

Foraging Behavior: Experience or Inheritance?

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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).

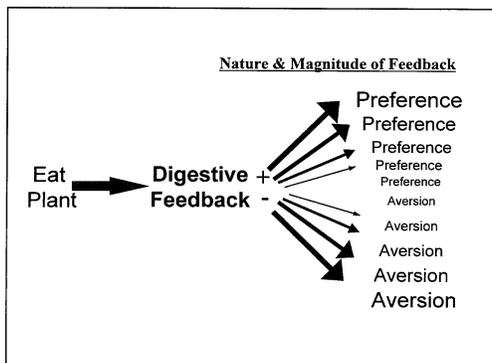


Figure 1. When herbivores eat a plant, they experience digestive feedback from energy and nutrient (positive feedback) or from plant allelochemicals (negative feedback). The nature and magnitude of this feedback determines the intensity of preferences or aversion formed to the plant.

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 fluoroacetates 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 (Shiple, 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 heels 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 vice 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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