwood and Rittenhouse 1997). In another study, one or two steers were in the lead when entering a patch, and the other two or three steers followed (Bailey 1995). This suggests that movements and grazing patterns of cattle herds could be changed by selectively culling a few key animals.

However, Prins (1996) reported from his studies of African buffalo that there were no herd leaders, and lead animals consistently changed during grazing and while traveling to feeding sites. Data from these studies suggest that the decision where to graze is a communal decision made at the end of a resting bout and before the grazing bout begins. If the results observed in African buffalo are confirmed for domestic livestock, then selectively culling high social ranking animals will have little impact on overall herd movements. The apparent contrast between the studies of cattle and African buffalo may be explained by differences in herd and pasture size. The cattle studies were conducted with small herds where individual animals may have more influence than in large herds of buffalo. In addition, decisions where to graze may be more distinct in large acreages than in the small pastures used for these cattle studies because animals often travel further before actively grazing. Obviously, more research is needed to evaluate the impacts of social interactions on herd movement patterns during grazing.

## Will Selection for Grazing Distribution be Effective?

The most important component of a grazing distribution selection program is its effectiveness. To my knowledge, no direct tests of this approach have been completed. However, Mosely (this volume) and Mcdonald and Mosley (this volume, abstract) suggest that social competition may force subordinate individuals away from preferred areas. Correspondingly, other cows may fill the "vacuum" if cows grazing preferred areas are removed, and a culling and selection program would be ineffective. Our research center will begin a study next year to answer this question. We will observe cattle that have spent more time in the last two years in bottoms and near water in foothills pastures as well as cattle that used steeper slopes and higher elevations in separate, but similar, pastures. If the resulting forage utilization patterns differ and if the cattle that preferred more rugged topography exhibit a more even grazing pattern, selecting cattle for grazing distribution may become an important tool for modifying livestock grazing use in large pastures.

## Animal Age and Status

It has long been recognized that yearling steers, yearling heifers or dry cows (without calves) will utilize extensive pastures more evenly than cow-calf pairs (Bell 1973). The presence of a nursing calf may hinder movement of cows; this effect may be more pronounced when the calf is young. As mentioned earlier, cows with older calves used steeper slopes and higher elevations

Table 3. Residual Correlations Between Grazing Distribution Patterns and Characteristics of the Cow

| Behavior | Cow wt. | Hip height | Body condition score | Milk production (early lactation) | Milk production (late lactation) |
|---|---|---|---|---|---|
| Slope | | | | | |
| Pasture 1 | .146<br>(.05) | .060<br>(.42) | .056<br>(.45) | .078<br>(.43) | .071<br>(.48) |
| Pasture 2 | -.026<br>(.73) | -.002<br>(.98) | -.101<br>(.18) | .018<br>(.85) | -.020<br>(.84) |
| Horizontal distance to water | | | | | |
| Pasture 1 | .037<br>(.62) | .003<br>(.97) | -.021<br>(.78) | .069<br>(.49) | .132<br>(.19) |
| Pasture 2 | -.224<br>(.01) | -.110<br>(.14) | -.090<br>(.23) | .033<br>(.74) | -.094<br>(.35) |
| Vertical Distance to water | | | | | |
| Pasture 1 | .107<br>(.15) | .067<br>(.37) | -.001<br>(.99) | .159<br>(.10) | .081<br>(.42) |
| Pasture 2 | -.073<br>(.32) | .001<br>(.99) | -.101<br>(.17) | .132<br>(.18) | -.013<br>(.90) |

Note: P-values are in parenthesis below the residual correlations. If the P-values are less than or equal to 0.05, the correlation between the grazing distribution behavior and the performance trait can be considered statistically significant.

Table 4. Residual Correlations between Grazing Distribution Patterns and Calving Date and Weaning Weights

| Behavior | Calving date | Actual weaning wt. | 205-day adjusted weaning wt. |
|---|---|---|---|
| Slope | | | |
| Pasture 1 | -.033<br>(.68) | .050<br>(.53) | .004<br>(.96) |
| Pasture 2 | -.205<br>(.01) | .148<br>(.06) | .098<br>(.22) |
| Horizontal distance to water | | | |
| Pasture 1 | -.086<br>(.28) | .099<br>(.21) | .063<br>(.43) |
| Pasture 2 | -.047<br>(.55) | -.027<br>(.74) | -.040<br>(.62) |
| Vertical distance to water | | | |
| Pasture 1 | -.089<br>(.26) | .137<br>(.08) | .082<br>(.30) |
| Pasture 2 | -.163<br>(.04) | .152<br>(.05) | .106<br>(.18) |

Note: P-values are listed in parenthesis below the residual correlations. If the P-values are less than or equal to 0.05, the correlation between the grazing distribution behavior and the performance trait can be considered statistically significant.

than cows with younger calves (Bailey et al. 1998b). Dry cows used rougher terrain early in the season but not later in the season. However, Bryant (1982) reported that cows used Oregon mountain rangeland more evenly than yearlings. This apparent inconsistency may be the result of prior experience (Vallentine 1990). At our research center in northern Montana, first-calf heifers appear to use gentler slopes and lower elevations more than older cows with calves. More even cattle grazing distribution may be obtained in extensive rugged pastures if managers can graze yearlings or dry cows (e.g., after weaning).

## Conclusions

Livestock producers and land managers can manipulate grazing distribution by selecting the livestock or wildlife species. Some species are more adaptable to rugged terrain. Distribution of herded animals (e.g., sheep) can certainly be controlled more than free-ranging animals. Management and economical constraints must be carefully considered when selecting which species to graze. Within livestock species, opportunities exist to select breeds that are more adapted to extensive pastures. Some cattle breeds tend to travel further from water and use more rugged topography than others. Managers should also consider the effects of animal sex, age and status (nursing or non-lactating) on grazing distribution. The presence of nursing offspring may hinder livestock from traveling further from water and using steeper slopes.

Individual cattle tend to repeatedly use the same general areas of large mountainous pastures, which suggests that selecting for a more even grazing pattern may be effective. Potentially, distribution could be improved by culling undesirable and selecting desirable individuals, and culling social leaders within the herd that have undesirable grazing patterns. Individual cattle vary in their use of rugged terrain, which promises relatively rapid genetic progress if these traits are heritable. Identifying individuals with desirable and undesirable grazing patterns is labor-intensive. Readily identifiable behaviors must be found so that the general grazing patterns of individuals can be characterized. No adverse relationships between livestock grazing patterns and animal performance have been observed, and cows that use more rugged terrain tend to have older calves at their side with higher weaning weights. Although the potential to use selection to modify and improve livestock grazing distribution is promising, more research is needed before we can conclude if it will be an effective and practical technique.

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# Influence of Social Dominance on Habitat Selection by Free-Ranging Ungulates

Jeffrey C. Mosley

## Abstract

**Social dominance hierarchies (i.e., pecking orders) exist among species, herd subgroups, and individual free-ranging ungulates. Dominance hierarchies influence habitat selection. High-ranking individuals and subgroups occupy the preferred habitats or, where home ranges overlap, dominant individuals or subgroups preferentially use habitat resources (e.g., food, water, cover). Social competition intensifies as resource conditions deteriorate, and subordinate animals are displaced. Knowledge of these relationships between social dominance and habitat selection can be used to improve management of rangeland, livestock, and wildlife resources. For example, application of this knowledge can increase success when translocating animals into new habitat, and improve efforts to manipulate ungulate distribution.**

## Introduction

Grazing managers strive to control four variables: the timing, frequency, intensity, and selectivity of grazing. Management strategies must consider foraging behavior because controlling the four grazing variables requires manipulation of: 1) where animals graze; 2) when they graze; 3) how long they graze a site; and 4) how selectively they graze among tillers of individual plants, among the plants on a site, and among sites within the landscape. The ability of grazing managers to manipulate these variables is affected by ungulate social behavior, and dominance hierarchies (interspecific and intraspecific) are influential components of ungulate social behavior.

Social dominance exists when the behavior of an animal is inhibited or altered by the presence or threat of another animal (Beilharz and Zeeb 1982, Drews 1993). Wild and domestic ungulates are able to recognize other individuals and maintain consistent dominance hierarchies. Animals high in the hierarchy have priority to important habitat resources such as food, shelter, and water (Van Kreveld 1970).

Interspecific and intraspecific social competition is largely a passive process in which subordinates avoid conflict. Dominant animals often make few overt attempts to supplant subordinates. Instead, low-ranked animals monitor their spatial relationships relative to dominant animals. As subordinates get closer to dominants, subordinate animals may reduce their bite rate, stop feeding, or move away, but behavior of dominants is largely unaffected by their proximity to subordinates (Thouless 1990). Thus, movements by dominant animals may displace subordinates, and dominants enjoy greater freedom in habitat selection. This may restrict the amount or quality of resources available to subordinates (Van Horne 1983).

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## Interspecific Dominance Hierarchies

Social dominance hierarchies help partition resources among species of free-ranging ungulates(Morse 1974). Dominant species may preclude subordinate species from occupying certain habitats, or dominant species may preferentially use the food, shelter, or water in an area that is shared with subordinate species.

Interspecific dominance hierarchies are complicated because the social rank of an individual animal intraspecifically also influences its interspecific relations. Timid, low-ranking animals intraspecifically also interact this way interspecifically, at least with species of similar size (Kramer 1973, Fisler 1977). Several studies that report dominance relationships among rangeland ungulates are listed in Table 1. These studies document interspecific dominance hierarchies among wild ungulates, and between livestock and wild species. All of these dominance hierarchies listed in Table 1 were reported to be stable. I have synthesized the results in Table 1 into one interspecific dominance hierarchy for the major rangeland ungulates in North America: bison > horses > cattle > sheep > elk > mule deer > bighorn sheep > pronghorns > white-tailed deer.

Table 1. Examples where interspecific dominance hierarchies have altered habitat use by free-ranging ungulates.

| Interspecific Dominance Hierarchy | Reference |
|---|---|
| Angora goats > white-tailed deer | McMahan (1966) |
| bison > elk > mule deer > pronghorns > white-tailed deer | McHugh (1958) |
| bison > horses | McHugh (1958) |
| cattle > bighorn sheep | Steinkamp (1990) |
| cattle > elk | Mackie (1970)<br>Knowles & Campbell (1982) |
| cattle > mule deer | Linsdale & Tomich (1953)<br>Kramer (1973) |
| cattle > pronghorns | McNay & O'Gara (1982) |
| cattle > white-tailed deer | McMahan (1966)<br>Michael (1967)<br>Ellisor (1969)<br>Kramer (1973)<br>Suring & Vohs (1979)<br>Prasad & Guthery (1986)<br>Compton et al. (1988)<br>Cohen et al. (1989) |
| feral horses > mule deer > bighorn sheep > pronghorns | Berger (1985) |
| horses > mule deer | Linsdale & Tomich (1953) |
| mule deer > white-tailed deer | Anthony & Smith (1977) |
| sheep > bighorn sheep | Buechner (1960)<br>Dean (1977) |
| sheep > elk | Rouse (1957)<br>Stevens (1966) |
| sheep > white-tailed deer | McMahan (1966) |
| wild ponies > cattle | Tyler (1972) |
| wild ponies > fallow deer | Tyler (1972) |

## Interspecific dominance among wild ungulates

Interspecific dominance hierarchies among wild ungulates are often veiled because other factors also help partition habitat use, such as differences in predator avoidance strategies and differences in diet selection. For example, ungulates that rely on their ability to see and run to escape predators (e.g., pronghorns, bighorn sheep) prefer areas with low cover (Kindschy et al. 1982, Van Dyke et al. 1983), whereas many other species prefer taller, more dense hiding cover. Portions of the landscape where palatable browse or herbaceous forage are abundant correspondingly attract ungulate species that are typically browsers or grazers (Kingery et al. 1996, Shipley this volume). Also, dominance hierarchies are often subtle, especially between species that forage closely together. Animals often feed together, mutually unconcerned, but the subordinate species readily gives way if the dominant animal happens to move too close. Anthony and Smith (1977) observed that mule deer and white-tailed deer foraged closely together in southeastern Arizona, but mule deer were clearly dominant. Most of the agonistic interactions occurred when the two species foraged together during the hottest, driest months of the year (April-July). Succulent forage was limited, and mule deer exerted their dominance when selecting preferred foods and bedding sites.

## Interspecific dominance between livestock and wild ungulates

Dominance relationships between wild and domestic ungulates also are complicated by predator avoidance strategies and diet selection differences. In addition, the presence of herders, stock dogs, and vehicles associated with livestock make it difficult to discern whether a wild ungulate is subordinate to the livestock species, per se, or merely reacting to the human activities surrounding livestock. Pronghorns, for example, often associate with domestic sheep and the presence of sheep alone does not cause pronghorns to leave an area (Einarsen 1948, Clary and Beale 1983). At fawning time, however, a closely herded band of sheep can sometimes cause pronghorn does and their fawns to become separated and fawns to be abandoned (Einarsen 1948). Similarly, pronghorn does avoid cattle during the fawning season but these two species commonly feed together during the rest of the year (McNay and O'Gara 1982).

Social disturbance from sheep grazing can force bighorn sheep into less favorable habitat (Buechner 1960), and social dominance by sheep may exert more influence than forage competition (Dean 1977). Steinkamp (1990) observed that a translocated group of bighorn sheep moved away when cattle entered a core area of their home range.

White-tailed deer and mule deer usually ignore cattle, but cattle are dominant. Deer avoid being too close to cattle, but cattle make no effort to avoid them (Linsdale and Tomich 1953, McMahan 1966, Compton et al. 1988). Cattle can displace deer from shade and bedding sites (Michael 1967) and from watering facilities (Prasad and Guthery 1986). Deer usually remain on their home ranges despite the presence of cattle (Skovlin et al. 1976, Cohen et al. 1989), even when cattle stocking rate is high (Skovlin et al. 1968, Cohen et al. 1989). However, the stock density of cattle does matter; deer avoid large concentrations of cattle (Linsdale and Tomich 1953, Skovlin et al. 1968, Cohen et al. 1989). Deer will likely remain on their home range if they can shift thier habitat use slightly to temporarily avoid large concentrations of cattle. For example, in southeastern Texas white-tailed deer shifted back and forth between preferred habitats whenever concentrations of cattle approached either site, but deer were not displaced from their home range (Cohen et al. 1989). Large concentrations of cattle may displace deer into nearby habitat if that is the only escape option afforded the deer (Ellisor 1969).

Elk may leave mountain meadows and forage in adjacent forests after domestic sheep arrive (Stevens 1966), or elk may remain nearby and graze the meadows whenever the sheep are away from the meadow (Rouse 1957). Dominance relations between elk and cattle, and their effects on habitat use, are similar to those described above for cattle and deer. Elk sometimes ignore cattle (Ward 1973, Ward et al. 1973), and elk sometimes submissively select habitat away from cattle (Mackie 1970, Knowles and Campbell 1982). Stock density of cattle and the amount of forage, water, and shelter that is available to both elk and cattle probably determine whether cattle displace elk. The thresholds for displacement remain largely unknown. However, my colleagues and I recently began a research study that is trying to quantify some of these relationships. Our study area is near Cody, Wyoming and researchers from Montana State University and the University of Wyoming are collaborating in this project. The project is investigating elk/cattle relations on four large ranches in the North Fork and South Fork drainages of the Shoshone River. Results from this 3-year study should be available in Fall 2001.

### Influence of resource abundance on potential habitat use overlap and social competition

Differences in resource abundance probably account for many apparent contradictions in the literature concerning interspecific social dominance. Interspecific dominance hierarchies may not be readily apparent when resources are plentiful (Table 2). Kramer (1973) reported that in southwestern Alberta where the area's deer population was well below its capacity, neither mule deer or white-tailed deer appeared to dominate the other socially. Sympatry and the absence of agonistic encounters, however, do not deny the existence of dominance hierarchies. When resources are plentiful, species commonly feed and rest together. Dominants move less and displace subordinates less frequently. Few agonistic encounters occur.

Sympatry will also be high when resources are scarce (Milner 1995), but in this situation interspecific agonistic encounters will be common when the animals are clustered near scarce resources (Table 2). One example is where deer and elk feed together with cattle in winter on pastures, hayfields, and hay that has been disbursed to cattle. Interspecific clustering is high because there are few alternative foraging sites. The animals must graze where forage is available, but deer and elk commonly move away when cattle approach too closely (J. Mosley, personal observations).

The third scenario in Table 2 is when resources are adequate across the landscape, but not abundant enough for the animals to ignore each other's presence. In this situation subordinate species adjust their habitat use patterns. Potential habitat use overlap, at least temporally if not spatially, is low or moderate, and few agonistic encounters occur.

## Intraspecific Dominance Hierarchies

Habitat use and intraspecific dominance are influenced by resource abundance in the same ways as interspecific relations (Table 2). Animals that are dominant intraspecifically have priority access to available resources, including feeding areas, shade, salt licks, supplemental feed, and shelter from storms. These relationships are well documented in both wild and domestic ungulates (Table 3). Low-ranked animals are forced to relocate into areas of lower habitat quality or they must wait their turn until the more dominant animals are satisfied and leave the area. If the relative differences in resource utilization are great, dominant individuals and their offspring gain more weight and reproduce more successfully.

Current year's offspring are near the bottom of a herd's social hierarchy, but, when close to their mothers ($\leq$ 10 feet), offspring are elevated to their mother's status and receive the privileges attached to their mother's social rank. This has been documented in bison (McHugh 1958), elk (Altmann 1956), and wild ponies (Tyler 1972). Offspring of high-ranked mothers also tend to achieve high social rank as adults (Tyler 1972, Clutton-Brock et al. 1986). The mechanism for this is unknown. It may be that offspring learn to be aggressive by watching their mothers interact aggressively with other individuals. It may be that offspring inherit aggressive temperaments, or it may be that the other individuals in the herd learned to avoid the offspring when it was near its high-ranked mother and the other animals continue to avoid it after weaning (Tyler 1972).

### Leadership and intraspecific dominance

The concepts of leadership and dominance are often confused, but they describe two distinct behaviors. Animal groups are led by individuals that initiate an activity (i.e., grazing, traveling, resting) that is different from the remainder of the group. If the remainder of the group does not follow, the "leader" returns to the activity of the group (Sato 1982). Leaders are individual animals that consistently initiate movements that cause others to follow. Leaders exist within most groups of ungulates. One rancher I work with in western Montana has identified two leader cows in his herd. He doesn't begin herding any animals to a new pasture until he finds one of his leader cows. These individuals are used to facilitate

Table 2. Effects of resource abundance on habitat use and agonistic encounters.

| Resource Abundance | Potential Habitat Use Overlap | Frequency of Agonistic Encounters |
|---|---|---|
| Plentiful | High | Low |
| Adequate | Low/Moderate | Low |
| Scarce | High | High |

Table 3. Examples where intraspecific dominance hierarchies have altered habitat use by free-ranging ungulates.

| Species | Habitat Component in Demand | Reference |
|---|---|---|
| bison | feeding site | Green et al. (1989) |
| caribou | feeding site | Barrette & Vandal (1986) |
| cattle | shade | Bennett et al. (1985) |
| | supplemental feed | Sowell et al. (1995) |
| | supplemental feed | Wagnon et al. (1966) |
| elk | feeding site | Harper et al. (1967) |
| | salt lick | Altmann (1956) |
| | shade | Harper et al. (1967) |
| | storm cover | Altmann (1956) |
| feral horses | water | Miller & Denniston (1979) |
| red deer | feeding site | Appleby (1980) |
| | | Thouless (1990) |
| reindeer | feeding site | Espmark (1964,1974) |
| sheep | feeding site | Hunter & Milner (1963) |
| | shade | Lynch et al. (1985) |
| | shade | Sherwin & Johnson (1987) |
| | storm cover | Lynch et al. (1985) |

herd movements. In fact, a herd movement is not attempted unless a leader cow is included in the group.

Leaders appear to be animals that move purposely in a direction, attracting the attention of others (Tyler 1972, Greenwood and Rittenhouse 1997). Purposeful movement may come from having more knowledge of where resources are located (Greenwood and Rittenhouse 1997). This may explain why, in spring, adult ewes of bighorn sheep migrate to alpine range before yearling ewes (Festa-Bianchet 1988). However, Tyler (1972) found that any individual in a group of wild ponies could be a leader, even an immature animal.

Popularity or sociability may determine leadership. Syme (1981) found leaders in a group of sheep were the more sociable animals. Reinhardt and Reinhardt (1981) found that the leader in a group of cattle was the most popular cow; that is, the cow that was the preferred associate of many herd members. She was an average cow in terms of age, reproduction, weight, and social rank, but her movements were attentively observed by the other group members. Most other studies also have found little correlation between leadership and dominance, although Sato (1982) did observe a tendency for high-ranked cows to be leaders and low-ranked cows to be followers. This tendency appeared related to the fact that higher-ranked animals moved around more actively, and actively moving animals may have sometimes caused others to follow.

## Subgrouping and intraspecific dominance

Wild and domestic ungulates are socially organized in fusion-fission societies (Sinclair 1977, Lazo 1994) that operate with two levels of organization. At the high level, animals form stable social subgroups within a herd or local population. These "subherds" are often collections of matrilineal groups. Each subherd has a well-defined home range, or area over which the group habitually travels while engaged in its usual activities (Burt 1943). Home ranges of subherds are usually very consistent among years. At the low level of social organization, subherds separate into smaller, unstable groups termed "parties" (Lazo 1994). Parties fluctuate in size and composition according to environmental conditions (Arnold and Pahl 1967, Muller et al. 1976, Miller 1980). The larger, stable subherds reform when the smaller, unstable parties fuse. Contradictions in the literature about the stability and composition of ungulate subgroups probably arise because many studies only focus on one of the two levels of social organization (Lazo 1994).

Subherds rarely integrate. This was documented when several herds of cattle were combined and managed as a single herd on montane summer range, and cows preferred to graze near individuals from their home herd (Fayre 1976, cited in Arnold and Dudzinski 1978). Other studies also have documented intraspecific social exclusion by subherds of cattle (Lazo 1994, 1995), sheep (Winfield and Mullaney 1973, Winfield et al. 1981, Lawrence and Wood-Gush 1988), and white-tailed deer (Hawkins and Montgomery 1969).

Dominance hierarchies exist between subherds and parties, where higher-ranked groups limit access to resources by lower-ranked subgroups. A study of feral cattle in Spain found that a subordinate subherd reduced its home range area and relocated its home range when higher-ranked subherds came too close (Lazo 1994). Dominant subgroups (i.e., bands) of feral horses displace subordinate subgroups from watering locations. Horses within the dominant subgroups, in addition to the dominant stallions, display aggression towards horses in the subordinate subgroups. This behavior indicates that the hierarchy is an intergroup hierarchy and not just a hierarchy of the dominant stallions from each band (Miller and Denniston 1979).

## Management Implications

Knowledge of the relationships between social dominance and habitat selection can be used to improve management of rangeland, livestock, and wildlife resources. Translocation, herding, and selective culling are three management activities that can benefit from this knowledge.

### Translocation

Translocation is the intentional release of animals into the wild in an attempt to establish, reestablish, or increase a population. Translocation is largely responsible for the present distribution of many wild ungulate species in North America (Griffith et al. 1989). However, translocation is expensive, and new release strategies are needed to improve success rates and limit animal mortality.

Releases of group-feeding ungulates should consider the influence of social dominance on habitat selection. Translocated animals should be released in cohesive social units that, in time, will develop into subherds (Tear et al. 1997). Great effort should be made to translocate intact social subgroups, because subgroups missing key members may not remain cohesive (Jones et al. 1997). Many species (e.g., deer, elk, pronghorns) should not be released immediately before or after parturition because pregnant females become agonistic towards their subgroup associates, and subgroups may not remain together (Schwede et al. 1993).

Where resources are plentiful, releases should consist of large social groups. Plentiful resources allow the group to remain together which expedites social learning about desirable habitats in the translocation area. However, when releasing animals into particularly harsh environments where food, water, or shelter are widely dispersed and variable over time, it is better to release two or more smaller groups rather than one large group. As long as each group is large enough to cope with predators and to reproduce successfully, increased numbers of smaller groups increase the likelihood that at least one subgroup will soon develop a successful pattern of habitat use.

Translocation of animals into areas with established populations can be improved by structuring subgroups to include experienced, if not also high-ranked, individuals captured from the wild (Tear et al. 1997). A long prerelease time is required for the captured animal to bond with the other members of the subgroup. Upon release, the high-ranked or experienced animal should improve the habitat use efficiency of its translocated subgroup. This approach is applicable only when the established population is large enough to withstand the temporary removal of one or more experienced adults.

### Herding

Herding can be used to mitigate interspecific social competition between livestock and wild ungulates. Herding can help keep livestock concentrations small, and small concentrations will displace less wildlife. Livestock can be herded away from critical habitats at critical times (e.g., winter range during winter, fawning sites during fawning) to minimize social displacement of wildlife. When management prescriptions require livestock to be grazed during one of these critical times, or in high livestock densities, a rotational grazing system can be used to provide wildlife the opportunity to move into pastures where livestock are not present.

Livestock can be purposely grazed at high stock densities to control wild ungulate distribution. For example, livestock at high densities can help distribute wildlife away from highways in locales where wild ungulates are colliding with vehicles. Livestock grazing at high stock densities can also be used to deter wildlife depredation of nearby crops, pastures, or haystacks.

Herding is a proven tool for controlling livestock distribution, but herding must consider livestock social behavior to be effective. Cattle subgroups, for example, should be dispersed as a unit (Skovlin 1957, 1965, Roath and Krueger 1982). Otherwise, individuals separated from their subgroup will return to their former location. A herder should purposely relocate subgroups to alternative sites rather than merely harassing animals to disperse from a preferred site. Mere harassment often results in cattle returning within minutes or hours to their former site. Rather than trying to disperse large numbers of cattle at once, it is better to gather only one subgroup or a few subgroups at a time and then guide them to a new site. This approach is much like the old adage that suggests the best way to eat an elephant is one bite at a time. Upon arrival at the new site, the animals should be shown the location of water, salt, and palatable forage. The herder should then remain with the animals in their new location until the group has settled. This often requires 30 minutes to 2 hours. The approach is similar to when trailing cow/calf pairs to a new pasture and then waiting there to make certain that every cow has claimed its calf. The time spent ensuring that subgroups establish their new "home base" saves much time that would otherwise be spent repeatedly harassing animals away from their former locations. Budd (this volume) suggests that when moving cattle to a new grazing site, it is best to move them before they have watered, and when trying to relocate cattle to new loafing areas, it is best to move them soon after they have watered. These strategies make cows more inclined to graze or rest when they reach their new location, rather than immediately turning and heading back to their former location.

Individual animals sometimes do not respond to herding, and these individuals should be culled from a herd (Skovlin 1957, 1965). Here the old adage applies that one bad apple can spoil the whole bunch. Eliminating uncooperative individuals will help develop a group of animals that readily responds to herding. Cattle can be trained to use certain areas of a landscape even though they may prefer to use others. This example highlights the fact that habitat use patterns reveal relatively little about an animal's habitat use preferences (Peek et al. 1982).

## Selective culling

Some authors (e.g., Roath and Krueger 1982, Howery et al. 1996, 1998) have extended Skovlin's concept of selective culling to suggest that selective culling might be used to develop a herd of upland-dwelling cattle (see also Howery et al. this volume, and Bailey this volume). Their recommendation is based on the premise that certain individuals or subgroups within a herd prefer, or are accustomed to, riparian habitats, whereas others prefer or are accustomed to upland habitats. Selective culling on this basis should be considered cautiously because its effectiveness is unknown. Some individual herd members do spend disproportionally more time within riparian ares (Roath and Krueger 1982, Howery et al. 1996, 1998), but it is possible that in their absence and without diligent herding, the desirable habitat in the vacated riparian area would simply be reoccupied by other individuals within the herd. This is what occurred in Scotland when Hunter (1960) selectively culled sheep that had occupied the preferred grazing areas within a pasture. Hunter speculated that the sheep removed from the preferred grazing area had been a high-ranked group, and after their removal their home range was occupied by a lower-ranked group. In northern England, Rawes and Welch (1969) also found that stocking rate reductions of sheep did not alleviate grazing pressure on the better sites and only reduced use of the less desirable areas. Many similar examples exist in the western United States where reducing numbers of livestock has done very little to redistribute grazing pressure away from riparian zones. Selective culling has also been recommended for alleviating deer-human conflicts in parks and municipalities (Porter et al. 1991).

Macdonald and Mosley (this volume, abstract) are presently evaluating the effectiveness of selectively culling cattle that spend too much time in riparian areas. We are studying one rangeland cattle herd of 155 cow/calf pairs in southwestern Montana. We began by determining the social dominance hierarchy of the herd. This was accomplished by observing win/loss interactions between individual cows. In late spring-early summer 1998, more than 900 agonistic encounters were recorded during more than 340 hours of direct observation. To the best of our knowledge, this herd is the only commercial sized cattle herd to ever have its social hierarchy documented. During an 8-week period in summer, a global positioning system is used to record the location of each cow at least once daily. In 1999 and 2000 we will cull 20 to 30 cows each year from a cross-section of the herd's social hierarchy and compare summer habitat use patterns of cows and replacement females in the herd versus those cows that were culled.

If all ages of animals that inhabit desirable habitat are culled, the likelihood that the desirable habitat remains vacant (or used noticeably less) may depend on how closely young females remain to their natal home ranges. Desirable habitat is more likely to remain vacant if young females establish home ranges close to their mothers'. Young females that disperse widely in search of suitable habitat are more likely to reoccupy the vacated areas. The efficacy of selective culling also may depend on the degree of home range overlap among individuals or subgroups. Little or no home range overlap provides less chance for other animals to perceive the absence of the culled animals and less chance that the vacated area will be reoccupied. McNulty et al. (1997) selectively culled white-tailed deer from a forested environment where deer home ranges did not overlap appreciably and where young females did not disperse widely. After 14 of 17 white-tailed deer in one social group were removed, no deer in the adjacent area moved its home range into the removal area. However, although deer density was reduced in the vacated area, it is unknown whether the vacated area offered significantly better resource conditions than the adjacent, occupied home ranges. Caution must also be used when extending inferences to other environments or other ungulate species. For example, in rangeland and agricultural landscapes where fawning, water, and foraging sites are more limited, young female white-tailed deer disperse widely from their natal home ranges (Sparrowe and Springer 1970, Dusek et al. 1989, Nixon et al. 1991). And overlapping home ranges are common among individuals and subgroups of rangeland ungulates, including bighorn sheep, feral horses, sheep, and cattle. In these situations, selective culling of individuals or subgroups is less likely to work.

Selective culling will have longer lasting results when all females in a subgroup are removed. This ensures that reoccupation can only occur by dispersing females rather than reproduction by females that escaped culling. Selective culling will probably not be effective if a translocation is made. Translocated animals often do not assimilate into the subgroups of the existing population and instead establish new home ranges. Translocated animals will probably occupy the habitat vacated by selective culling. Similarly, selective culling has little chance of success with livestock if ranchers do not select replacement females from animals reared in the same pasture from which animals were selectively culled. Replacements reared elsewhere cannot return to their natal home range, will probably not integrate into existing herd subgroups, and will probably establish their home ranges in the vacated habitat. Finally, livestock managers using selective culling should also make certain that replacement females selected from the herd were not raised by cows whose home ranges included the targeted removal area. Otherwise the replacements will likely perpetuate the foraging pattern of their culled mothers.

## Conclusion

In conclusion, social dominance hierarchies influence habitat selection among species, herd subgroups, and individual free-ranging ungulates. Dominant animals preferentially select their habitat at all scales, from the feeding station to selection among regional landscapes (Senft et al. 1987). Management of rangeland, livestock, and wildlife resources can be improved by considering these social interactions. Failure to address these relationships will prevent grazing managers from achieving many of their resource objectives.

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# Management Strategies for Optimal Beef Cattle Distribution and Use of Mountain Riparian Meadows

**Tim DelCurto, Marni Porath, Mike McInnis, Pat Momont, and Cory Parsons**

## Abstract

**Current concerns regarding water quality, biodiversity and threatened and endangered species, combined with the economical importance of livestock production in the Pacific Northwest, dictate a need for research addressing livestock impacts on riparian ecosystems. In the Pacific Northwest specific issues relative to the ultimate survival of Chinook salmon, bull trout and La Hontan cutthroat trout clearly demonstrate a need for additional research and education. More specifically, research evaluating management techniques which help improve livestock distribution relative to riparian areas may be a critical factor in the future of the Pacific Northwest beef cattle industry, as well as other areas of the western United States. In fact, the continued use of public rangelands in the western United States by livestock industries may depend on the ability of university and agency research efforts to prove that livestock grazing can maintain and/or improve the ecological integrity of rangeland resources. Information does exist that suggests livestock grazing can be conducted in a fashion that maintains and/or improves riparian ecosystem integrity. However, most of the data, to date, are observational in nature and does not lend itself well to scientific scrutiny. This paper reviews factors that influence distribution of cattle relative to riparian areas as well as discusses past, current and future research efforts in Northeastern Oregon regarding livestock grazing distribution in riparian ecosystems.**

## Introduction

Beef cattle production is the number one agricultural commodity in Idaho and Oregon, generating over $1 billion dollars in revenue in 1995 (Oregon Agricultural Statistics, 1996). Currently, the beef industry is dominated by commercial cow/calf production with over 1.1 million producing females in the two states. Nearly 80 % of these cows are managed on ranches located in the eastern half of Oregon and the southern half of Idaho. This area of land also represents production units that are in many cases dependent on public land grazing and areas where riparian habitat is under increased public scrutiny. Uneven use of rangeland by livestock has been and continues to be a major problem confronting range managers (Holechek et al. 1989). Several studies indicate that today's rangelands, in general, are in better condition than 20 years ago (Busby 1979), others indicate that upland areas have shown greater improvement compared to riparian areas (Platts 1991). While improved upland conditions are crucial to the function of the riparian area, and the watershed as a whole, riparian areas should not be sacrificed in favor of uplands. Increased soil erosion, greater early spring runoff contributing to a net loss of late season water holding capacity, decreased plant and animal biological diversity, and poor water quality are some of the critical problems of poor riparian area management. In contrast to drier upland areas, however, riparian zones are dynamic communities which respond relatively quickly to changes in rangeland management. Thus, research and outreach education is a critical need for ranchers and other land managers in the western United States with respectto livestock distribution issues. Likewise, potential improvements in resource management relative to livestock grazing and riparian ecosystem integrity are attainable goals.

The problem of acquiring timely improvement in riparian ecosystems is two-fold: 1) identifying and developing grazing systems that are economically and ecologically compatible with riparian ecosystems and 2) persuading land managers to implement cost effective, beneficial management practices (Kinch 1989, Chaney et al. 1990, Meehan 1991, and Platts 1991). Historically, grazing management has focused on optimum utilization of forage from upland areas for maximum livestock production. Research efforts concentrating on wetland and riparian habitats in relation to livestock grazing are limited in number and scope. Years of training land managers through traditional ranch management practices have impeded the progress in improving riparian habitat.

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Proven, beneficial demonstrative and cost-effective management practices for grazing rangeland riparian areas are a critical need for ranchers and range managers.

## Grazing Distribution and Behavior

Grazing management aimed at minimizing uneven use of rangeland requires an understanding of natural factors that influence the grazing patterns of livestock. A series of pasture characteristics that include but are not limited to slope, water availability, vegetation characteristics, shade, and a combination of one or more of these factors have been found to influence grazing distribution to a significant degree. Understanding the natural factors that influence distribution allows for more successful manipulation of distribution using alternate management strategies.

### Slope and rangeland accessibility

Understanding distribution patterns on rangelands may begin with an evaluation of terrain and accessibility of the rangeland. In looking at both continuous and deferred-rotation grazing systems, Gillen et al. (1984) found that as slope increased cattle preference for a site decreased. This response was found throughout the grazing season, and may have been partially responsible for 75% utilization of riparian meadows vs. 10% utilization of uplands. Cattle in southeastern Oregon were generally found to prefer slopes less than 10%, and avoid slopes of greater than 20% (Ganskopp and Vavra 1987). These results were similar to those obtained by Pinchak et al. (1991) who discovered that cattle preferred slopes of less than 4% and found that over 90% of total use occurred on slopes of less than 7%.

### Vegetation type

While the previous work dealt primarily with the direct effect of slope on utilization, other work has focused more generally on the tendency for livestock to gather in riparian areas. This may be a function of level terrain, increased quantity and quality of vegetation, presence of cover, and availability of water (Kauffman and Krueger 1984). Free-ranging cattle, like wildlife, often form semi-independent groups, known as home range groups, that tend to share habitat use and distribution patterns throughout the grazing season. In a study of home range groups, Howery et al. (1996) found that cows utilized riparian habitat more frequently than upland steppe or upland forest. A similar pattern was observed in the Sierra Nevada when riparian habitat was preferredto clearcut, second growth forests, and burned habitats (Kie and Boroski 1996). On the Great Plains, intermittent drainage channels and adjacent communities were heavily grazed during the growing season, receiving 54% of growing season grazing in just 38% of the pasture areas (Senft et al. 1985a). While these studies noted disproportionate use of riparian areas, they also documented a decrease in the use of riparian areas as the grazing season progressed and forage became depleted (Goodman et al. 1989, Hart et al. 1991, Howery et al. 1996, Kie and Boroski 1996, Pinchak et al. 1991, Senft et al. 1985a). They suggest this is due to the need to venture to less desirable habitat to find enough forage to meet their nutritional needs. In a different study, Marlow and Pogacnik (1986) looked at habitat use as a function of season and physiological stage of the vegetation rather than previous use. The study utilized an 8 pasture system in which pastures were stocked heavily for 2-3 weeks and then evacuated. Results showed that riparian areas received greater use later in the grazing season compared to early season use. They suggested that the change in habitat preference was probably due to physiological changes in the vegetation; as upland forage dries up, riparian forage becomes even more desirable in comparison. Owens et al. (1991) noted distribution randomness in response to biomass. In an attempt to look at distribution patterns in pastures of uniform landscape and range site, increased randomness in distribution was noted as biomass decreased. When total biomass was limited, factors such as physical design of the pasture and vegetation composition had a dominant impact on distribution. Under high biomass conditions, plant related factors, such as total amount of vegetation and amount of grass and brush, played the most significant role in determining distribution. Preference for specific vegetative communities, despite water and slope constraints, was noted in Wyoming when cattle demonstrated preference for wetland/subirrigated sites even when other plant communities were available with similar slope and the cattle had similar access to water (Pinchak et al. 1991).

### Water

Water availability is another factor contributing to cattle distribution and behavior within a grazing system. Briske and Heitschmidt (1991) discuss the tendency for large herbivores to focus their foraging activity around water, stating that these ungulates seek the most energy-efficient sources of forage referenced to known water sources. This tendency was observed in cattle on a number of studies which evaluated grazing distribution relative to water sources. Cattle preferred to graze in areas within 215 yards of water while avoiding areas greater than 645 yards away from water under a continuous grazing system (Gillen et al. 1984). Under a deferred system in the same area, cattle avoided areas greater than 215 yards from water (Gillen et al. 1984). A similar trend was found when cattle on Wyoming foothill range concentrated

47% of their use within 320 yards of water (Hart et al. 1991). On the same foothill range, 69% of the available grazing land, which lies over 720 yards from water, sustained less than 12% of the use (Pinchak et al. 1991). In an area where most slopes were less than 20%, Kie and Boroski (1996) found that cattle observations were never farther than 240 yards from water during the two years of the study. Even though they described this area as being potentially available to cattle because of the moderate slopes, riparian areas played the dominant role in distribution.

Valentine (1947) determined that past range surveys and stocking rate levels were inaccurate because they had not taken distance from water into consideration. He noted that many studiesused valid production measures to determine stocking rates, but the ranges were still in decreasing trend. Senft et al. (1985b) pointed out that resting behavior, as it relates to water location, is also important when looking at distribution patterns because of its potential to occupy up to 50% of animal activity time. He concluded that 18-25% of resting in a Great Plains pasture occurred near the stock watering facility at all times of the year. In a related study on grazing patterns Senft et al. (1985a) noted that a zone immediately surrounding watering areas was preferred for grazing at all times of the year. The importance of water as a factor in cattle distribution is apparent throughout these studies. Furthermore, it seems that, depending on variation of factors such as slope, shade, and vegetation, cattle tend to spend the majority of their time within about 322 yards of water.

### Shade

McIlvain and Shoop (1971) addressed the role of shade in influencing cattle distribution on a site in northwestern Oklahoma with little natural shade. They looked at steers grazing with 1) artificial shade/shelter present, and 2) no shade or shelter present. Results showed that shade influenced distribution, as steers loafed under shade on cool days as well as hot days. Availability of shade was also credited for increased animal performance of 19 lbs over steers without access to shade. This response demonstrates the importance of shade in areas that typically receive little use.

Throughout this summary of research on the effects of varying range characteristics on cattle distribution, it is clear that no single characteristic is primarily responsible for explanation of cattle behavior and distribution. Cook (1966) demonstrated the complexity of cattle distribution and behavior in a study looking at the correlation between 21 factors in grazing distribution and utilization as measured by grass utilization on the site. Results showed that when all 21 factors were included in the analysis only 37-55% of variability was explained. It is apparent through the previous studies that water availability, shade, slope, and vegetation play a key role in cattle distribution. A combination of one or more of these factors would probably be most influential in determining distribution patterns. The complexity of cattle distribution demonstrates a need to evaluate interactions between all factors in creating and implementing management plans. Cook (1966) suggested that the utilization expected on mountain slopes can best be obtained by good management practices that involve herding animals and salting and watering appropriately. He emphasizes that no single factor can be used as a reliable index in predicting range utilization.

## Management Strategies and Opportunities

Grazing management systems designed to protect the integrity of riparian systems while sustaining cattle production must consider: 1) distribution patterns of cattle, and 2) season and degree of use that would have minimal impact on that particular riparian area. In order to maintain a productive operation, the nutrient requirements of the cattle must also be satisfied.

Research has been conducted on management strategies that encourage more uniform livestock use throughout the pasture and potentially decreases riparian grazing pressure without fencing. While it seems that cattle exclusion through fencing is the common solution to protection of riparian areas, in most cases it is not economically feasible and inhibits movement of some species of wildlife. Fencing is expensive both in terms of the initial cost and annual maintenance of the fence, as well as the forage lost in the total exclusion of grazing from the riparian area (Bryant 1982). Some strategies that have been evaluated as a substitute for fencing included use of salt and supplement, alternate water, and manipulation of stocking rates and class of animal. Other strategies that have been used less extensively include herding, culling based on distribution tendencies, and the use of electronic eartags.

### Salt and supplement

Ares (1953) looked at the effects of supplying a cottonseed meal-salt mixture to cattle grazing southwest ranges. Results showed that supplying the meal-salt mixture at water and away from water was not as effective as providing the mixture away from water only. Feeding the meal-salt mixture away from water eliminated areas of excessive use, as defined in his protocol, decreased areas of heavy use by 50%, increased areas of proper use by 84%, and decreased areas of light or no use by 29%. A similar study in the southwestern U.S. looked at use of 1) block salt at water, 2) block salt with meal-salt added (Nov.-Apr.) at water, 3) block salt away from water, and 4) block salt with meal-salt added (Oct.-June) away from water to increase uniformity of distribution throughout the pasture (Martin and Ward 1973). There was no significant difference in the treatments, however, trends of increased utilization in light use zones when the salt or meal salt was fed away from water were noted. The authors suggested that use of salt or meal-salt cannot be expected to cure a serious distribution problem. McDougald et al. (1989) investigated the effectiveness of strategically placed supplemental feeding locations in decreasing grazing pressure on the riparian areas of hardwood rangelands. Shifting supplementation sites resulted in residual dry matter changes in the riparian area. On a whole, the strategy reduced the area of low residual dry matter from 48% to 1%, and increased the area of high residual dry matter from 13% to 72% of the riparian area.

While these strategies may be effective in areas where supplementation is an integral part of grazing management, many areas do not require supplementation, other than a trace mineralized salt, to meet nutrient requirements during summer months. Also, supplementation may not be a feasible option due to the policies against the introduction of agricultural products such as alfalfa and other supplements onto public lands in some BLM and Forest Service allotments. Therefore, the use of supplementation may not be the most feasible option to increase the uniformity of grazing distribution throughout the pasture.

### Stocking rate and class of animal

Data has also been collected on effectiveness of altering stocking rates and class of animal in improving distribution. Because improper riparian grazing often results in decreased stocking rates in future seasons, Huber et al. (1995) attempted to determine the effects of decreased stocking, and its effectiveness in protecting riparian areas. They reported that cattle stocked at a low stocking rate spent more time grazing in the streamside vegetation than those stocked at a moderate rate. The authors suggested that during drought conditions low stocking could cause cattle to spend a greater amount of time grazing and loafing in streamside vegetation; however,because of the greater number of animals at the moderate stocking rate, total use of the streamside vegetation may have been equal or greater. Bryant (1982) reported that both cows and yearlings spent disproportionate amounts of time in riparian communities but cows used a wider range of slope classes and plant community types overall than yearlings. Bryant (1982) also suggested that greater maintenance requirements of cows may force them to travel farther in search of available forage. He attributes the tendency for cows to remain closer to the stream compared to yearlings during the early part of the grazing season to a greater water requirement by lactating cows.

### Offstream water

The use of offstream water to alter distribution of animals and decrease riparian grazing pressure is a management strategy that would intuitively have positive effects; however, few studies have evaluated the effects of offstream water on cattle distribution relative to the stream. Miner et al. (1992) looked at the effects of using an offstream water source during winter feeding in a riparian meadow to reduce time spent in the stream by cows. During the winter feeding period, cattle responded to the alternative water source by spending less time loafing in the stream. The tank was over 99% effective in attracting animals away from the stream during the times of day when thirst was the attractant, and 80% effective during the rest of the day when cattle were loafing. In a separate study, Godwin and Miner (1996) used an animal-operated pasture pump to determine the effectiveness of providing an offstream water source in reducing water quality impacts. Animals with access to alternate water spent significantly less time at the stream than those with no water trough. This response decreases direct fecal contamination of the stream, due to the fact that more fecal matter is deposited further away from the stream. It also creates a better opportunity for filtering of the bacteria, nitrogen, and phosphorus present in the fecal matter, by riparian vegetation.

While these studies each evaluated the effect of an alternate water source on cattle distribution relative to the stream, they dealt with winter feeding situations, and small riparian pastures. Little, if any, research has been devoted to the effects of an alternate water source on cattle distribution in herds grazing summer rangeland.

## Grazing Systems and Season of Use

Strategies aimed at minimizing damaging effects to riparian areas from livestock grazing include manipulation of stocking rate, grazing system, and season of grazing. Results from a study looking directly at sediment loss from 1) heavy, continuous grazing (HCG), 2) moderate continuous grazing (MCG), and 3) short duration grazing (SDG) in both shortgrass and midgrass communities indicated sediment loss from the midgrass community in the MCG pasture was relatively stable throughout the study and sediment loss from the shortgrass pasture decreased throughout the study (McCalla et al. 1984). This demonstrates the potential for pastures with different vegetative communities to respond differently to the same management strategies aimed at the protection of riparian and stream ecosystems. In a similar study, Gamougoun et al. (1984) looked at the effects of 1) no grazing, 2) heavy continuous grazing, 3) moderate continuous grazing, and 4 ) two pastures from a four-pasture heavy rotation system on infiltration rates in south-central New Mexico. This study indicated that exclusion of grazing did not create responses significantly different from moderate stocking. Although the heavy continuous and moderate continuous systems had higher infiltration rates than the rotation pastures, it was suggested that the heavy continuous pastures had undergone a shift in species composition toward more forbs, and evidence of disturbance was more apparent in the vegetation shift than the infiltration rate.

A study conducted in northeastern Oregon examined the effects of grazing cattle on riparian areas from late-August to mid-September (Kauffman et al. 1983). Examination of succession, composition, productivity, and structure between riparian communities that were grazed and ungrazed indicated that fall grazing did influence some communities while not affecting others. Kauffman et al. (1983) suggested that late season grazing may be acceptable as a management strategy but this is dependent on the objectives of the management system. Sedgwick and Knopf (1991) conducted a similar study in Colorado that evaluated the effects of October and November grazing on moderately stocked riparian communities compared to ungrazed pastures. They reported no difference between treatments in total biomass production following fall grazing, and only three species (prairie cordgrass, *Spartina pectinata*; and willow, *Salix exigua and Salix interior*) showed any response to grazing. The resilience to grazing under these conditions was attributed to 1) grazing at moderate levels, and 2) grazing late in the year during the dormant season.

The previous review of literature focuses on a number of management strategies aimed at either increasing the uniformity of livestock use over a pasture or decreasing livestock pressure on the riparian area specifically. Research reveals that a number of factors including class of animal, grazing experience of animal, terrain of the land, climatic conditions, and vegetation composition can have a significant impact on the success of various management strategies. These interactions add to the complexity of riparian area management. Seldom will single management practices alleviate long-term, overutilization of riparian habitat. Grazing practices that are beneficial for one region may not prove successful for all areas, as management is often specific to local environments. While some of the studies have documented grazing distribution as it pertains to the time livestock spent grazing specific areas, there is virtually no quantification as to how cattle distribution affects riparian ecosystems.

## Riparian Grazing Research in Northeastern Oregon

Oregon State University and numerous cooperators have been actively evaluating riparian grazing systems for a number of years. Several articles have been published relative to riparian grazing systems, livestock performance and vegetation responses of riparian grazing relative to research conducted at "Meadow Creek" in the Starkey Experimental Forest in the Blue Mountains (Bryant 1982, Holechek and Vavra 1982, Holechek et al. 1982, Kauffman and Krueger 1984, Vavra 1984); or "Catherine Creek" on Oregon State University's Hall Ranch at the base of the Wallowa Mountains (Kauffman et al. 1983, Vavra 1984). In addition changes in channel morphology of Catherine Creek have been documented with and without cattle grazing over a 20-year period (Johnson et al. 1995).

### Recent research in Northeastern Oregon

We recently completed a study that evaluated offstream water and salting for altering cattle distribution. Oregon State University's Hall Ranch was the research location. Vegetation types were grand fir (*abies grandis*) forest on the north slopes, mixed conifer forest, wet meadow and riparian. Dominant plant species are grand fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), ninebark (*Physocarpus malvaceus*), ocean spray (*Holodisus discolor*), snowberry (*Symphoricarpos albus*), pine grass (*Calamagrostis rubescens*), elk sedge (*Carex geyeri*), and Kentucky bluegrass (P*oa pratensis*).

In this study, three treatments were compared: 1) non-grazed control; 2) grazed without offstream water/ salt; and 3) grazed with offstream water and trace mineral salt (TMS) to alter distribution. The study period spanned from mid-July to late-August with two intensive monitoring periods within the 42-day period (days 14-21, and 35-42). The study was conducted over a two-year period.

Distinct differences in cattle distribution patterns were observed between cattle with offstream water and TMS and those without (Fig. 1). Cattle with offstream water and TMS (W) displayed a more uniform average distance from the stream throughout the day, while cattle without offstream water and TMS (NoW) began the day further from the stream ($P < 0.05$), but moved closer to the stream as the day progressed. During the early evening hours NoW cattle began to move away from the stream again. Differences in daily grazing patterns between treatment groups were most pronounced during 1996, although similar patterns were observed in both years. The less pronounced response in 1997 may have been a response to slightly cooler weather.

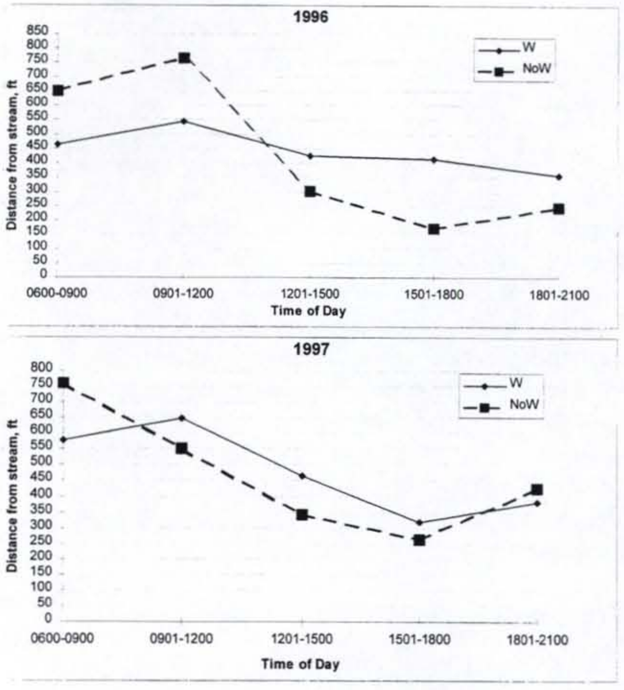

**Figure. 1**. Effects of offstream water and trace mineralized salt on the distance of cattle from the stream throughout the day during 1996 and 1997. Values are averaged over early and late season. Treatments include: 1) W = cattle with access to offstream water and trace mineral salt, and 2) NoW = cattle without access to offstream water and trace mineral salt.

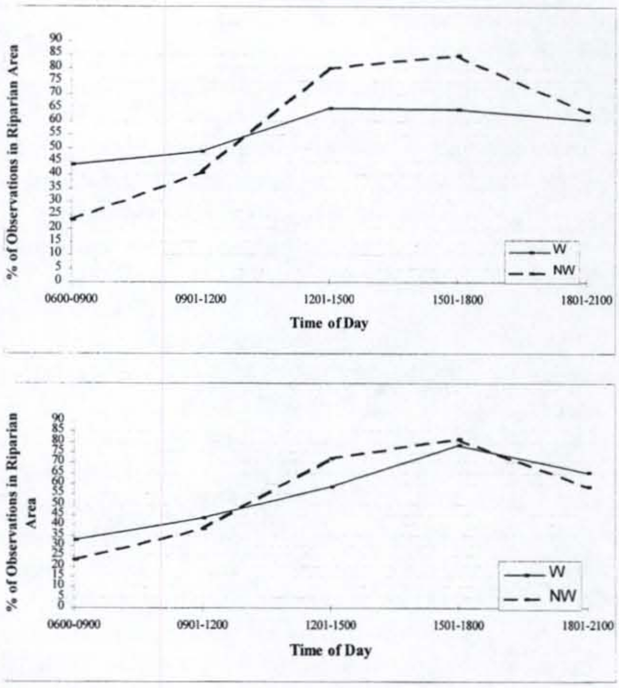

**Figure. 2**. Effects of offstream water and trace mineralized salt on the proportion of cattle observations in the riparian area during the early (22-28 July) and late (19-25 August) part of the grazing season. Values are averaged over 1996 and 1997. Treatments include: 1) W = cattle with access to offstream water and trace mineral salt, and NW = cattle without access to offstream water and trace mineral salt.

Effects of offstream water and TMS on cow/calf distribution patterns were also reflected through the percentage of cattle observations in the riparian areas compared to the uplands (Figure 2). Distribution in the different areas of the pasture followed the same pattern as average distance from the stream, as a larger proportion of W cattle were observed in the riparian area from 0600-0900 ($P < 0.05$), while in the afternoon a larger proportion of NoW cattle were observed in the riparian area ($P < 0.05$). This pattern occurred during early and late season; however, late season distribution differences were less pronounced than early season differences.

The difference in distribution patterns of the two treatments appears to be a response to the tendency for cows to graze during the early morning hours, then search for water and finally seek shade, or graze less intensively during hot afternoon hours. During the search for water W animals were given a choice of two water sources, while NoW animals were forced to use the stream for water. Cattle tended to spend the afternoon in the same areas as they drank, then move away during the evening period. Documentation of water disappearance from stock tanks during a 6-day period in early August showed that despite mean water temperatures of 69.3°F in the tank compared with 59.9°F in the stream, average daily disappearance of water from the tank was 5.7gal/pair per day and TMS consumption averaged 0.30 lbs/pair per day.

The amount of time spent grazing did not differ between W and NoW cattle ($P = 0.25$). Cattle in both treatments followed a daily grazing pattern in which peak grazing occurred from 0601-0900 and 1801-2100. The period from 1201-1800 seemed to be part of the late afternoon/evening grazing period, accounting for about 34 % of the daily grazing activity. This period coincides with the period of highest riparian area occupation for NoW animals, indicating that riparian areas in NoW pastures were receiving greater grazing pressure than W pastures during this afternoon period. Total daily grazing time did not differ between treatments ($P < 0.60$) as cattle grazed about 664.8 minutes/day. Cattle in both treatments appeared to graze more from 0301-0600 during the early season than the late season, and during the late season they grazed more from 0601-0900 than they did in the early season. This is probably a response to the decrease in daylight during the late season. Travel distance, measured with pedometers, indicated that use of offstream water and TMS had no effect on daily travel distance ($P = 0.55$).

Cow and calf weight gains were improved by the presence of offstream water and TMS. Cows with access to offstream water and TMS gained 25.3 lbs more over the 42-day grazing period than cows without offstream water and TMS ($P < 0.05$; Table 1). Calves had a similar response, gaining 0.31 lbs/day more in the pastures with offstream water and TMS ($P < 0.05$). Body condition score was not affected by the presence of offstream water and TMS.

The reason for increased weight gain by W animals is unclear; however, more uniform grazing and less patch grazing may have occurred in W pastures. Additionally, greater vegetation production in W pastures compared to NoW pastures may have contributed to the weight differences.

Inappropriate management of livestock grazing in riparian areas can contribute to declines in water quality by removing protective vegetation and decreasing streambank stability through trampling. We also tested the hypothesis that W cattle would have less of an impact on streambank stability and cover than NoW. Measurements of streambank cover and stability followed protocol of Platts et al. (1983) as modified by Bauer and Burton (1993). Results are summarized in Table 2.

The proportion of covered/stable streambank declined due to grazing but was not different ($P \leq 0.05$) between W and NoW pastures. The uncovered/stable class did not vary among grazing treatments. Proportions of the covered/unstable class did not differ between non-grazed and W pastures. However, pastures lacking off-stream water and minerals had a higher proportion of streambanks in this class compared to non-grazed controls. The amount of uncovered/unstable streambank increased due to grazing, but was less in W pastures compared to NoW pastures. No differences ($P \geq 0.05$) were observed in streambank cover between non-grazed and W pastures, but in pastures lacking off-stream water, cover declined six percent compared to control pastures. Streambank stability was not different between non-grazed and intensively-managed pastures. However, streambanks were less stable in pastures lacking off-stream water and mineral supplements compared to non-grazed pastures.

There was a shift from covered/stable to uncovered/unstable streambanks due to grazing (Table 2). The increase in uncovered/unstable streambank in W pastures (3.5%) was less ($P \geq 0.05$) than in NoW pastures (8.6%), indicating off-stream water and mineral supplement was effective inreducing the impact of cattle on streambanks.

**Table 1.** Effects of offstream water and trace mineral salt on cow weight and condition change, and calf weight gain over the 42-day study period (mean S.E.). Values are the average of both years.

| | Treatment[1] | |
|---|---|---|
| Item | W | NoW |
| Cow | | |
| Weight change (lbs) | $64.24 \pm 1.80^{a}$ | $38.94 \pm 1.65^{b}$ |
| Condition score change | $0.18 \pm 0.10$ | $0.09 \pm 0.09$ |
| Calf | | |
| Weight gain (lbs/day) | $2.22 \pm 0.013^{a}$ | $1.91 \pm 0.011^{b}$ |

[1] W= cattle with access to Milk Creek and offstream water and trace mineral salt, NoW= cattle with access to Milk Creek with no offstream water and trace mineral salt.

[ab] Values within a row with different superscripts differ ( $P < 0.05$).

**Table 2.** Percent change in streambank parameters between initiation of grazing (June) and removal of cattle (August).[1]

| | | Percent Change ($\pm$ SE) | |
|---|---|---|---|
| Parameter | No Grazing | W | NoW |
| Covered/Stable | $0^{a}$ (0) | $-9.9^{b}$ (3.5) | $-14.1^{b}$ (3.8) |
| Uncovered/Stable | 0 (0) | -0.4 (0.8) | -2.5 (1.5) |
| Covered/Unstable | $0^{a}$ (0) | $6.0^{ab}$ (3.3) | $8.1^{b}$ (2.4) |
| Uncovered/Unstable | $0^{a}$ (0) | $3.5^{b}$ (0.9) | $8.6^{c}$ (1.2) |
| Bank Cover | $0^{a}$ (0) | $-3.9^{ab}$ (0.2) | $-6.0^{b}$ (2.7) |
| Bank Stability | $0^{a}$ (0) | $-9.5^{ab}$ (4.2) | $-16.6^{b}$ (3.0) |

[1] Negative values indicate a decrease and positive values indicate an increase. Means within rows with different superscripts are significantly different (LSD, $p \leq 0.05$); n=3.

This project has also documented water quality attributes before and after grazing with measurements including total phosphorus, ortho phosphorus, total coliform, and E. coli. Water quality attributes have been, in turn, related to the concentration of cattle feces within a 3-ft distance from the stream.

## Current research in Northeastern Oregon

Our current research is evaluating the influence of timing of grazing on the distribution of cattle relative to riparian areas. Early grazing (28 days from mid-June to mid-July) is being compared to late grazing (28 days from mid-August to mid-September). We are beginning the second year of a two-year project. Like the offstream water and salting study, the goal is to provide useful information about management strategies for sustainable riparian systems and viable grazing management alternatives to exclusion fencing. We hope our methodologies are being improved as we continue with this research program.

Another project conducted on Oregon State University's Hall Ranch involves the use of radio transmitters and receivers to control livestock movement and distribution (Quigley et al. 1990). The concept of the transmitters and receivers is similar to a shock collar used for training dogs. The cattle wear a radio receiver eartag that is the size of a small transistor radio. In turn, a battery operated transmitter is placed in a area of desired livestock exclusion and is manually set to send out a signal that creates an exclusion zone to the animals wearing the eartag receivers (Figure 3). When an animal wearing an ear tag receiver approaches the signal boundary from the transmitter (exclusion zone), the animal receives an audio signal and, if they do not return to the grazing zone, a maximum of four electronic signals. The signal from the transmitter and subsequent stimulus received by the eartag trains the animals to avoid exclusion areas.

Research to date has indicated that this technology has substantial potential in discouraging livestock use of riparian areas. In short, the electronic eartags have been shown to effective change grazing patterns (Quigley et al. 1990). Furthermore, our research suggests that this technique does not adversely stress animals. In a 56 day project, animals diverted from riparian areas with electronic ear tags had lower weight gains as compared to nondiverted control heifers (Table 3). The lower weight gains, however, appear to be associated with lower nutritional qualities of upslope vegetation diets, rather than stress induced performance depressions.

Currently, patents have been granted relative to this technology. The major hurdles to use the widespread of this technology are related to making the equipment practical to actual ranch and grazing land managers. The ear tags are too heavy, difficult to maintain an animal's ear and the transmitters are somewhat inconsistent in establishing a stable zone of exclusion. A development company is currently working on new and better prototypes and grants proposals are currently pending that would provide significant funds for the development of this equipment. If these grants are obtained, we have made tentative plans to conduct field tests evaluating the effectiveness of this technology and the impact on animal nutrition and stress physiology.

The future use of this technology is encouraging. Fenceless livestock control has significant advantages to exclusion fencing particularly related to other uses of public lands (ie. Recreation and wildlife, esthetics, etc.). The advent of global positioning technology and its potential use in technology such as electronic diversion may open up even greater potential in the near future.

## Conclusions and Implications

Our past research, as well as current projects, provide valuable insight to managed livestock grazing and maintenance and/or improvement of riparian ecosystems. Controlled research with replicated designs, multi-disciplinary teams and multi-agency participation will provide a critical vehicle to ease conflict over future management of riparian areas in the western United States. We believe that our research and outreach education program has begun to accomplish two general goals: 1) encourage and educate land managers to improve distributional management of livestock associated with critical riparian areas, and 2) educate other stakeholders relative to the compatibility of managed livestock grazing with riparian ecological integrity.

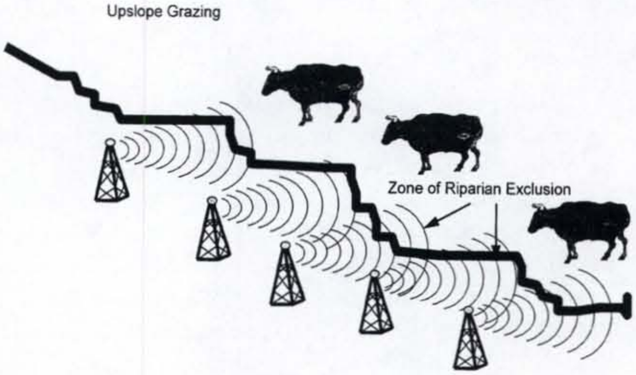

**Figure 3.** Electronic diversion of livestock involves setting up an exclusion zone established by radio transmitters. Cattle are equipped with eartags that, when within the zone, will emit audio followed by electronic stimuli that effectively discourages riparian grazing.

**Table 3.** Influence of electronic diversion form riparian areas on livestock grazing behavior, nutritional physiology, stress physiology and performance.[1]

| | Treatments | | | |
|---|---|---|---|---|
| Item | Diverted | Control | SE | P-value |
| Heifer performance: | 1.46 | 1.76 | | |
| Weight gain, lb/day | 1.46 | 1.76 | .09 | .02 |
| Body condition score change | 1.05 | .86 | .11 | .23 |
| Intake, lb/day | 14.12 | 15.12 | .58 | .19 |
| Distance traveled, miles/day | 3.23 | 3.51 | .31 | .53 |
| Grazing time, hr/day | 7.26 | 7.68 | .40 | .60 |
| Diet composition: | | | | |
| Crude protein, % | 13.40 | 16.90 | .74 | .03 |
| Acid detergent fiber, % | 41.80 | 41.30 | .66 | .60 |
| Physiological performance: | | | | |
| T3, ng/ml | 1.61 | 1.62 | 5.37 | .96 |
| T4, ng/ml | 55 | 53 | .12 | .33 |
| Cortisol, ng/ml | 57 | 51 | .69 | .59 |
| Serum urea N, mg/dl | 12.1 | 13.2 | .40 | .19 |

[1] Diverted heifers had electronic eartags, whereas, control heifers were in adjacent pastures with free access to riparian vegetation. Thirty-six heifers were randomly allotted to three replications of the above two treatments (n = 3).

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# Livestock-Big Game Relationships: Conflicts and Compatabilities

Martin Vavra, Mitchell J. Willis, and Dennis P. Sheehy

## Abstract

**Competition between livestock and wild ungulates is an ongoing concern of both wildlife biologists and livestock operators. Scientific evidence for competition is scarce. Even if two species share similar food habits, competition does not occur unless those food resources are in limited supply and in using those resources one species causes a decline in population performance of the other. The potential for competition is influenced by incomplete or compressed habitats resulting from such things as weather changes, human activities and animal densities. Minimizing the potential for conflicts between domestic and wild ungulates may be antagonistic or harmonious in approach. Antagonistic methods have historically been the methods of choice. These methods usually involve forceful attempts such as harassment or trapping and transport to move animals away from the area of concern. Another approach is to consider wild ungulates a part of the overall system and then develop management plans accordingly. Most western states' wildlife agencies have programs that provide assistance to landowners. Future problems involving wild and domestic ungulate relationships include the role of herbivory in post-disturbance succession, forest health and foraging habitat quality.**

## Introduction

Landowners, land managers and researchers have long been concerned with the concept of competition between livestock and native ungulates. In 1943, Pickford and Reid in the Journal of Wildlife Management voiced concern over livestock–elk competition on the Whitman National Forest in northeastern Oregon. In their article, they summed up the situation quite well. "It is well known that elk and livestock compete for forage...but the nature of this competition has been described largely by conjecture because specific information is meager." In the 1950's several articles in the Journal of Range Management addressed the issue for various states in the West. Has anything changed? Lonner and Mackie (1983) stated, "...It (competition) remains largely an issue of conjecture." These same authors found that most competition studies showed better evidence for coexistence and adaptability. Recently, some authors have termed livestock grazing as the most pervasive land use that has greatly degraded wildlife habitats. Conversely, livestock operators complain that big game grazing on private lands affects their ability to maintain livestock production. While deer numbers have declined in much of the West in the last 25 years, elk numbers are at an all time high. What is known is that rangelands in the West support a large number of ungulates (livestock) that did not evolve with the vegetation and a large human population with concomitant land use incompatible to wildlife. Competition and loss of habitat remain important topics of discussion on both private and public lands.

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## What is Competition and Can it be Quantified?

Free-ranging herbivores are faced with the dilemma of extracting sufficient nutrients from rangeland vegetation to meet their minimum requirements for growth and reproduction. The forage base is frequently limited in amount and constantly changing in quality. Various species of herbivores have evolved to meet their specific nutrient requirements by adapting feeding strategies that tend to optimize levels of nutrient intake, and minimize feeding time (important where predators are a factor). In the process of food selection and rejection, herbivores influence structure and composition of vegetation, potentially influencing their own population dynamics and those of sympatric herbivores. Theoretically, sympatric herbivores with similar food habits will compete and those that have dissimilar food habits will not. Although competition between herbivores may appear obvious, relationships between herbivores may not necessarily be competitive and may even be beneficial.

Interspecific competition has to be judged on two criteria: 1) two species compete when they share a resource that is present in short supply, and 2) in using that resource, each species reduces the other's population performance to levels below what these measures would be in the absence of the other species. In theory, animals that evolved sympatrically do not compete because one or the other should have gone extinct. Livestock, on the other hand, did not evolve in western U. S. ecosystems so competition with native herbivores is possible. Additionally, if resources are not in short supply then competition does not exist, even between livestock and wildlife. Studies frequently demonstrate dietary overlap among sympatric herbivores, but such overlap may not result in the reduction of population performance of either species. It is no surprise that scientific evidence for the existence of competition among large herbivores is scarce. However, the perception of competition often results in the removal or reduction of livestock from areas considered important to wild ungulates. Livestock operators often observe the presence of deer and elk on private lands and perceive there is a reduction of forage available to livestock. Sportsmen often resent the presence of livestock on areas they hunt and envision that removing livestock would allow increased big game populations. Wildlife and land managers suffer from the criticisms of both groups and because they bear the burden of proper management, often react to that pressure. The bottom line is that whether or not competition can be scientifically proven, people believe it is occurring. For the purpose of this paper, we will make the assumption that it is possible. For a more complete discussion of competition and a list of references from which the previous discussion was drawn see Vavra et al. (1989) and Wisdom and Thomas (1996).

## Influencing Factors

What makes competition so difficult to determine? The acquisition of nutrients by herbivores is complex (Provenza and Launchbaugh this volume). In general, large herbivores evolved either to consume large quantities of low quality forage or rely on carefully selecting a diet of higher quality forage but eat less of them (Bunnell and Gillingham 1985). Some herbivores must also minimize their exposure to predation. Generally, larger animals are quantity oriented and smaller animals are quality oriented. For example, horses forage by increasing quantity, while pronghorns are more selective. However, forage availability is the ultimate driver. When resources are in short supply, competition may occur. This is possible during severe winters with extensive snowpack, at the end of winter prior to the initiation of new growth or on long overgrazed ranges with simplistic plant communities. Hanley and Hanley (1982) present an excellent detailed discussion on diet selection.

The major problem with wild ungulates is the human population and concomitant land use practices: agriculture, cities, roads, and all the other trappings of civilization. Wild ungulates once migrated seasonally over wide areas and were able to choose a wide array of habitats depending on season of the year, forage and weather conditions. Wild ungulates now exist in ecologically incomplete or compressed habitats (Vavra and Sheehy 1996, Wisdom and Thomas 1996). Lower elevation spring, fall, and winter ranges are the most affected as many of these are now private lands devoted to agriculture or human habitation. The potential for competition (real or perceived) is highest on these lands.

In most of the western U.S., "average" weather conditions rarely occur; annual variation is the name of the game. The amount and timing of precipitation influences the amount of forage produced, the array of plant species growing, and their nutritional quality. Cold winters with heavy snowpacks can limit the amount of winter range available. Animals that would normally occupy different winter habitats are forced to coexist on limited ranges. Cool springs that delay the initiation of new growth can stall seasonal migration of animals at lower elevations and create areas of overuse. Usually there is a time lag between wild ungulate migration to higher elevations and livestock turn-out that allows vegetation recovery. This may not occur in cool springs with heavy snowpacks when the up-slope migration is delayed. Heavy snow years may also force wild ungulates to nontraditional winter ranges such as hay meadows or croplands like winter wheat. These new areas may then be adopted as winter range in following years even though weather moderates. New habits are formed. The same situation may occur in dry years when animals are forced to search for water. In some areas where late summer forage quality becomes limiting to lactating animals, movement to areas of higher forage quality may occur. Late summer movement by deer and elk to alfalfa fields provides an excellent example.

Increased human activities may force animals to seek new ranges for security. The obvious example is animals moving from areas exposed to hunters to those where hunting is not allowed. On public lands, increased human activity such as commercial mushroom harvest, intense logging, firewood gathering, and recreation coupled with high road densities often drives animals to private lands for solitude.

As with other "land wars", water is often an important consideration in any examination of ungulate competition in the western United States. In the years following World War II, the Oregon Game Commission and Bureau of Land Management cooperatively built many water holes in the xeric portions of southeastern Oregon (Trainer et al. 1983). These developments made vast tracts of otherwise very marginal rangeland available to wild, feral, and domestic herbivores. Was this work effective at reducing competition or merely spreading it to new areas? Competition at water has been reported between feral horses and pronghorns while coexistence or synergistic benefits have also been speculated. Water developments have traditionally been a significant range improvement for both domestic and wild herbivores. By providing sufficient water in appropriate places, water can be used to shift utilization and decrease competition.

Good range management may even be a cause of competition. Livestock operators often practice rotational systems or specialized grazing systems that use an early cattle entry to condition forage for a later grazing entry. These and other forage and ecological enhancement practices (e.g., reseeding, prescribed burning) may attract wild ungulates to well managed rangeland. On private lands, throw in the "solitude factor" for another attractant. The results are increased big game numbers on lands grazed by livestock and a resultant potential for competition. Immediate access to croplands is another associated problem (Nolte this volume).

Many factors obviously affect interactions between livestock and wildlife. The important point is that competition is a moving target. In some cases, where compatibility appears to be the norm, some event (e.g., weather pattern, reseeding) may shift herbivore use patterns and create a problem where none had previously occurred. It may be temporary or it may not.

As the relative density of deer and elk increases, several events or conditions may increase competition with livestock. The most obvious mechanism is spatial in nature. Crowding prompts increased dispersal, which increases the chance of negative encounters. Forage quantity and quality may also be influenced by changes in relative herbivore density. Even at low densities, sites with desirable forage or in desirable places show signs of heavy use. At very high ungulate densities, some areas are still unused. Active management may be quite effective at temporing either of these situations by influencing the distribution or density of the ungulates.

Several studies have addressed the role or viability of conditioning forage (Anderson and Scherzinger 1975, Vavra and Sheehy 1996, Alpe et al. 1999). The outcome of conditioning forage is ultimately dependent on grazing intensity and herbivore density. Too many or too few animals through a site for too short or long a period may result in a significant departure from the desired preparation for later grazing. Competition may be influenced by population density and potentially diminished through density dependence functions after populations reach high levels. These actions typically impact productivity, survival, and recruitment. What triggers density dependence functions, and even when or how they occur are subject to great debate and personal interpretation. The essence for this discussion, however, is that wild ungulates may demonstrate some form of self-regulation through density dependent functions (e.g., lower survival, decreased calf crops, etc.). Resolving competition conflicts in the future may somehow utilize these natural processes to help relieve conflicts in a more cost-effective manner than current depredation mitigation.

## Minimizing the Potential for Competition

Minimizing the potential conflicts between wild and domestic herbivores can be accomplished in a variety of ways. Methods can be antagonistic (e.g., hunting, harassment, trap and transport, exclusion fencing) or harmonious (e.g., adjusting stocking rates, complementary grazing systems, reseeding, salting, feed grounds).

Antagonistic measures have historically been the methods of initial choice. Hazing and harassment of big game animals, setting up traps and transporting animals to low conflict areas, and as a last resort, exclusion fencing have all been used particularly on areas of minimal winter range availability and where croplands abut winter ranges. In some cases, specialized hunts have been effective as a harassment method. Some western state wildlife agencies have damage policies and procedures in place outlining increasingly severe actions to alleviate damage. However, landowner resistance often occurs on the grounds that hunters are a bigger problem than the offending animals.

In some cases, conflict and competition are not really resolved by management efforts to minimize competition, but are merely rotated. Consider an elk population which discovers and invades alfalfa fields in late summer or hay stackyards in late fall or winter. By displacing elk through antagonistic techniques the initial problem is resolved, but a neighbor or another ranch down the road is suddenly subjected to the same problem. Once elk shift their fall or winter use onto agricultural lands, whether through hard winter, displacement, or random chance, they are hard to remove. A domino effect is often put into play with initial efforts of antagonistic management.

Some ranchers have also used heavy grazing with livestock with the attitude that "I'm going to get it before the elk do" on spring and summer ranges, or that late season use will deny winter range use by elk. These methods seldom work because forage remains in areas that cattle do not use. Also, if timely precipitation and consequent forage regrowth occur, the availability of high quality forage may actually attract wild ungulates.

Quantifying the loss of grazing value due to wildlife on rangelands is a near impossible task. Most importantly, if resource damage is occurring, payments will not improve ecological conditions unless stocking rate adjustments also occur. Payments have to be used by the landowner to acquire additional forage and not just pocketed.

Other methods can be tried. Consideration should be given to the particular needs of the problem wild ungulate. The trick is to deny that species some requirement. Security, usually provided by solitude or cover is probably the requirement of choice. The limitations of denying forage have already been discussed. Denying security might include selective logging of important forest habitat. However, opening a forest canopy may improve forage enough that the animal is willing to compromise security needs to obtain the forage. Even worse, the forage may draw more animals. Harassment of animals using grasslands may move them to cover (forest or rough topography) where harassment is not possible. Areas adjacent to that cover then become more important and animal use may be concentrated in those areas resulting in localized damage worse than what occurred previous to the control attempt.

Providing alternatives, diversions, or barriers to stackyards and alfalfa or other crop attraction is sometimes highly effective at minimizing competition (Nolte this volume). Developing elk feeding grounds is a management option subject to great controversy given the many benefits and detriments. In some cases (for example the White River Management Area in Oregon), elk are fenced from agricultural land and fed through the winter somewhat successfully. At Jackson Hole, Wyoming, every winter an ever-increasing number of elk descend on a finite winter range. Here elk are fed pelleted rations throughout the winter with more controversial results. Brucellosis concerns for elk and neighboring cattle are bringing attention to the area. Staging and dispersal of elk are undoubtedly also causing concern with the owners of homes and ranchettes on land adjacent to the winter range.

Positive approaches to livestock/big game conflicts are possible if the landowner or land manager adopts the attitude that wild ungulates are part of the system he/she operates in. Cooperation with state wildlife managers and public land managers is imperative in developing workable alternatives. In most western states programs are now available to assist landowners in this approach.

Access and habitat enhancement programs are potentially harmonious solutions that are used by several western states to varying degrees. Oregon has such a program in place funded by a $2 hunting license surcharge and revenues from up to 10 raffled tags each for deer and elk. Regional committees with landowner and hunter representation submit project proposals to a state board. Typical projects have included vegetation manipulation, water development, road closures, and fencing. One very desirable aspect of the program is that 75% of the costs can be paid out up-front. Deer and elk tags can be allocated for providing access or improving habitat as well as monetary support. A Green Forage Program is in place to assist landowners experiencing crop damage problems. The Deer Enhancement and Restoration (DEAR) program assists landowners wanting to improve mule deer habitat on private lands. Oregon also has a habitat improvement program funded by Pittman-Robertson dollars, a federal excise tax on arms and ammunition, to improve habitat for wildlife in general. The Green Forage and DEAR Programs are to be dropped if help does not come through the state legislature. Nevada has a rather unique program where a landowner can schedule a cooperative big game inventory with a biologist. A voucher for tags is issued on the spot at the rate of 1 tag per 50 deer or pronghorn. These tags may be used by the landowner or sold for use during the general season. In Idaho, an access program is in place, but is not used extensively. However, damage payments are made in Idaho with the stipulation that access be granted to public hunting. Wyoming has a program in which coupons attached to big game tags are presented to landowners and subsequently cashed in to the state for compensation. A program to feed and attract deer and elk from critical lands towards public and even some private land, is in place in Washington, and is managed by their enforcement branch. Damage hunts are commonly held in lieu of cash payments for damage. Colorado has two special programs: Habitat Partnership Program and Ranching for Wildlife. The first is designed to alleviate livestock-big game conflicts. Local committees develop prioritized lists of conflict areas and then draft, with public input, solution plans. Utilizing earmarked license funds, plans may include habitat improvements, special hunts, fence improvements or repair, or even direct payments. Ranching for Wildlife creates a new value for big game through the exchange of tags (from Colorado Division of Wildlife) for wildlife habitat improvements and limited public access (from major landholders).

Contrary to the European approach to wildlife management, wildlife ownership in the United States is granted to the people and is entrusted to management by the states. In much of Europe, the landowner or a collective of landowners, has responsibility not only for crops, timber, and other commodities, but also for wildlife management, particularly harvest. In this country, one of the most fundamental benefits of our structure is the hunting opportunity provided for all citizens with the interest and at least modest means. In Europe, hunting is essentially restricted to the well-to-do. Wildlife in Europe represent a commodity, and as such become another avenue of income to the landowner. When wildlife provide significant revenue, competition becomes allocation, and frowns turn to smiles. An increasing number of landowners in this country are adapting the European philosophy by charging for the right to trespass. Commensurate with this shift is a general increase in tolerance of depredation by big game.

Controlled livestock grazing can be used to improve foraging habitat available to wild ungulates and may also influence their distribution across the landscape (Mosley 1994, Severson and Urness 1994). Grazing by one herbivore (livestock) modifies the vegetation in such a way that it is more acceptable (compared to untreated areas) to another. Severson and Urness (1994) provide four methods to enhance forage for wild ungulates. Livestock grazing can alter the composition of the vegetation, increase the productivity of selected species, increase the diversity of the habitat by altering structure, and increase the nutritive quality of the forage. Anderson and Scherzinger (1975) provide the hypothesis and a working example. Other examples of application are provided by Vavra and Sheehy (1996), Frisina and Morin (1991), Alt et al. 1992, and Frisina (1992). When a winter range encompasses both private and public lands, a management scheme that treats all properties as one management unit is the most desirable.

## Future Issues

It is generally accepted that forests in the interior Northwest are in an undesirable ecological condition due to past practices that include fire suppression, and improper grazing and timber management. These conditions have lead to a high risk of large wildfires (100,000+ acres). In fact, several of these have occurred in recent years and there will undoubtedly be more. After a fire occurs, land management agencies initiate aggressive fire rehabilitation programs. The end result is usually a landscape that has an overabundance of herbaceous cover that provides aggressive competition to shrub and conifer seedlings. Additionally, livestock are generally excluded for a time period to prevent utilization of recovering vegetation. The exclusion of livestock results in grass plants that develop persistent material from previous year's growth (i.e., wolfiness). This old material essentially makes the grasses "herbivore proof" or at least decreases palatability drastically. Native ungulates attempting to optimize diets are forced to search for alternative forages. The result is increased utilization of recovering shrubs in uplands and riparian zones, and potential increased utilization of conifer seedlings. When livestock are allowed to re-enter the burned areas the same problem occurs. Usually, stocking rate is light enough that only small highly preferred areas are grazed. Small patches of high nutrient content forage then occur. These same areas may be grazed heavily in subsequent years while most of the area remains ungrazed and "wolfy".

It is possible to provide carefully controlled livestock grazing to reduce the amount of herbaceous forage present (see Severson and Urness 1994). The most effective livestock use should be in the first half of the grazing season when grasses are still green. Cattle should utilize primarily grasses at this time. The result is a reduction in competitve ability of the grasses so that shrub and conifer seedling growth and survival is improved (Severson and Urness 1994). Additionally, carefully timed livestock grazing can modify grasses so a more palatable and nutritious regrowth component is present for subsequent use by wild ungulates. This should also decrease the use by the wild ungulates of the shrub and conifer component of the landscape. Skovlin et al. (1976) reported increased use of grasslands and decreased use of shrubs by mule deer and elk following cattle grazing on the Starkey Experimental Forest.

One additional option is available on large burned areas. Usually, livestock are returned to burned areas at the same stocking rate as before the burn. Stocking rates are not sufficient to utilize the increased forage production. If other nearby non-burned pastures or allotments are in need of rest for riparian restoration or other concerns, then cattle could be moved over to the highly productive burned areas to provide efficient forage use. Better utilization of the herbaceous component of burned areas should then benefit wild ungulates.

Forests in the West were traditionally subjected to periodic heavy harvest of trees as the primary management objective. Recently, timber harvest has declined substantially. This change in management may have brought about profound changes in important habitat for elk, deer, and summer grazing for livestock as well as the increased fire intensity discussed previously.

Timber harvest has an immediate and dramatic impact on almost all aspects of a forest stand. It immediately increases light reaching understory layers, releases water and nutrients to herbaceous and woody plants, and changes the dynamics of stand and habitat structure. In general, herbaceous species will initially be favored after harvest by increasing density, cover, and yields. Shrub dominance may soon follow on some sites. As succession progresses, understory productivity declines as overstories increase. Most interior Northwest forests now suffer from this condition; too many trees. Both forage quantity and diversity for herbivores decrease. A decline in wild ungulate production and/or redistribution of these animals onto private lands is possible.

Managed forest habitat can be conceptualized as occurring along a successional response curve, because of periodic harvest, that varies temporally and spatially. Elk, deer and cattle may not benefit equally or at the same time along the curve. Wildlife habitat in young to mid-aged stands may be regarded as dynamic and as transitory for a number of species. Although changes occur in forests following harvest, great dissimilarity in results can be expected. Understory release has important implications for herbivore carrying capacity, potential competition among large herbivores, and grazing management plans. Maintaining habitat for large herbivores will require planning harvest with consideration of temporal and spatial relationships of the understory components.

The issue of continued livestock grazing on public lands has important ramifications for the management of wild ungulates. We have already established that controlled livestock grazing is important to wild ungulates through the process of improving forage. Removal of livestock from rangelands will result in a redistribution of wild ungulates to foraging areas where the best array of nutrients is available. This more than likely, will be private land. Additionally, the shrub component, both riparian and upland, on public land may receive increased utilization (see previous discussion). Evidence for this hypothesis exists in the Hell's Canyon Recreation Area where elk winter range is located on vacated sheep allotments. Once the sheep left, elk use declined on the vacated allotments and increased on spring and fall seasonal rangelands that are privately owned and grazed by cattle.

## Conclusions

In this paper we have attempted to describe the difficulty in identifying competition between wild and domestic herbivores, describe possible alleviation methods and discuss potential future problems. What is left is the search for solutions. That search has to begin in one place, and that place is where the word "cooperation" is used exclusively. Once landowners, land and wildlife managers, and interested publics can respect each other and discuss the issues, resolution of problems through the development of remedial management plans is possible. Cooperative management plans that incorporate resource areas and attempt to ignore property boundaries may be the best approach. Remember, the problems are not simplistic, and therefore, simplistic solutions may only create new problems. Hopefully, the ideas we presented in this paper can form the basis for discussion and action that will insure ecologically viable landscapes that provide wildlife values and sustainable commodity outputs.

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# Livestock, Wildlife, Plants and Landscapes: Putting It All Together

## (Lessons from Red Canyon Ranch)

**Bob Budd**

## Abstract

**Rangeland management at Red Canyon Ranch considers: 1) landscape-scale ecological processes, 2) economics, and 3) cultural values. Inclusive collaborative planning has helped stimulate creative thinking and empowered people to try new solutions to old problems. Low stress animal handling and herding based on cattle behavior, have been used to better control stocking rates, stock densities, duration of grazing, and season of use. This, in turn, has improved wildlife habitat, increased biological diversity, and increased the health of uplands and riparian areas. Increased cattle performance and decreased production costs may also result.**

## Introduction

Central to discussing livestock and wildlife interactions is understanding that we can and must have compatible economic uses of natural landscapes in order to maintain ecological and human community values. That is not to say that we should not endeavor to have places which are managed for "natural" assets, or other areas which are managed for economic returns. It is possible to have all of these values within a watershed, a county, or on an individual ranch.

To develop land management strategies that will lead to sound ecology, economy, and culture, it is important to understand the landscape-scale processes that shaped the history of any given habitat or set of habitats. Areas that evolved with a history of large animal grazing, fire, and flood will lead us to different strategies than those employed in areas that may have evolved under different circumstances. It is equally important to visualize the types of animals that may have coevolved with the systems in which we now live. By doing both, it may be possible to adapt operations to the existing natural landscape, or "retrofit" our operations to a more natural setting.

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Too often, the issue of livestock and wildlife is boiled down to an "either-or" proposition. This notion is then cast over millions of square miles of rangeland, as if there were no mix of livestock and wildlife compatible with biological diversity, cultural integrity, and economic security. At times, there will be situations where livestock and wildlife, or wildlife and plant communities, or wildlife and wildlife cannot be optimized. However, on a scale large enough to be valuable to diversity of species, we can usually achieve multiple objectives. However, we must first be able to accept the fact that we truly know very little about all of the "pieces and parts" of a functioning ecosystem; and that some of our "conventional wisdom" may be flawed.

## Goals and Collaborative Management

In designing successful management strategies, several approaches have been used to ferret out targets and objectives to guide ranching operations. The first essential ingredient is a ***common goal***, or vision, which people can understand and support. The coordinated resource management (CRM) framework, and the holistic resource management (HRM) decision-making process both work exceedingly well to achieve that objective. This may also be called integrated resource management (IRM) or another moniker, but all of these processes work in the same manner, and are based upon the same principles. Inclusion of other points of view, especially the knowledge of other people, is the basic operating premise. We engage people of different backgrounds and knowledge in order to create a group capable of acting or reacting to challenges faced in managing for a multitude of values. Members of the CRM team serve as individuals with expertise, and a common goal of managing the landscape without undue regard for jurisdictional or ownership boundaries.

## Joy in Failure

To be successful, there is an immediate need for acceptance of, or better yet, excitement for, mistakes. A prime challenge we face in contemporary society is a quest for perfection, which is admirable. However, as all of us who work with natural resources and living creatures know, there is no such thing as perfection. There is elegance, wonder, incredible complexity, and stark simplicity, and over time, infinite interactions. The time frame of natural systems may be geologic. Therefore, it is not entirely possible for us to overlay our short generational lives on the duration of an ecosystem. Attempting to overlay perfection on nature is defeating and leads to a fear of failure, which clouds our ability to think creatively. We become unwilling to be innovative and find new (or old) ways of managing. In our quest for perfection, we never leave the box. Call it paralysis by analysis - it is a serious malady. Thus, if we want to succeed, the most important commodities we can bring to resource management are an open mind, a true concern for other people's values and needs, and a willingness to fail and learn from the effort.

## Dietary Overlap

It might be worthwhile to follow some of the rationale which led to our successes and failures at Red Canyon Ranch over the past five years. The first step was to understand that our natural system evolved with grazing, browsing and other natural relationships. Second we tried to ascertain how those relationships might have worked. Our working theory did not revolve around bison; but rather, bighorn sheep, elk, mule deer, and antelope. In analyzing dietary overlaps, cattle were the domestic animal that best fit the mix because they had a strong dietary similarity with elk and bighorn sheep; which were the dominant species in the landscape a few centuries ago. While it helped to consider the bison as an occasional user of the area, we viewed elk and bighorns as the primary native species in the system.

## Removal of Fire

Complete removal of fire from the system shaped our current environment, leading us to wonder what the dynamics of the system might have been. It is easy to document the encroachment of conifers and juniper in the absence of fire, and the subsequent loss of aspen and other deciduous trees and shrubs. This is further substantiated by nearly unilateral agreement by community elders that "there used to be more water in the old days." These are significant changes to the natural processes that shaped our environment. Another indicator of what happened in our system is the present performance and behavior of wildlife species. Elk and whitetail populations are exploding throughout the region, while mule deer and sage grouse are declining, or at best, holding their own. Mule deer and sage grouse appear to need some level of disturbance and a lower successional level that is maintained by both grazing and fire. Consequently, plant and animal indicators pointed simultaneously to the loss of two major habitat modifiers: grazing and fire.

## Entropy

Entropy is a slow process that is often difficult to observe amidst the seasonal and yearly dynamics of natural ecosystems. The complete removal of grazing can result in stark changes in standing crop; leading some to conclude that herbivory was a "problem." In riparian systems that experience chronic heavy utilization, the release following rest can be spectacular leading to a conclusion that may not be substantiated by longer term analysis. If we look at riparian systems subjected to prolonged overuse, the pattern of recovery may be unexpected. Following the initial flush or release by woody plants, many areas slowly begin losing woody plants to competition from grasses (especially smooth brome). These systems may lose the diversity once there, and regress to a community of some grasses, a few hardy woody plants, and a variety of annual or biennial plants. The coincidental loss of beaver habitat contributes mightily to slow dewatering of the system, and we find ourselves in either a degrading or stable condition we do not desire.

One of the basic premises guiding our grazing program is the need to look at the whole system, including natural processes, and ecological and cultural values. That does not imply a "natural regulation" theory; we work, live, and draw a living from a managed environment. Instead, it moves us toward a concept of sustainability. The tools we believe will lead to the desired result include management of: stocking rates, stock density, duration of grazing, season of use, type of animal, rest, and animal behavior. Each of these can be used to address the two most serious concerns relative to the long-term health of the rangeland resource; entropy and succession.

## Energy Flow

By coupling our knowledge of the present landscape with the landscape our ancestors knew, we can draw a picture with less conifers and more deer, aspen, deciduous shrubs, and water. This land was also characterized by large herds of animals which were moved by predation, weather, and foraging opportunity. In the early-day cattle operations, nearly every region had extensive roundup crews moving livestock across the local landscape in response to weather and foraging opportunity. Until fifty years ago, fire may have been disdained, but was largely uncontrolled.

Seventy years ago, the Depression, followed by World War II and massive growth in technology, virtually eliminated practices and realities previously used in animal agriculture. Those changes also led to the loss of small- to moderate-scale ranches with cooperative management of large herds of livestock. Larger size led to greater needs for technology. We were able to produce more and bigger animals through animal health aids, by producing more feed (through tillage, fertilization, pumping of water, and fire suppression), and a host of other measures, that changed our connection with the land immeasurably. Two things came out of this change. The first was a concentration of animals along privately owned riparian areas, that occurred out of convenience, as a result of regulation of the public domain, attention elsewhere, and a variety of other reasons. The second was an increase in season-long grazing on upland rangelands resulting from the cessation of roundups and riding, loss of rights to forage, attention elsewhere, and other reasons. At the same time, the size and type of livestock began to change markedly. Bigger, more docile beasts from other lands hit our shores. Predators and labor problems reduced the number and scale of sheep operations. Consequently, management options changed.

The effects of these changes were barely noticeable at first, as is the case with entropy. However, change occurred, and when people noticed, the outcry could not be denied. In the last 50 years, public opinion and action has led to reductions in the number of animals grazing on public lands, virtual elimination of natural fire, and an increase in grazing on privately owned riparian and wetland areas. Furthermore, there has been an increase in conifer encroachment, an explosion in rural homesites and habitat fragmentation. These events and activities are a very serious challenge to species we barely recognize as declining. Some of these are now cause for worry (e.g, mule deer, burrowing owls, neotropical migrant songbirds, fish, and sage grouse). It may be cavalier of me to simplify the causes, for it is not any one, but the combination of many, that have led us to our current dilemmas.

## Less Is Not More

Our management approach at Red Canyon Ranch assumes that we cannot manage for landscape integrity with fewer animals, for economic reasons certainly, and possibly, for other reasons as well. In attempting to mimic natural interactions between grazing animals, wildlife habitats, and economic realities, we have to tease out some of the basic premises of the system, as follows:

1. *Animals* are a renewable source of carbon, nitrogen, and energy to natural systems.

2. Natural systems must have varying levels of disturbance, at differing scales, at different times - mid-seral is neither attainable nor the "desired" condition unless it is applied at a landscape scale.

3. All disturbances are not created equal.

4. Treatment radically different from natural disturbance will advance entropy. We should be very careful when we select stocking rates, use spring fire, herbicides, and other treatments which may radically alter the processes we are trying to mimic.

5. Disturbance need not always be followed by rest.

6. Confusion and disarray are the norm, not the exception, and should be the goal instead of being regarded as a challenge.

7. Continuous use of a treatment leads to entropy, whether it is same-season grazing, burning the same area every year, complete rest over time, or other excessive-compulsive disorders of natural resource management.

8. Short-term costs to change follow the same path as succession, with sudden response followed by longer-term trends. This is not something that will pay immediate economic or ecological returns.

9. Management which mimics or includes a natural process is the goal, even if that does not rest well with us intellectually. An example may be the notion that we should rest for two years after prescribed fire.

10. Domestic animals (including bison) are a tool which MUST be used to move succession, generate energy, create and maintain habitats for wildlife, and shape ecosystem function.

Human management of animals ultimately determines parameters that can be addressed. It is human creativity, that is most severely depressed at this point in time.

## How Much Forage Is There?

One of the primary tenets of our management program is the notion that there is a whole lot more forage out there than we have been using. To date, I have not found many operations where that is not true. In fact, federal agencies have long characterized some ranges as "unsuitable" for grazing, based on such criteria as slope, distance from water, and cover. I am not criticizing the agencies here - the cattle they were accustomed to were largely incapable of using certain ranges; and, the practice of reducing numbers to achieve ecological objectives was so institutionalized that it became the norm. Therefore, stock density is not a tool available to alter animal behavior.

Given the general fact that the forage is there, the question becomes, how can we better use the landscape? There are several means to improve animal distribution from simple water distribution and fencing to those that capitalize on the animals themselves. At Red Canyon, our CRM group was adamant that fences were not the answer, but of primary concern because they impede migratory wildlife. A second concern was the added cost of fence maintenance and construction. Water is a constant factor, but not the only answer; again, cost is a major hurdle.

The three key elements we looked at were time (duration of grazing), timing (season of use), and stock density. By decreasing time, constantly changing season of use, and maintaining large numbers of livestock, we have seen some radical shifts in both production and forage composition. We added rest to the mix three years ago. After five years, the results are: increased animal numbers and weaning weights; full and complete rest of land (as much as 5,000 acres per year); increased hay and irrigated forage; and, reduced death loss from all causes. Keep this trendline moving upward is our objective; though only time will tell. All indications are that we can maintain these trends without substantial cost.

## Animal Behavior

Absolutely critical to these changes is an understanding of the animals we use as ecological and economic tools. In working with "learned behavior," there is none so powerful as that which is passed between humans. As humans, we hate like hell to unlearn a wrongheaded practice and replace it with another. We still speak of "breaking" horses, though few of the modern horsemen ever have a horse really buck hard beneath them. Plenty of ground time, trust, and repetition lead to a mutual "breaking" of man and horse. Cows are equally trainable. Some of the better cow trainers use a whistle to evoke the desired response. My neighbor uses a 9030 Versatile tractor for most of his cow moving and it is a very low-stress method. Unfortunately, in many of the ranges we utilize even a 9030 can't make the trip. So, we have to train the cattle, and they us. By watching and listening to many people, we have found that we can move a lot of cattle, with a few people, MOST of the time. We expect and accept a major screw-up once a year from each of us. We *could* blame the cows, because most of our screw-ups involve cows in some way. However, one recent revelation of mine is that the more people involved in moving livestock, the better chance you will have some large-scale mess. We are pretty gentle with our cattle. We do not own a hotshot or a whip. We have about three sorting sticks, and when we work cattle, we usually don't use those. We are advocates of the Bud Williams schools because his techniques work. The best attestment to the fact that these techniques are valid is the use of the name "Bud Williams" as a verb. It is not uncommon to hear about "Bud Williams-ing" a heifer into the barn, or "putting a little Bud" on a group of cows.

## Eat, Sleep, and Chew Your Cud

These three items pretty well sum up the life of a cow or most other grazing animals. They directly parallel the three requirements of a habitat - food, water, and shelter. Anything we do that affects one of these three requirements can shape behavior. An easy example is water development in uplands, but others include movement of animals to desirable areas at the time they desire to be there. Travis Clyde, our cattle manager, has found that to get cattle to rest and chew their cud in a certain location, he simply needs to move them there after they water, which is highly predictable. (Travis says you can set your watch by them). After they water, he moves them to a shady spot in conifers, or a ridge where the breeze will keep the bugs down. The animals will adapt to this action in about two or three days. If he chooses to move them to a new location, he moves them before watering, and lets them locate on a new water source.

## The Buffet Lunch Theory

Cows never order and eat a single meal. They are constantly at the buffet line making choices; choosing differently at different times of year. As a result, we can shape the landscape by managing the time of grazing. We have begun to manage cheatgrass by grazing in early spring, with removal as soon as we begin to see the desired perennial grasses elevating. This has led to a short-term increase in western wheatgrass and needlegrasses on that range. It may or may not decrease the amount of cheatgrass, but that is a minor concern. Our goal is abundant native perennials. The same approach works well in riparian areas, where the animals are anxious to eat green grass in the spring. They are used to clean up old feed and defoliate grasses that may compete with new willow sprouts in these lush areas. By removing rapidly growing brome (until woody plants, sedges and other desirables are elevated) we are able to use the animal behavior and dietary preference to move our landscape in a direction we desire.

## Race You to the *Pascopyron smithii*!

One of the most serious consequences of reducing management intensity and replacing it with reduced livestock numbers has been the increase of animals in areas that can't withstand constant use; and, decreasing animal influence on other portions of the environment. A variety of factors enter into the result, such as opportunity cost and the conversion of native grazing lands to crops, housing and other uses. One of the most important long-term effects may be the selection of plants and habitats by grazing animals. Stock density can influence foraging behavior in two ways. First, it drives selection of the forages that will be consumed. Long-term grazing on a site allows animals to select and repeatedly select individual plants, leading to shifts in type of vegetation, and possibly, reducing plant vigor. This is shown in pastures which have long served as "spring" pastures in the shortgrass prairie. Within about 10 years, the pasture quality decreases as cool-season plants are selected by grazers, and the pasture is ultimately dominated by warm-season species of little value in a spring pasture. This is one reason that managing for biological diversity has direct positive economic implications, along with the obvious beneficial effects on natural systems.

The other influence of stock density is that at higher densities, cattle will use discreet portions of the pasture (with or without traditional range improvements such as water). As animals learn that portions of a pasture are good foraging areas, they will return to those areas, and increase the amount of forage available. The economic returns from increased numbers and availability of marginal foraging areas should offset the costs of increased management, independent of other benefits, such as reduced death loss.

## Ms. Bovine, Your Child Is at the Front Register

Instead of attacking a herd of cattle in order to move them, we spend a great deal of time riding through them, opening gates in advance, and pairing them up before and after movement. Most "wrecks" occur because animals are not ready to move. We move a lot of cattle in the middle of the day or the evening, which is not the "cowboy way". However, if you watch a cow with her calf, she will step out and walk, while a mother without her calf will drag back, and eventually run back, taking most of the herd with her. This behavioral trait cannot be denied, and is even seen in human mothers in large department stores when their children have wandered off. When we reach the place we want animals to stay, they are paired before being let out of the bunch, at which time they can go freely to feed, water, or lay down. This is the Harry Day theory, and it works very well. Before long, the cows seek out their calves and are allowed to leave. By fall when we ship, more than half of the cows will be worked with their calves at their sides.

## Head 'Em Up and Leave 'Em Be

We have found over time that even if we do a really great job of scaring a herd of cattle from one pasture to the next, that we will *always* have to "backride" the pasture. We also know that two or three of us can move 300 to 400 animals with ease. Planned grazing and daily monitoring of utilization (by ocular estimate) led us to moving cattle over a period of days, instead of a single gather. This practice has several benefits for us. First, it reduces the amount of labor required to move a large number of cattle. In addition, we are able to gather a portion of the pasture which may be more heavily utilized, or where we may desire more or less use. By leaving animals in areas where utilization is more difficult to achieve, we can "gain grass" while not overusing key areas or areas with different management objectives. Lastly, animals which are moving happily (paired up, not confined, and at a pace and direction they choose), will draw other animals to them. This is pure Bud Williams, and it works astoundingly well. Cattle moving freely in the general direction we want to go will get there much quicker and with less stress than animals being forced to follow a road or human route. They will often run, if given the freedom to choose their direction. It may be more important to look behind us when moving cattle than ahead so we can confirm that we are moving away from the area we want to leave, without worrying about the direction we will take to get to the nextpasture.

## "Vaya Con Dios", You Old Rip

I have known a few cows who were a bit cranky and I have been kicked, gored or chased by several others who were not. I have also known some cows who were poor mothers, constantly searching for their calf, and producing little milk while growing fat as sows. The reason I speak in the past tense, is that those cows have all become either someone else's problem, or burger. Landscape management being part of the goal, it only takes a handful of cows to make the process less than optimal. We call these "culls." In analyzing these cull cows some will raise a good calf on irrigated meadows, or in riparian areas, but most bring back an "average" calf. The reasons are fairly simple – a cow staying in a grazed-out area all summer is not going to produce on a par with a cow constantly on fresh forage. To the converse, the cows which produce our heaviest calves are rarely seen during the summer, unless you are riding rimrocks. This is learned behavior. Over time, the same cattle, including mothers and daughters, will forage in the same manner on the same parts of the pasture.

## Why Does a Cow Dog Bark?

Travis asked this question one morning, and took me by surprise, something he likes to do. His answer was very simple – "a cow dog barks for the same reason a human being yells at cattle – they are frustrated." This was a revelation for me, and it taught me a lot; most of all, the notion that as our yelling and the dog's barking increases, the less chance we have of working cattle successfully. We strive to handle animals with a minimum of stress, to them and to us, and that can be directly measured in decibels. If the cattle are quiet, they will be moving. If the dogs are quiet, the cattle will be moving in the right direction. If the humans are quiet, chances are great that the other two will occur at the same time.

## The Glory of Confusion

In natural systems, disturbance and confusion are the rule, not the exception. This has been captured in much of this discussion, but should be stated overtly and underscored. Our management at Red Canyon Ranch is predicated on the notion that plant communities abhor a vacuum; and in that vacuum energy, will be diminished and monocultures advanced. Grazing management should use confusion as a basis, a rule or maxim. A plant community in constant flux should armor itself in many ways, including different species' adaptations to herbivory. Examples are numerous, in all types of systems, although response times are highly variable.

## Summary

We could carry this discussion forever, and some of us will. Management of animals on rangelands is an inexact science. Much of the progress made in enhancing wildlife values, economics, biological diversity and other values of this immense resource will come as a result of shared anecdotal information between people willing to explore interactions between many of these areas. To make informed decisions, we must be open to other thoughts and ideas. We must also be aware of the economic needs of ranch managers and owners, willing to make mistakes, and constantly attentive to the history and potential of our natural systems. In the near term, there are a variety of tremendous inputs being discussed.

Some of those most captivating inputs are interrelationships between fire regime, water cycling and grazing, but there are more. Plant reproduction (through seed germination) may be overstated, leading us to consider rest in a entirely different light. Plant species competition in riparian areas may be more severe than once thought over the long-term. Theories of stable states and energy flow should be explored. By looking back at the way natural systems have evolved under management, it is possible to make the assertion that the needed correction brought about by the Taylor Grazing Act may have done what we see most often, that is, to overcorrect and make no concession for management. All of these topics could occupy the next conference, and will take up great amounts of time. However, the one real truth we should remember is that we will need animals to act appropriately, and an understanding of their behavior will be essential to choosing the proper action.

# Abstracts for Poster Presentations

**DIFFERENCE IN LUPINE INGESTION BY CATTLE AS A RISK FACTOR FOR LUPINE-INDUCED CROOKED CALF DISORDER AND POSSIBLE MANAGEMENT BY REDUCING EXPOSURE TO LUPINES EARLY IN PREGNANCY.** C. Gay, E. Motteram, S. Parish, L. Pritchett, J. Cleasby, D. Lovely *(Field Disease Investigation Unit, Veterinary Clinical Sciences, Washington State Univ., Pullman, WA 99164),* K. Johnson *(Animal Science Dept., Washington State Univ., Pullman, WA 99164)* and K. Panter *(USDA Poisonous Plant Res. Lab., Logan, Utah. 84321).*

There are two major lupine species on rangelands in the channelled scablands of central Washington with potential to cause crooked calf disorder–*Lupinus leucophyllus* and *L. sericeus.* In the herds we examined, the birth of crooked calves could be related to lupine preferences by individual cows. We observed differences in the grazing frequency of lupines between pastures and between and within lupine species. In a preliminary trial, nine heifers were penned and fed either dried *L. leucophyllus* or *L. sericeus* mixed in dried ground alfalfa in randomized replicate feedings. Three heifers showed a strong aversion to lupine and three were indifferent. There was no apparent difference in selection between lupine species.

In a second trial we examined if crooked calf disorder can be minimized by not pasturing pregnant cattle (40 to 70 days gestation) on lupines and by avoiding grazing of lupine in the seed stage. Hereford heifers were grazed on lupine-free pastures in early pregnancy and allowed to graze pastures containing *Lupinus sericeus*, *L. leucophyllus* and *L. sulphureus.* Different growth stages through the spring and the summer period in lupine were examined for anacyine concentrarions. There were few periods in the spring and summer that were present on lupines. The incidence of crooked calf at subsequent calving in both years was approximately 25% with a significant proportion of affected calves affected seriously. Extrapolation of conception dates from recorded calving dates indicated that the period of susceptibility to teratogenic alkaoids is not limited to the first 90 days of gestation.

**EATING BEHAVIOR OF SHEEP IDENTIFIED AS HIGH AND LOW CONSUMERS OF SAGEBRUSH.** M. J. Fraker, and K. L. Launchbaugh *(Rangeand Ecology & Management, University of Idaho, Moscow, ID 83844).*

Sagebrush (*Artemisia spp.*) contains several essential oils, mainly monoterpenes, that limit the digestibility and intake of sagebrush. Several adaptive behaviors have been suggested as ways to limit the deleterious effects of these allelochemicals and therefore increase sagebrush consumption. These ingestive behaviors include increased time spent chewing or ruminating to expel the volatile oils before they yield negative post-ingestive effets. In our research, we examined over 800 sheep and identified 10 high and 10 low sagebrush consumers, placed them in pens and offered ad libitum sagebrush (*Artemisia tridentata*) branches for two-hour periods. The number of bites, chews, and rumination bouts, were observed for individuals from both high and low consumer groups. The number of feeding bouts, time spent feeding, and number of bites and chews were not significantly different between consumer groups. Predictably, animals that consumed a greater than average amount of sagebrush, regardless of consumer group, spent more time feeding, had more frequent feeding bouts and a higher number of bites and chews. However, time spent ruminating and the number of ruminating bouts were significantly higher ($p$=0.07, and $p$=0.07, respectively) for high consumers than low consumers. Individuals consuming more than the average amount of sagebrush, regardless of consumer group, also spent more time ruminating and had more frequent rumination bouts. This exhibited difference in rumination patterns suggests that sagebrush consumption may be facilitated by specific ingestive behaviors.

**INCREASING INTAKE OF SAGEBRUSH BY LAMBS WITH FOOD SUPPLEMENTS.** R.E. Banner *(Rangeland Resources, Utah State University, Logan, UT 84322-5230),* J. Rogosic *(Institute for Adriatic Crops and Karst Reclamation, Put Duilova, Croatia),* E.A. Burritt, and F.D. Provenza *(Rangeland Resources, Utah State University, Logan, UT 84322-5230).*

Big sagebrush is recognized as intolerant of intensive browsing by herbivores. Although it is widely distributed and dominant in many plant communities, minimal use occurs in most situations. There is interest in both applying browsing pressure as a means of suppressing it, as well as increasing its value as a forage plant. While it is known to be nutritious, big sagebrush also contains terpenes which are toxic and thought to deter feeding by herbivores. We sought to increase intake of big sagebrush by lambs by supplementing them with barley and activated charcoal. Barley provides macronutrients which may facilitate detoxification of terpenoids and activated charcoal may adsorb these compounds, allowing animals to increase sagebrush intake. We ran feeding trials to evaluate the role of supplemental barley plus charcoal and barley alone in sagebrush intake by lambs with two subspecies of sagebrush, mountain big sagebrush and basin big sagebrush. We also evaluated effects of supplemental barley plus charcoal, barley alone and no supplement in sagebrush intake by lambs with time-restricted and highly time-restricted access to high quality foods. Collectively, the results indicate that activated charcoal and supplemental barley increase intake of sagebrush by lambs by 50-100%. Sagebrush intake increased over time for all lambs suggesting that some conditioning takes place. Availability of alternative high quality foods dampens sagebrush intake by lambs, supplemented and not supplemented. These results indicate that, through management, it is possible to manipulate big sagebrush stand densities while deriving the benefit of nutritious forage.

### DOES ENERGY FEEDBACK FROM CARBOHYDRATES AFFECT DIETARY PREFERENCES IN GRAZING ANIMALS?

E.R. Smith, K.L. Launchbaugh *(Rangeland Ecology & Management, University of Idaho, Moscow, ID 83844)*, and T.C. Griggs *(Washington State University Cooperative Extension, Ephrata, WA 98823)*.

In natural foraging environments, herbivores must select from a wide array of plants that vary greatly in kinds and amounts of nutrients and toxins to acquire a nutritionally adequate diet. Ruminants generally prefer plants or foods that yield the greatest digestible energy. For that reason, we hypothesized that ruminants might form preferences for foods that yield energy feedback quickly after ingesting, over those that yield delayed energy feedback. To examine this hypothesis we offered 24 lambs flavored wheat straw and then administered intra-ruminal infusions of cornstarch (energy feedback) within 90 minutes or 6-8 hours after the consumption of straw. As a result, lambs significantly preferred the flavor of straw yielding the quick energy feedback to those flavored straws yielding delayed or no energy feedback. We then hypothesized that ruminants would prefer foods high in soluble carbohydrates (yielding the quick energy feedback) to those foods containing a higher proportion of fermentable carbohydrates (yielding a delayed energy feedback). We examined this hypothesis with 12 lambs offered 3 prepared diets that differed in the proportions of soluble, fermentable, and non-fermentable carbohydrates. Contrary to our hypothesis, lambs preferred the diet containing the greatest proportion of fermentable carbohydrates (delayed energy feedback). These results suggest that ruminants are sensitive to the delay between ingestion and energy liberation. However, this is not the only characteristic of plants which influences the formation of preferences by grazing animals.

### EFFECT OF TIMING AND INTENSITY OF GRAZING ON *AGROPYRON SPICATUM* AND *FESTUCA IDAHOENSIS.*

D. Lucas *(Montana State University Extension, Philipsburg, MT 59858-0665)*, L.R. Schmidt, *(Montana State University Extension, Whitehall MT, 59759)*, and J. Mosley *(Animal & Range Sciences, Montana State University, Bozeman, MT 59717-2820)*.

Resource managers across the West are faced with the challenge of balancing increasing demands for early spring forage with enhancing or maintaining the health of native grass species. Elk (*Cervus elaphus)* populations have dramatically increased in most western states, and are consequently increasing the intensity of grazing use on historical early spring range. Often, early spring range found on private lands has been allocated for early spring use by domestic livestock, and a conflict over resource allocation and demand has arisen. This investigation has been undertaken to aid in evaluating the effect of timing and intensity of grazing on two native grass species, bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*), and to aid in developing appropriate range management strategies. This study was designed to assess the effects of early spring grazing by large ungulates on these species ability to regrow after grazing. Six 50' x 50' exclosures were built to prevent grazing for two years. Random plots within the exclosures will be clipped either at spring green-up or during boot stage at stubble heights representing low, medium, high and no grazing. Average stubble height on random plots outside the exclosures will measure actual grazing use during early spring green-up and boot stage. Average stubble height will be measured after senescence on each plot within and outside each exclosure. Results will quantify the effects of early spring grazing on the ability of *Agropyron spicatum* and *Festuca idahoensis* to regrow during the same growing season, and to maintain health in the longer term.

### INFLUENCE OF GRASS PLANT ARCHITECTURE ON INTAKE AND PREFERENCE BY SHEEP.

E.D. Reid and K.L. Launchbaugh *(Rangeland Ecology & Management, University of Idaho, Moscow, ID 83844-1135)*.

Much research has examined the influence of plant nutritive quality on animal grazing preferences, but plant architectural characteristics also can affect diet selection. We conducted several trials to test whether the architectural plant structure of individual grass plants influenced intake and preference by sheep. A set of artificial plants were constructed using individual tillers from1 of 4 grass species to examine sheep grazing response to tiller and canopy arrangement. The 4 grasses were big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), and silver bluestem (*Bothriochloa laguroides*). Four distinct plant architectures were constructed by using two different tiller densities and tillers with a high or low number of leaves. The four treatments (one plant each) were simultaneously presented to individual sheep. Preferences for plants constructed from vegetative tillers (i.e., primarily leaves) were affected more by tiller densities than by the number of leaves per tiller. By contrast, preferences for plants constructed from reproductive tillers (i.e., stems and leaves) were affected more by the number of leaves per tiller than by tiller density. The different response to vegetative or reproductive tillers may be a result of the differences in nutrient distribution in a plant. In vegetative plants, the distribution of nutrients is more uniform (i.e., nearly every bite yields similar nutrient value). However, in reproductive tillers, distribution of nutrients is less uniform as leaves are substantially more nutritious than stems. When eating grasses in a reproductive state, sheep were more selective and had smaller bite sizes, slower bite rates and lower intake rates than vegetative grasses. Consequently, architecture needs to be considered when examining forage selectivity.

## FORAGE QUALITY IMPROVEMENT ON ELK WINTER RANGE USING DOMESTIC SHEEP GRAZING.

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Carefully-managed livestock grazing has been suggested as a tool to improve the forage quality of graminoids on big game winter range, however, formal testing of this theory has been done using hand clippers rather than livestock grazing as the forage conditioning agent. We report winter standing reproductive culm, crude protein, *in vitro* dry matter digestibility, and dry matter yield responses of bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and elk sedge (*Carex geyeri*) to late spring domestic sheep grazing. The study was conducted in 1993 and 1994 on a big game winter range in the Blue Mountains of northeastern Oregon. Sheep grazing and exclusion treatments were applied to 20-ha plots at 3 sites on the study area. Grazed plots received 50% utilization of graminoids during the boot stage of bluebunch wheatgrass. Grazing did not influence the number of standing reproductive culms per plant in bluebunch wheatgrass but did, in some cases, reduce standing Idaho fescue culms relative to sheep exclusion. Crude protein and *in vitro* dry matter digestibility of bluebunch wheatgrass in grazed plots relative to ungrazed plots increased by as much as 1.7 and 7.6 percentage points, respectively. Grazing reduced dry matter yield of bluebunch wheatgrass by as much as 202.4 kg/ha. Crude protein of Idaho fescue in grazed plots was 2.6 percentage points greater than in ungrazed plots. Crude protein , *in vitro* dry matter digestibility, and dry matter yield responses of elk sedge were inconsistent between years and this may be related to differences in sheep utilization between years. The levels of forage quality improvement in bluebunch wheatgrass and Idaho fescue obtained in this study could produce beneficial effects on the foraging efficiency and nutritional status of wintering Rocky Mountain elk (*Cervus elaphus nelsoni*). The effects of forage conditioning treatments on the winter forage quality of elk sedge require further study.

## APPROACHES TO ESTIMATING ELK CARRYING CAPACITY IN NORTHEASTERN NEVADA.

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During the 1990s, 93 elk (*Cervus elaphus*) were translocated into the Jarbidge Mountains of northeastern Nevada. Livestock grazing is the main use of public and private rangelands in the Jarbidge area; 36 federal grazing allotments provide seasonal forage to cattle and domestic sheep on 146,000 ha (65.6% USFS, 25.6% BLM, and 8.8% Private). Our objectives are to obtain several estimates of carrying capacity to understand and predict which mechanisms promote or limit elk population growth in this area. Forage has often been viewed as the most limiting factor of ungulate carrying capacity. However, interactions of elk with other ungulates, predators, and humans to some degree influence forage and habitat availability and selection. The quantity and quality of critical habitats such as winter range are other factors that may influence carrying capacity. Our approaches to estimating carrying capacity include: (1) Estimating dietary overlap between elk, mule deer, and livestock, and in relation to utilization levels, (2) Estimating forage quantity and quality, (3) Estimating the quantity and quality of critical habitats used by elk, and (4) Spatially assessing the effect of livestock locations in relation to elk habitat selection. Preliminary results from 1998 field work indicate elk demonstrate seasonal selection for forage and habitat and in relation to other factors including livestock.

## CO-SPECIES GRAZING OF SHEEP AND CATTLE IN SAGEBRUSH STEPPE.

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Co-species grazing can increase animal production from vegetatively diverse rangeland. Little is known about which combinations of cattle and sheep optimize livestock performance in sagebrush steppe. During 2 summers, 4 combinations of cattle and sheep AUMs were compared: 100% cattle; 100% sheep; 75% cattle:25% sheep; and 50% cattle:50% sheep. Botanical composition of livestock diets was estimated by microhistological analysis of feces. Hand-plucked diet samples of forage were analyzed for CP and NDF. Experimental design was completely randomized with 3 replicates per grazing treatment. Repeated measures ANOVA was used to determine whether diet botanical composition, diet nutritive quality, or livestock performance differed among treatments. Preliminary results indicate that stocking rate combinations did not affect botanical composition or nutritive quality of sheep or cattle diets. Average daily gain by cattle was not affected by the presence of sheep, but sheep gained more when grazed with cattle. Total gain/hectare in a dry year was greatest with $\leq$ 50% sheep, and in a wet year with $\geq$ 50% sheep. Therefore, allocating livestock AUMs at 50% cattle:50% sheep may maximize gain/hectare over the long-term.

## OFFSTREAM WATER AND SALT AS MANAGEMENT STRATEGIES FOR IMPROVED CATTLE DISTRIBUTION AND SUBSEQUENT RIPARIAN HEALTH

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This study was designed to quantify the effect of offstream water and trace mineralized salt on cattle distribution relative to riparian areas. From 15 July to 26 August, 1996 and 1997, 3 treatments were randomly assigned to 1 pasture in each of 3 blocks. Sixty cow/calf pairs were then randomly allotted to the grazed pastures. The treatments included stream access with: 1) access to offstream water and trace mineralized salt W), 2) no access to offstream water and trace mineralized salt (NW), and 3) ungrazed control (C). Response of cattle to access to offstream water and salt was measured through visual observations of cattle distribution, grazing behavior, cow/calf performance, vegetation utilization patterns, water quality, and fecal deposit distribution. Distribution patterns of the cattle, measured as the distance of cattle from the stream, was characterized by a time of day x treatment x year interaction ($P<.05$). NW cattle began the day further from the stream than W cattle, but moved closer to the stream after the morning grazing period (0600-0900). Grazing behavior of cattle was not affected by the presence of offstream water and trace mineral salt. Increased gains of .27 kg per day for cows, and .14 kg per day for calves, were observed in W cattle compared with NW cattle ($p<.05$). Analysis of water samples indicated no response of water quality to cattle grazing or grazing treatment. Overall, cattle distribution patterns and cow/calf performance were influenced by the presence of offstream water and trace mineral salt, however, grazing behavior, forage utilization, and water quality responses were either not observed or unclear.

## DO SOME INDIVIDUAL COWS OR SUBGROUPS PREFER TO GRAZE UPLANDS RATHER THAN RIPARIAN AREAS?

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Low-cost cattle grazing strategies are needed for improved stewardship of riparian areas. One possible strategy is to cull from a herd those cows that over utilize riparian habitats. This strategy is based upon the hypothesis that individual cows differ in their habitat use preferences. However, less riparian use by individual cows may be caused by social competition that forces subordinate animals onto less preferred uplands. If dominant animals occupy preferred riparian habitats, and these dominant animals are culled from the herd, subordinates may reoccupy the space created. Our project seeks to: 1) determine whether cows of higher social rank spend more time in riparian habitat; 2) examine the influence of social rank on subgrouping behavior; and 3) examine the effects of culling on habitat use patterns of individual cows and subgroups. We are studying one rangeland cattle herd of 155 cow/calf pairs. Social hierarchy within the herd is determined by observing win/loss interactions between individual cows. GPS is used to record the daily location of each cow for 8 weeks in summer. Environmental conditions are recorded at each cow location. Thirty cows are culled each year from a cross-section of the herd's social hierarchy, and nonparametric tests will be used to compare habitat use patterns of cows that remain in the herd versus those that were culled. Cluster analysis will be used to identify subgroups, and home range behavior will be analyzed using GIS and CALHOME. Regression will be used to relate social rank to habitat selection by individual cows and subgroups.

## EFFECTS OF SEASON OF USE ON BEEF CATTLE DISTRIBUTION IN RIPARIAN ECOSYSTEMS.

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The study was conducted to quantify the effects of season of use on beef cattle distribution relative to riparian areas and subsequent riparian health. These data will be used to design better grazing strategies aimed at decreasing grazing pressure and alleviating negative impacts to riparian ecosystems. Treatments consisted of 1) non-use or control, 2) early season (E) grazing (June 9-July 7), and 3) late season (L) grazing (August 18 to September 16). Nine pastures were arranged in a randomized complete block design (3 treatments replicated within 3 blocks). Fifty-four and 52 cow/calf pairs, were randomly allotted to the grazed pastures for the early and late seasons of use, respectively. The pastures were stocked according to dry matter production at 50% utilization for 28 days. Responses of cattle to season of use were measured through water quality, fecal deposit counts within 1 meter of stream, visual observations of cattle distribution, grazing activity, cow/calf performance and vegetation utilization. Final data will be presented. The results of this study will be incorporated with current information and practices to assist both ranchers and land management agencies to create sustainable grazing systems relative to riparian areas.

## A SURVEY OF BIG GAME IMPACTS ON PRIVATE GRAZING LANDS IN SOUTHWEST MONTANA.

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Big game wildlife population increases have been reported in southwestern Montana over the past few decades. This coupled with shortages of year-round habitat on public lands has caused problems on private grazing lands. Big game wildlife species use private grazing lands, as well as public lands, and compete with livestock for forage, utilize stored hay, and damage fences. This poses conflicts to ranchers who need their private grazing land resources to support livestock. A survey of private landowners in five southwestern Montana counties was conducted during the spring and summer of 1998 to determine how wildlife are utilizing private grazing land resources, to see if management is still possible from a private landowners perspective, and to assist in developing workshops to provide technical assistance. A total of 1,803 surveys were sent out and 245 (14%) of those were returned. The majority of respondents have from 100 to 2,500 acres of private grazing land under their control, do not utilize a public grazing allotment, have beef cows and horses, and ranching is their primary livelihood. Ninety-five percent of respondents indicated that their private land provides habitat for big game. Although 71% of respondents consider big game use on their private lands to be tolerable, 72% of those who feel it is intolerable recognize that big game are a part of nature but are frustrated because they do not have a voice in big game management. Only 40% of survey respondents plan for big game use in their grazing land management plan. It is apparent that big game use is occurring on the majority of private lands at the expense of the forage resource. Results from this survey will assist resource technicians in developing programs for managing livestock and wildlife on private lands to conserve grazing land resources in southwestern Montana.

## CAPABILITIES AND LIMITATIONS OF THE MULTI-SPECIES STOCKING CALCULATOR FOR DETERMINING CARRYING CAPACITIES OF WILDLIFE AND LIVESTOCK OCCURRING ON SYMPATRIC RANGELANDS: A USER'S PERSPECTIVE.

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Developing management plans for grazing lands in the western United States often involves taking into account the forage demands of both domestic livestock and big game species of wildlife. The interactions between the two may be viewed as a conflict for limited resources or as an opportunity for diversification and enhanced lifestyle. The Multi-Species Stocking Calculator complements behavioral interactions by using plant composition and production, livestock and big game forage demand, seasonal forage preferences of the grazing animals, and harvest efficiencies to determine the carrying capacity of a targeted land unit. The ability of this tool to analyze habitat and help determine the numbers and combinations of big game and livestock that can cohabit a specific site, when complemented with knowledge of behavioral interactions, enables land managers to make better informed decisions regarding their resource management objectives. The effects of various range improvement practices can also be modeled. The capabilities and limitations of this software will be demonstrated using "real-life" situations in Colorado and Montana.