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Conditioned food aversions: principles and practices, with special reference to social facilitation

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Conditioned food aversion is a powerful experimental tool to modify animal diets. We have also investigated it as a potential management tool to prevent livestock from grazing poisonous plants such as tall larkspur (*Delphinium barbeyi*), white locoweed (*Oxytropis sericea*) and ponderosa pine (*Pinus ponderosa*) on western US rangelands. The following principles pertain to increasing the strength and longevity of aversions: mature animals retain aversions better than young animals; novelty of the plant is important, although aversions can be created to familiar plants; LiCl is the most effective emetic, and the optimum dose for cattle is 200 mg/kg body weight; averted animals should be grazed separately from non-averted animals to avoid the influence of social facilitation which can rapidly extinguish aversions. Social facilitation is the most important factor preventing widespread application of aversive conditioning. When averted animals see other animals eat the target food they will sample it, and if there is no adverse reaction they will continue eating and extinguish the aversion. However, if averted animals can be grazed separately, aversions will persist. Aversive conditioning may provide an effective management tool to prevent animals from eating palatable poisonous plants that cause major economic loss.

Diet selection: Conditioned food aversion: Social facilitation: Poisonous plants

'Conditioned food aversion is the strongest experimental tool that we know of to modify diet selection. Yet, social facilitation is able to extinguish even strong aversions' (Galef, 1986). We have developed procedures to avert livestock to specific poisonous plants on extensive rangelands of the western USA. Aversions appear to last indefinitely while averted animals graze separately. However, when averted animals are placed with non-averted cohorts that are eating the target plant, aversions gradually extinguish. Social facilitation is a strong detrimental force to maintaining aversions in mixed grazing situations.

We first review the diet selection process on extensive rangelands and discuss the learning process by which animals select safe and balanced diets. Next we present principles of creating food aversions and describe the adverse impacts of social facilitation in maintaining aversions in mixed grazing settings. Finally we present results of our research to develop aversions as a management tool to prevent animals from eating palatable poisonous plants.

Diet selection

Diet selection is complex. The situation is made even more complex for cattle and sheep grazing the rangelands of the western USA because of the spatial and temporal patterns of vegetation on offer. A ranching enterprise in the Intermountain region of the western USA is characterized by seasonal migration of animals from low elevation (2000 m) desert ranges in the winter to high elevation (3000 m) mountain ranges in the summer. The gestating cow or ewe spends the winter grazing on salt-desert shrub rangelands, where temperatures range from an average minimum of −12° to a maximum of 2°, with extremes dropping to −30°. Total annual precipitation averages 200 mm, with most coming as winter snow. Evergreen shrub species (*Atriplex*, *Artemisia* and *Eurotia*) supply protein and minerals, whereas dormant grasses (*Oryzopsis hymenoides*, *Elymus elymoides* and *Hilaria jamesii*) provide energy. Vegetation is sparse, resulting in low carrying capacities; it requires 4–10 ha to provide feed for one cow for 1 month. Water sources are

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erratic and generally animals rely on snow. If sufficient forage is available, animals fare quite well.

Before lambing or calving in the spring, animals are brought close to the ranch headquarters, generally located within sagebrush (*Artemisia* spp.) communities in the foothill zone, where the young are born. They are often supplemented with lucerne (*Medicago sativa*) hay before parturition until new-season grass is available in the late spring. In May, animals are grazed on monocultures of cool-season crested wheatgrass (*Agropyrum cristatum* and *A. desertorum*) designed to provide abundant and highly nutritious forage during early lactation and the breeding season. In early summer, both cattle and sheep are trailed to the mountain summer range (2300–3300 m elevation). Plant communities are variable and complex, ranging in elevation from mountain brush (gamble oak (*Quercus gambleii*), mountain maple (*Acer glabrum*) and mountain mahogany (*Cercocarpus ledifolius*)) to mountain sagebrush–grass plant communities, to aspen (*Populus tremuloides*) trees with a tall forb understory, and finally to sub-alpine meadows dominated by a variety of forbs and grasses scattered among spruce–fir forests.

In any of these plant communities, there are at least thirty to forty plant species. The shrubs, although succulent and high in N, often have high levels of tannins, terpenes and cyanogenic glycosides. Forbs are highly digestible, yet have varying levels of alkaloids and glycosides. Grasses vary in abundance, but are generally the staple of diets. In each community there are three to five plant species considered to be poisonous, and one or two cause significant economic loss. On top of the complexity of the vegetation, each plant changes in its nutrient (Fisher *et al*. 1997) and toxin concentration within the day and as it matures seasonally.

In spite of the complexity of land forms, plant communities and phenological changes, grazing animals are generally successful in selecting balanced diets to optimize production (according to the Optimization Theory; Emmans & Kyriazakis, 1995), most of the time.

Our research efforts have sought to understand how animals select the right amount and combinations of plants to supply the right amount and specific mix of nutrients, yet avoid toxins that are prevalent. Provenza (1995) suggests that animals learn which plants or foods to eat and which to avoid through interactions between a food’s flavour (odour, taste and texture) and the post-ingestive consequences of nutrients and toxins.

Palatability is typically defined as pleasant or acceptable to the taste, and hence fit to be eaten or drunk. This definition highlights the role of flavour, but ignores the role of post-ingestive feedback. Palatability is best understood as the interrelationship between the senses and post-ingestive feedback, as influenced by the physiological condition of an animal and the chemical characteristics of a food (Provenza, 1995, 1996). Taste and smell enable animals to discriminate among foods, and provide hedonic sensations associated with eating. Post-ingestive feedback calibrates hedonic sensations from taste and smell commensurate with the homeostatic utility of a food.

Palatability increases, even for poorly-nutritious foods like straw and grape pomace, when ingestion of those foods is paired with intra-gastric infusions of energy and protein (sheep: Burritt & Provenza, 1992; Villalba & Provenza, 1996, 1997*a,b,c*; rats: Sclafani, 1996). Conversely, palatability decreases, even for foods rich in energy and protein, when ingestion is paired with intra-gastric infusions of toxins (sheep: Provenza, 1995, 1996; rats: Garcia, 1989). Animals typically limit intake of toxin-containing nutritious foods to the amount of a particular toxin they can detoxify (Freeland & Janzen, 1974; McArthur *et al*. 1991; Launchbaugh *et al*. 1993). When macronutrient and toxin concentrations vary in foods herbivores (Wang & Provenza, 1996, 1997) and omnivores (Kimball, 1997) prefer foods high in macronutrients and low in toxins, regardless of the flavour (Wang & Provenza, 1997) or the physical characteristics (Villalba & Provenza, 1999) of the food.

The neural integration of the senses (taste, smell) and post-ingestive consequences of food influence palatability. The senses interact with the body through neurophysiological feedback loops (Scott, 1990; Provenza, 1995; Provenza *et al*. 1998). Sensory receptors respond to gustatory (i.e. sweet, salty, sour and bitter), olfactory (i.e. a diversity of odours) and tactile (i.e. astringency and pain) stimuli. These receptors then interact with visceral receptors that respond to nutrients and toxins (chemoreceptors), osmolality (osmoreceptors) and distension (mechanoreceptors). Preference increases when foods contain macronutrients required by the animal (Villalba & Provenza, 1996, 1997*a,b,c*, 1999). Toxins and excesses or deficits of nutrients reduce preferences (Provenza, 1995). Responses to nutrients and toxins operate along a continuum from preference to aversion, depending on the type and intensity of stimulation (Provenza, 1995, 1996). Aversions may be pronounced when foods contain toxins or excessive levels of rapidly-digestible nutrients that cause malaise (e.g. some forms of N and energy). These mechanisms can be used to induce aversions to specific plants or foods to steer selection away from these foods.

Food aversions

Conditioned taste aversion is a prominent field of research in the behavioural sciences (Braveman & Bronstein, 1985). It has also been used to prevent coyote (*Canis latrans*) and wolf (*Canis lupus*) predation on livestock and rodent depredation on crops (Gustavson & Gustavson, 1985), and in treatment of alcoholism in human subjects (Logue, 1985; Nathan, 1985). Zahorik & Houpt (1977, 1981) first demonstrated that cattle, sheep and horses could be partially averted to specific foods. Provenza (1995) used aversions extensively to develop his theories on diet preferences based on post-ingestive consequences. Laycock (1978) suggested that aversions may have potential to prevent livestock from eating poisonous plants. Our research programme at the USDA/ARS Poisonous Plant Laboratory has been to develop the procedures to avert livestock to specific poisonous plants as a management tool to prevent poisoning. We have successfully developed aversions to tall larkspur (*Delphinium barbeyi*; Ralphs, 1997), white locoweed (*Oxytropis sericea*; Ralphs *et al*. 1997) and ponderosa pine (*Pinus ponderosa*) needles (JA Pfister, unpublished results).

Other scientists have studied aversion conditioning to evaluate selective grazing behaviour. Provenza *et al*.

(1990) reported that naive goats initially grazed both old growth and current-season growth blackbrush (*Coleogyne ramosissima*), but quickly formed aversions to current-season growth due to the high tannin concentration. He suggested that native animals develop natural aversions to many poisonous plants through individual learning of post-ingestive consequences. Kronberg *et al*. (1993) reported that secondary compounds in leafy spurge (*Euphorbia esula*) caused complete aversion to a novel grain–lucerne pelleted feed in cattle. They reasoned that cattle develop natural aversions to spurge which prevent them from grazing this noxious weed. Sheep and especially goats tolerate spurge, and are used as biological control agents to suppress spurge. Kyriazakis *et al*. (1997, 1998) and Duncan *et al*. (1998) demonstrated that aversions could be created to flavoured lucerne hay using oxalic acid, a naturally-occurring toxin in many plants.

Principles of aversive conditioning

Drugs

Any chemical or physiological state which affects the upper gastrointestinal tract or the emetic centre of the brain can cause an aversion (Garcia & Holder, 1985). Riley & Tuck (1985) listed fifty-six drugs (including some toxins) which have been effective in creating aversions. Cyclophosphamide and thiabendazole have been used to create aversions in wild animals. LiCl is currently the most-widely-used emetic in behavioural studies with animals and in human clinical applications. It causes nausea without dangerous side-effects (Provenza *et al*. 1994). The different methods of administering LiCl (mixed in food, orally, bolus or subcutaneous or intraperitoneal injections) appear equally effective in creating an aversion (Nachman & Ash, 1973; Shumake *et al*. 1982). As a result of its caustic nature the relatively large quantities required to create aversions in livestock (80–200 mg/kg body weight) must be administered into the rumen either orally in solution or in boluses, allowing dilution in rumen fluid. Li is retained at significant levels in the body for up to 96 h (Johnson *et al*. 1980; Ralphs, 1999). Treated cattle are most severely ill the second day after dosing, requiring a recovery period of at least 3 d.

Apomorphine is another common emetic used in large animals, and we tested it as an alternative to LiCl. Apomorphine given intramuscularly at 0·1 or 0·2 mg/kg body weight caused a very intense but short-lived illness, but did not create total aversions to flavoured lucerne pellets, and the partial aversions extinguished rapidly (Ralphs & Stegelmeier, 1998). Apomorphine may not work because of its short duration. Testa & Ternes (1977) suggested that the duration of illness should correspond with the natural gastric stimulation following a meal, and continue through the digestion process.

Dose

The strength of the aversion and its resistance to extinction varies with the intensity of the induced illness (Dragoin, 1971; Testa & Ternes, 1977). Increasing doses of LiCl increased the strength and retention of aversions in rats and sheep. Total aversion was obtained from doses of 130 mg/kg body weight in rats (Nachman & Ashe, 1973) and 150 mg/kg body weight in sheep (du Toit *et al*. 1991). We found the optimum dose for cattle was 200 mg/kg body weight (Ralphs & Cheney, 1993). Dose rates of 300 mg/kg body weight did not increase the strength of the aversion, but greatly increased the intensity and duration of illness. The lethal dose of LiCl to cattle lies between 250 and 500 mg/kg body weight (Johnson *et al*. 1980).

Taste cue and familiarity of food

Novelty and intensity of the taste cue are also important in acquiring and retaining an aversion (Rozin & Kalat, 1971; Nachman *et al*. 1977; Testa & Ternes, 1977; Launchbaugh *et al*. 1993). Taste elicits the orienting response to a new food (Garcia, 1989). Thus, the more novel or unique the taste, the stronger is its association with the induced illness (Best & Barker, 1977).

It is difficult to create aversions to familiar foods (Burritt & Provenza, 1996). Foods that have not caused harm in the past fall into a ‘learned safety’ status (Kalat & Rozin, 1973), based on the nutrients they provide (Villalba & Provenza, 1996, 1997*a*,*b*,*c*). As little as one lengthy exposure or several short exposures to a food before pairing it with an emetic is detrimental to forming an aversion (Best & Barker, 1977; Burritt & Provenza, 1996). Several pairings of taste with illness are required to form aversions to familiar foods, and aversions extinguish rapidly (Fenwick *et al*. 1975, JD Olsen and MH Ralphs, unpublished results). The difficulty in creating aversions to locoweed was dramatically different in naive steers compared with experienced steers that had been eating it (Ralphs *et al*. 1997). Naive steers required a single dose of LiCl (200 mg/kg body weight), and totally abstained for the remainder of the grazing trial. Steers that were familiar with locoweed required at least two doses in the conditioning phase in the pen, and continued eating locoweed when released in the locoweed-infested pasture. We were finally able to create aversions in these steers by reinforcing the aversion each time they grazed locoweed in the field. They were observed closely and brought back into the pen and dosed with LiCl whenever they consumed any locoweed. These steers required three or four doses of LiCl following consumption of locoweed in the field to create a complete aversion.

Aversions can be formed with long delays (up to 12 h) between the taste cue and the induced illness (Garcia *et al*. 1966); however, aversions are stronger when the cue and consequence are in close proximity. The strength of the aversion declines when the interval goes beyond 4 h (Andrews & Braveman, 1975; Burritt & Provenza, 1991).

Hunger

Food deprivation before conditioning has little direct influence on success in forming aversions (Revusky *et al*. 1980). Hungry animals may eat more during conditioning, thus enhancing the flavour stimulus (Braveman & Crane, 1977). We have typically fasted animals for 1–3 d to force them to consume the target plant.

On the other hand, hunger during testing or extinction trials can reduce the strength of the aversion (Grote & Brown, 1973; Wellman & Boissard, 1981). Hungry animals eat even though the food has been associated with illness and 'tastes' bad. A choice of two foods during testing eliminates the forced consumption of the averted food, and thus is a more sensitive measure of the aversion (Dragoin, 1971; Grote & Brown, 1973). A single food test is a severe test of the aversion.

Animals are also likely to sample foods that are constantly available to them (Zajonc, 1968). Offering an averted food intermittently in test trials is more likely to preserve the aversion than continually offering the food free choice.

Age

Learning ability varies with age. Livestock may learn to forage most efficiently around the time of weaning (Provenza & Balph, 1988). Thereafter, acceptance of new foods declines as animals mature (Squibb *et al*. 1990). However, the inquisitive character of young animals in sampling new foods may be a liability in maintaining an aversion. For example, weanling and preweanling rats form weaker aversions and extinguish them faster than adults (Steinert *et al*. 1980; Springer & Fraley, 1981; Franchina & Horowitz, 1982; Guanowsky *et al*. 1983). Thorhallsdottir *et al*. (1990) presented conclusive evidence that lambs extinguished aversions to calf manna (a very palatable concentrated feed) in a two-choice social facilitation trial, while their mothers retained the aversion to a greater degree. We found that mature cows required a lower dose of LiCl (200 mg/kg body weight) to maintain aversions to sugarbeet pulp compared with yearling heifers (300 mg/kg body weight; Ralphs & Cheney, 1993). Thus, aversions created in mature animals may be more resistant to extinction than those in younger animals.

Context of learning

All learning occurs within the context of previous experiences, and in an environmental context defined by the location, time and specific features of the task at hand. All basic learning phenomena, including appetitive and aversion conditioning, have been shown to change with contextual manipulations (Best *et al*. 1977; Balsam, 1985). Stimulus differences between the location where a response is learned and where it is expressed have strong and usually detrimental effects (Miller & Schachtman, 1985). Thus, food aversions may be difficult to maintain in new environments (Ralphs & Olsen, 1990; Burritt & Provenza, 1997).

Although taste is the primary sense involved in creating an aversion, the environmental context can influence the strength and retention of the aversion (Archer *et al*. 1985). It is necessary to utilize this relationship to strengthen, rather than hinder, the aversion. Lubow *et al*. (1976) proposed that learning is stronger when either the stimulus or the environment is novel relative to each other; i.e. the aversion is stronger if a novel food is presented in a familiar environment, or a familiar food is presented in a novel environment. Kruz & Levitsky (1982) tested this hypothesis in rats and found that the aversion was strongest when a novel food was presented in a familiar environment. However, no aversion was created when a familiar food was presented in a novel environment. Mitchell *et al*. (1975) also found that aversions to novel items were not learned in a less-familiar environment. In a new environment everything is novel and the stimulus is not salient. Burritt & Provenza (1997) recommended that animals be averted to specific plants in environments where they will encounter the plant.

Social facilitation

Social facilitation has been the greatest impediment in retaining aversions in our mixed grazing trials with averted and non-averted cows grazing together (Ralphs & Olsen, 1990, 1992; Ralphs, 1997). Social facilitation has been defined as an 'increase in the frequency or intensity of responses, or the initiation of a particular response, when shown in the presence of others engaged in the same behavior at the same time' (Clayton, 1978). Social facilitation is an extremely strong force influencing animals to sample plants or foods they see others eating. This situation is illustrated in two grazing trials showing casual acceptance of locoweed as a novel food (Ralphs *et al*. 1994). Naive cattle ate very little woolly locoweed (*Astragalus mollissimus*) while grazing separately in New Mexico, but when they were placed with experienced cattle that were eating locoweed, consumption quickly increased to levels similar to those of the experienced cows. In the second trial on mountain rangeland in northwest Utah, naive yearling cattle grazed very little white locoweed (3 % intake), but when placed with experienced cattle locoweed consumption increased to 25 % intake.

Galef and his research group (Galef, 1985, 1986; Galef *et al*. 1985) have systematically evaluated the influence of social facilitation on diet selection in rats. Simple exposure to a food did not enhance preference. However, the presence of a demonstrator rat that had eaten a specific food, even if that food was consumed at another location, enhanced the observer rats' preference for that food (Galef *et al*. 1985). Delays of up to 4 h between the demonstrator's meal and interaction with the observer did not impede the establishment of preference for the food. He also reported that social facilitation was strong enough to overcome established food aversions (Galef, 1985). Rats which had formed mild aversions to a specific food abandoned their aversion to that food following interaction with one demonstrator that had eaten the food at a distant location. When interacting with two or more demonstrators even strong aversions were extinguished. He concluded that aversion conditioning is the most potent known experimental determinant of diet selection, yet social facilitation was able to extinguish even strong aversions.

Galef (1986) went on to compare social facilitation with other factors that influence diet preferences. Palatability, Na deficiency and mechanical impediments were all significantly modified by social facilitation. He concluded that a rat 'will abandon, to a greater or lesser extent, reliance on information it personally has collected concerning the value of a food, in favor of information it acquired from others'.

Although social facilitation is a strong force compelling animals to sample a food they see others eating, the utility of that food, positive or negative, will dictate its continued acceptance. Provenza *et al.* (1993) designed an experiment to test the relative strength of a mother's influence (social facilitation) compared with adverse post-ingestive consequences in selection of elm leaves (*Ulmus procera*) by lambs. Lambs generally avoided elm if their mothers avoided it, and consumed it if the mothers did. However, if the mothers ate it but the lambs were given a mild dose of LiCl, the lambs abstained in spite of the mother's influence. Provenza *et al.* (1993) concluded that the post-ingestive consequence of LiCl was stronger than the mother's influence. Social interaction will influence an animal to sample a plant, but post-ingestive consequences will ultimately determine its palatability and continued acceptance.

The practical problem remains as to how to maintain an induced aversion in field grazing or foraging conditions. If an averted animal is compelled to sample the target plant and there is no adverse post-ingestive feedback, the aversion will quickly extinguish. Gustavson & Gustavson (1985) reviewed several reports of predators being averted to prey, but the aversion was extinguished through the influence of social facilitation. Lambs also extinguished aversions to mountain mahogany when grazing in the presence of non-averted lambs (Burritt & Provenza, 1989). Both ewes and lambs extinguished aversions to calf manna in a group-feeding situation with non-averted sheep (Thorhallsdottir *et al.* 1990).

Social facilitation has been the most important factor inhibiting the retention of aversions in cattle to larkspur in our mixed grazing trials with averted and non-averted animals grazing together. Lane *et al.* (1990) created aversions to larkspur in heifers by feeding fresh larkspur in a pen, then dosing them with LiCl (100 mg/kg body weight) through a rumen catheter. The heifers associated the induced illness with the taste of larkspur, and avoided eating larkspur when it was offered in the pen. When released in larkspur-infested mountain pastures the heifers abstained from eating larkspur for 2 years. However, when the averted heifers were placed with non-averted cohorts that were freely grazing larkspur they started sampling larkspur and the aversion extinguished.

We conducted several experiments to try to overcome the influence of social facilitation and maintain the aversion under field-grazing conditions when averted and non-averted cattle grazed together. We first attempted to reinforce the aversion by dosing heifers with LiCl whenever they consumed larkspur in a group with non-averted cohorts that were freely eating larkspur (Ralphs & Olsen, 1990). We next tried using native cattle that were familiar with the plant community, under the assumption that their preferences were established and they would be less likely to be influenced by social facilitation (MH Ralphs, unpublished results). We finally used larkspur alkaloid extract as the emetic, so that if a cow subsequently ate larkspur in the field the indigenous alkaloids would create an internal feedback to reinforce aversions (Ralphs & Olsen, 1992). None of these procedures was successful. We concluded that if animals sample plants without adverse consequences, they will continue to eat them and the aversion will eventually be extinguished. Thus, averted cattle must be grazed separately to maintain the aversion. If averted animals can be grazed separately, conditioned food aversion may be a practical management tool to train animals to avoid eating specific plants or foods.

Aversion to poisonous plants

Tall larkspur

Tall larkspur is an important poisonous plant on mountain rangelands. It is palatable to all livestock, especially in its later stages of growth, but is acutely toxic to cattle. Its toxic alkaloids block acetylcholine receptors at the neuromuscular junction, resulting in muscular paralysis and rapid death from respiratory failure. Cattle do not form lasting natural aversions to larkspur. Pfister *et al.* (1997) showed that cattle reduced larkspur consumption following sublethal doses of the toxic alkaloid. However, after 2–3 d recovery they increased consumption of larkspur, presumably because of positive feedback from its high level of nutrients. Apparently, more intensive levels of nausea are required from non-lethal emetics to create total and lasting aversions.

LiCl at 200 mg/kg body weight was used to create aversions to larkspur that lasted 3 years while cows grazed separately on larkspur-infested mountain rangeland (Ralphs, 1997). We also implemented a ranch-scale demonstration project to determine if aversions will be practical on a large scale. The ranch was a 300 cow enterprise in Yampa, CO, USA, and the larkspur problem was on a 2000 ha Forest Service grazing allotment that had a history of serious losses to larkspur. More than 10 % of the herd had died from larkspur poisoning in two recent years. In 1997 forty-five cows were averted to larkspur, seventy-seven cows were averted in 1998, and the remainder of the herd will be averted in 1999. The cows were fasted overnight, then twenty head at a time were brought into a smaller corral and offered freshly-picked larkspur. They were observed closely, and those that consumed larkspur were restrained in a handling stall and orally administered LiCl at 200 mg/kg body weight by a stomach tube. Those cows that did not eat were held and offered larkspur later when they were more hungry. About 80 % of the cows ate larkspur and were averted. The cows were allowed to recover for 3 d, then they were trailed to the mountain grazing allotment. A rider observed them each day to see if they consumed any larkspur. About 10 % of the cows started to consume larkspur. They were removed from the allotment to prevent intoxication and social facilitation from influencing other cows to start eating (MH Ralphs, unpublished results).

Locoweed aversion

Locoweed is the most widespread poisonous plant on western US rangelands. It is relatively palatable to all classes of livestock, and causes chronic poisoning that affects weight gains, fertility and even causes abortion. A New Mexico rancher adopted the strategy of averting his yearling replacement heifers to white locoweed each year. Thus, over a period of years, he would replace his entire herd with averted cows. In the spring of 1998, forty-three heifers were averted to white locoweed. Another twenty-four heifers were averted in the autumn of 1998 immediately after weaning. The heifers were penned and not offered feed for 24 h. Five heifers at a time were run into an alley and offered freshly-picked locoweed in rubber feed troughs. They were closely observed and those that did not eat were separated into another pen. Those heifers that ate substantial amounts of locoweed were restrained in a handling stall and dosed with LiCl at 200 mg/kg body weight by bolus. Those heifers that did not eat locoweed were held in the corral and offered locoweed later. The heifers averted in the spring were transported to a locoweed-infested pasture in mid May. Before being released they were again offered locoweed to test the aversion, but all refused. The heifers were watched closely to see if they would graze locoweed in the pasture. Eleven heifers were observed eating locoweed and were returned to the corral and dosed a second time. All the heifers abstained from eating locoweed for the remainder of the grazing season (MH Ralphs, unpublished results).

Conclusion

Conditioned food aversion is a powerful experimental tool to modify animal diets (Galef, 1985). We have shown that it is a potential management tool to prevent livestock from grazing poisonous plants like larkspur (Ralphs, 1997), locoweed (Ralphs *et al*. 1997), and ponderosa pine (JA Pfister, unpublished results). The following principles will increase the strength and longevity of aversions: mature animals retain aversions better than young animals; novelty of the plant is important, although aversions can be created to familiar plants; LiCl is the most effective emetic for large animals; the optimum dose for cattle is 200 mg/kg body weight, and for sheep is 150 mg/kg (du Toit *et al*. 1991); and averted animals should be grazed separately to avoid the influence of social facilitation which will extinguish the aversion.

Social facilitation is the most important factor preventing widespread application of aversion conditioning. If averted animals see others eating the target food, they will sample it. If there is no adverse reaction, they will continue eating and eventually extinguish the aversion. However, if averted animals can be grazed separately, aversion conditioning may provide an effective management tool to prevent animals from eating palatable poisonous plants.

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