

Utah State University

DigitalCommons@USU

Green Canyon Environmental Research Area,
Logan Utah

Quinney Natural Resources Research Library,
S.J. and Jessie E.

1995

Tracking Variable Environments: There is More than One Kind of Memory

Frederick D. Provenza
Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/grcanyon>



Part of the [Life Sciences Commons](#), and the [Social and Behavioral Sciences Commons](#)

Recommended Citation

Provenza, F. (1995). Tracking variable environments : there is more than one kind of memory. *Journal of Chemical Ecology*, 21(7): 911-923.

This Article is brought to you for free and open access by the Quinney Natural Resources Research Library, S.J. and Jessie E. at DigitalCommons@USU. It has been accepted for inclusion in Green Canyon Environmental Research Area, Logan Utah by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



TRACKING VARIABLE ENVIRONMENTS: THERE IS MORE THAN ONE KIND OF MEMORY

FREDERICK D. PROVENZA

*Department of Rangeland Resources
Utah State University
Logan, Utah 84322-5230*

(Received February 14, 1995; accepted March 10, 1995)

Abstract—Three kinds of memory help herbivores track changes in the environment. The first is the collective memory of the species with genetic instructions that have been shaped by the environment through millennia. This includes skin and gut defense systems. Auditory and visual stimuli and sensations of pain impinge upon the skin defense system that evolved in response to predation. The taste of food and the sensations of nausea and satiety are an integral part of the gut defense system that evolved in response to toxins and nutrients in plants. The second kind of memory in social mammals is represented by the mother, a source of transgenerational knowledge, who increases efficiency and reduces risk of learning about foods and environments. The third kind of memory is acquired by individual experience. Post-ingestive feedback from nutrients and toxins enables individuals to experience the consequences of food ingestion and to adjust food preference and selection commensurate with a food's utility. The three memories interact, each linking the past to the present, and collectively shape the present and future of every individual. Thus, the dynamics of foraging involves appreciating the uniqueness of individuals and subgroups of animals, each with their own genetic and behavioral history, and recognizing that foraging behaviors may not be stable, optimal, or even predictable in the conventional sense.

Key Words—Evolution, ecology, learning, memory, foraging, habitat, spotted owl.

INTRODUCTION

Organisms rely on experience and memory to cope with hazards in the environment. In the absence of memory, every facet of the environment would ceaselessly be experienced for the first time and immediately forgotten. As Luis Bunuel lamented while in the process of losing his memory: "You have only

to begin to lose your memory, if only in bits and pieces, to realize that memory is what makes our lives. Life without memory is no life at all Our memory is our coherence, our reason, our feeling, even our action. Without it, we are nothing . . . (I can only wait for the final amnesia, the one that can erase an entire life, as it did my mother's . . .)" (in Sacks, 1990, Chapter 2).

There are three kinds of memory. The first is the collective memory of the species, the genetic instructions that have been shaped by the environment throughout millennia. The second is represented in social mammals by the mother, who is a source of transgenerational knowledge. The third kind of memory is acquired by individual experience. The three memories interact and link consequences of behavior from the past to the present and shape the present and future of every individual. This paper discusses the three types of memories and how they are related.

EVOLUTION AS MEMORY

Genes are the cumulative memory of how environment has shaped the species through millennia. Skin and gut defense systems are part of these genetic instructions in species are diverse as fruit flies, snails, fish, lizards, tiger salamanders, pigeons, hawks, rats, cats, dogs, sheep, baboons, and humans (Garcia et al., 1985; LeDoux, 1994; Provenza, 1995). Auditory and visual stimuli and sensations of pain 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 plants. As Garcia (1989) suggests "all organisms evolved coping mechanisms for obtaining nutrients and protective mechanisms to keep from becoming nutrients" too soon.

Evolution has created skin and gut defense mechanisms that facilitate interactions with a virtually infinite variety of objects in the environment. Each system is underlain by two kinds of memory; one provides the emotional content of the experience, whereas the other renders specific details about objects and events. Collectively, these systems are designed to interact with and to be shaped by the environment during each animal's lifetime. This flexibility increases the likelihood of survival of the individual and of the species, given the fact that the environment is ever-changing and that the average lifetime of a species is several million years (Wilson, 1992). This plasticity is clearly one of the most important outcomes of evolution.

The way skin and gut defense systems work is illustrated in experiments in which hawks were fed distinctively colored or flavored mice (Brett et al., 1976; Garcia and Garcia y Robertson, 1985). Hawks fed white mice with impunity, but occasionally given a black mouse followed by an injection of the toxicant lithium chloride (LiCl), would not eat either black or white mice,

because both mice tasted the same. But when a distinctive taste was added to black mice, hawks learned to avoid black mice on sight after a single black mouse toxicosis event. The taste cue potentiated the color cue.

Such experiments show that not all cues are readily associated with all consequences. Cue-consequence specificity refers to the fact that when animals are made ill following exposure to audiovisual and taste cues, they 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 and Koellin, 1966). The same kind of response has been demonstrated for food and place aversions. Toxins like LiCl cause strong food aversions, but they do not cause rats to avoid the place where they ate a particular food (Lett, 1985; Coil et al., 1978). Conversely, compounds such as gallamine, which causes muscular paralysis, causes rats to avoid the place where they ate but they do not stop rats from eating the food (Lett, 1985).

The incorrigible nature of such responses is illustrated further by the fact that animals acquire aversions even when they know the food did not cause the illness (Garcia and Garcia y Robertson, 1985; Provenza et al., 1994a). For instance, many of us remember acquiring an aversion to a particular food, even though we knew the illness (e.g., nausea caused by flu, reaction to a vaccine, seasickness, chemotherapy) was not related to food. This knowledge does not alter the newly acquired aversion to the taste and odor of the food.

Such seemingly irrational responses occur because gustatory and visceral afferent nerves converge at common central neural pathways that are generally distinct from audiovisual and somatosensory integrative neural systems (Garcia et al., 1985; LeDoux, 1994). Olfactory pathways have access to both skin and gut defense systems. Odor cues are associated with taste cues (i.e., taste potentiates odor) during a meal, and these two senses provide information concerning the flavors of particular foods. Conversely, odors of predators serve as warnings for the skin defense system. Thus, evolution arranged the central nervous system in a manner that affords relatively direct and independent integration of skin defense and gut defense systems.

Skin and gut defense systems were designed differently to accomplish different objectives. The skin defense system functions on a scale of milliseconds to seconds; rapid responses are required to avoid predation (LeDoux, 1994). Conversely, the gut defense system integrates information about tastes (and potentiated odors) of foods and the postingestive effects of nutrients and toxins over time frames of minutes to hours; digestion and absorption are relatively slow processes (Garcia et al, 1985; Provenza, 1995).

Skin and gut defense systems are also mutually inhibitory. Fear abolishes appetite and gastric motility, whereas a large meal is followed by drowsiness and muscular relaxation. As Robert Capa (*Newsweek*, May 23, 1994) noted in

his diary on D-Day: “The mess boys of the *U.S.S. Chase* wore immaculate white jackets and served hot cakes, sausages, eggs and coffee with unusual zest and politeness. But the pre-invasion stomachs were preoccupied, and most of the noble effort was left on the plates”

Two kinds of memory underlie skin and gut defense systems, one renders specific details about objects and events, whereas the other provides the emotional or affective content of the experience (LeDoux, 1992, 1994). Declarative (cognitive) memory is the process by which earlier conscious experiences are recalled. The original learning and remembering are conscious events mediated by the hippocampus. Memories of snakes (skin defense) and various foods (gut defense) and locations where they have been encountered are examples. In contrast, emotional (noncognitive) memory operates independently of conscious awareness, and it is mediated by the amygdala. Fear (skin defense), nausea and satiety (gut defenses) are examples. Emotional memory may be stored within declarative memory, which can activate emotional responses through the amygdalic system. Thus, emotion is not merely unconscious memory, rather it exerts a powerful influence on declarative memory and on behavior.

Emotional and declarative memories provide insights into the distinction between food preferences and food selection. Neurally mediated interactions between the senses (i.e., taste and smell) and the gut (i.e., nausea and satiety caused by toxins and nutrients) cause changes in food preferences that do not involve cognitive processes (i.e., they constitute an emotional memory). The noncognitive aspect of this phenomenon has been verified in a variety of species under various conditions, e.g., animals acquire food aversions when anesthetized (Roll and Smith, 1972; Bermudez-Rattoni et al., 1988; Provenza et al., 1994a), tranquilized (Forthman Quick, 1984), and when their electrocortical activity is depressed (Davis and Bures, 1972; Buresova and Bures, 1973). In contrast, animals use declarative memory to select (avoid) particular foods and foraging locations.

THE MOTHER AS MEMORY

The mother as a memory shapes food and habitat selection by her offspring and increases their likelihood of survival. The importance of this transgenerational link is clearly illustrated in instances when wild and domesticated ruminants are moved to unfamiliar environments. Compared with animals reared in the environment, naive animals spend more time foraging but ingest less forage; they spend more time walking and walk for greater distances; they suffer more from predation, malnutrition, and ingestion of toxic plants (reviewed in Griffith et al., 1989; Provenza and Balph, 1990).

The mother increases efficiency of learning about nutritious foods (Provenza, 1994). Lambs exposed to wheat with their mothers for as little as 1 hr/day for five days ingested more wheat than did lambs exposed to wheat without their mothers; intake of wheat was nearly 10 times higher as many as three years later with no intermittent exposure (Lynch et al., 1983; Green et al., 1984). Likewise, lambs exposed to the shrub *Amelanchier alnifolia* and to barley with their mothers ingested considerably more of these foods than did lambs who were exposed without their mothers (Thorhallsdottir et al., 1990). Finally, lambs who ate either of two palatable shrubs (*Cercocarpus montanus* or *Amelanchier alnifolia*), showed a marked preference for the shrub they ingested with mother (Nolte et al., 1990).

In the same manner, the mother reduces the risk of overingesting toxic foods (Provenza, 1994). For instance, a lamb learns quickly to avoid harmful foods and to select nutritious alternatives, when with its mother who exhibits this behavior (Mirza and Provenza, 1990, 1992). As a result of such interactions, a lamb acquires preferences for foods its mother eats, and avoids foods its mother avoids (Mirza and Provenza, 1994).

Experiences early in life with the mother also shape habitat preferences of offspring. Wild herbivores of the same species often occupy different home ranges within an area (Gruell and Papez, 1963; Geist, 1971; Fiesta-Bianchet, 1986a,b, 1988; Cederlund and Okama, 1988; Cederlund et al., 1987; Porter, 1992). This phenomenon also occurs in livestock (sheep: Hunter and Milner, 1963; Lawrence, 1990; cattle: Yeates and Schmidt, 1974; Martin, 1979; Reinhardt and Reinhardt, 1981; Roath and Krueger, 1982; Hall, 1988; Howery et al., 1995a; goats: O'Brien, 1984). Cross-fostering experiments with sheep (Key and MacIver, 1980) and cattle (Howery et al., 1995b) show that habitat selection preferences are transferred from mother to offspring. For instance, lambs whose mothers preferred native pastures were cross-fostered with lambs whose mothers preferred seeded pastures. After weaning, the lambs strongly preferred the location where their foster mothers had foraged. Individuals reared in different environments often have disparate dietary habits (Biquand and Biquand-Guyot, 1992), which in turn affects their preferences for foraging locations (Scott et al., 1995).

As a result of selecting particular foods and foraging in certain locations, the preferences of individuals can become quite rigid, to the degree that they appear to be genetically fixed. This phenomenon is illustrated in field studies of Criollo goats grazing savannas of Martinique, French West Indies (Biquand and Biquand-Guyot, 1992). The diets of mature female goats, which came from four different locations, strongly reflected their area of origin on the island, despite grazing a common area for four years. These mothers produced four lots of female offspring. Diets of the cohorts born in successive years were strongly affected by experiences early in life, which were a reflection of the

diets of their mothers and peers, as well as differences in plant species that were available the year they were born.

Research on moose provides another example of the persistence of behaviors learned from the mother (Andersen, 1991; Histol and Hjeljord, 1993). A population of moose in central Norway migrates from low-lying summer areas to winter areas situated at higher altitudes, which is contrary to the general pattern of migration to lower elevations near the sea. Archeological evidence along the migration route shows that the migratory behavior of this population has not changed since 5000 BP, despite deterioration in the quality of their winter range. The low calf production of the population (0.6 calves/cow) compared with neighboring populations (0.8–1.3 calves/cow) evidently reflects the poor winter ranges. Migratory traditions passed on from mother to offspring are inflexible, and changing migratory routes to utilize better quality range may take many generations, if it ever occurs.

THE INDIVIDUAL AS MEMORY

Experience is the memory of the consequences of behavior to the individual. The importance of individual experience in foraging is illustrated in experiments with the mother and her offspring. For instance, when a lamb experiences mild toxicosis from eating a food its mother prefers, the lamb acquires an aversion to the food even though its mother continues eating the food avidly (Provenza et al., 1993a). Thus the mother may facilitate the acquisition of foraging behaviors by her offspring, but continuation of the behaviors depends on the consequences to the individual (Galef, 1988).

Postingestive feedback enables individuals to experience the consequences of food ingestion, and it causes changes in preference for the flavor (taste and odor) of particular foods (Provenza, 1995). Animals acquire preferences for flavors of foods that cause satiety, the pleasant sensation that occurs when animals ingest adequate kinds and amounts of nutritious foods. Conversely, animals acquire aversions for the flavors of foods that cause malaise, the unpleasant feelings of physical discomfort that occur from ingesting excesses of nutrients and toxins and from nutrient deficits. What constitutes excesses, deficits, and satiety depends on the animal's nutritional requirements, which vary with age, physiological state, and environmental conditions. Thus, postingestive feedback adjusts food preferences commensurate with the food's utility. In the absence of flavor–feedback interactions, animals are not likely to select a nutritious diet because they generally can not directly taste and smell nutrients and toxins in foods.

Flavor–feedback interactions cause changes in preference (affective value), and changes in preference cause changes in food selection (Garcia, 1989; Provenza, 1995). Taste plays the pivotal role in both cases. Affective processes

integrate the taste of food and its postingestive consequences, aversive or positive, thereby causing changes in incentive to eat particular foods; they involve neurally (i.e., primarily brain stem and limbic system) mediated interactions between the sense of taste and the body, and they are noncognitive. Cognitive processes involve use of the senses of smell, sight, and hearing to select foods that cause positive consequences and to avoid foods that cause malaise; they involve interactions between higher cortical centers and the limbic system. Affective and cognitive processes function in parallel to regulate the internal environment. The taste of food is continuously calibrated according to its effect on the internal environment, and on that basis animals select foods that are nutritious and avoid those that are toxic.

Affective and cognitive processes both operate when animals forage, for instance when goats choose between current season's (CSG) and older growth (OG) twigs from the shrub blackbrush (*Coleogyne ramosissima*). Even though CSG contains more nitrogen (1.04% vs. 0.74%) than OG and is more digestible (48% vs. 38%), goats prefer older twigs containing lower levels of a condensed tannin that causes a learned food aversion (Provenza et al., 1990). When both types of twigs are offered to goats who have never consumed blackbrush, goats do not exclusively choose either type, but when they finally eat more CSG than OG in a meal (44 g and 16 g) and eat enough CSG to acquire an aversion (about 44 g), they ingest less CSG from then on (Provenza et al., 1994b). Thus, the relative amount of food eaten within a meal controls the acquisition of an aversion to CSG. The change in preference for CSG involves the brain stem and limbic system and requires no cognitive ruminations on the part of the goat, whereas the change in food selection by the goat involves the senses of sight and smell and higher cortical centers.

An animal's experiences, particularly early in life, exert a profound influence on food preference (Provenza and Balph, 1990; Provenza, 1994). As a result of eating particular foods and not eating others, young animals acquire dietary habits. They prefer familiar foods, and they become reluctant to eat novel foods. Accordingly, familiarity and novelty come to control taste-feedback interactions within meals. For instance, when animals eat a meal of novel and familiar foods and experience malaise, they avoid the novel foods (Revusky and Bedarf, 1967; Burritt and Provenza, 1991), and they exhibit the same response when the flavor of a familiar food changes (Launchbaugh and Provenza, 1993; Provenza et al. 1993a, 1995). Furthermore, when they eat a meal of only novel foods and experience malaise, they avoid the foods that are most novel (Kalet and Rozin, 1970, 1971; Kalat, 1974; Provenza et al. 1994b). For instance, lambs fed rolled barley (familiar food), with a low and a high concentration of a flavor, consume small amounts of both foods, regardless of flavor concentration (Launchbaugh et al. 1993); but after they eat a meal of both foods, and then receive a mild toxin dose, they avoid the barley with the highest concen-

tration of the flavor (i.e., the barley that is most different (novel) from plain barley). Conversely, when animals experience mild malaise following a meal of familiar foods, they avoid foods eaten too frequently or in excess (Provenza et al. 1993b, 1994b; Phy and Provenza, 1995; Burritt and Provenza, 1995). Thus, eating any familiar food to satiety is apt to cause mild malaise, which will cause animals to eat a varied diet (Provenza, 1995).

Young ruminants remember foods that provided either aversive (Lane et al., 1990; Burritt and Provenza, 1990) or positive (Green et al., 1984; Squibb et al., 1990) consequences for at least one to three years without intermittent exposure, and they sample novel foods cautiously (Chapple and Lynch, 1986; Chapple et al., 1987; Thorhallsdottir et al., 1987; Burritt and Provenza, 1989, 1991). The ability to discern novel from familiar foods is illustrated in experiments when lambs were given 10 different foods during a seven-month period (Provenza et al., 1995). Any time lambs were offered a food they had previously eaten, their initial intake was high (e.g., >600 g in 30 min). Conversely, when they were offered a novel food, their intake was low initially (e.g., <50 g in 30 min) and gradually increased over several days. Intake decreased (increased) any time a novel (familiar) flavor was added to a familiar (novel) food. Thus, lambs remembered at least 10 foods, a number similar to that typically comprising the diets of animals foraging on rangelands. For instance, goats encounter over 100 species/ha in tropical savannas, but they eat only seven species in significant amounts (10% or more of the diet), and five species constitute 65% of their diet (Biquand and Biquand-Guyot, 1992).

Animals discriminate among novel foods to the degree dictated by the environment. Goats first introduced to blackbrush-dominated rangelands sample all foods in the area during the first few hours, including potentially toxic plants like *Juniperus osteosperma* (bark and green leaves), *Gutierrezia microcephala* (a forb), and *Marrubium vulgare* (a forb), as well as nontoxic shrubs like *Prunus fasciculata* and *Purshia tridentata*. They also sample and learn to distinguish among different plant parts, for instance, current season's and older growth twigs from the shrub blackbrush. Within a few days, however, goats discriminate among and ingest different amounts of various foods, evidently on the basis of neurally mediated interactions between taste and postingestive feedback (Provenza et al., 1994b; Provenza, 1995). Considering the importance of food for survival, the design of the central nervous system, and the fact that ruminants spend as many as 8–12 hr foraging every day, it should not be surprising that herbivores can learn to discriminate among several novel foods on the basis of flavor–feedback interactions.

CONCLUSION

One of the most important outcomes of evolution is the plasticity to be shaped by the environment during an animal's lifetime. Beliefs concerning evo-

lution should be tempered with the realization that food and habitat selection are dynamic processes, adapted to environmental change. Learning is vital for adaptation, and it involves elements of history and change such as prior experiences; social interactions; neuro-, morpho-, and physiological feedbacks and feedback time lags; individual variability in responses to nutrients and toxins; forage sampling; and random events. It is prudent to recognize that learning can activate a self-perpetuating series of consequences that are nonoptimum, sensitive to perturbation, difficult to predict, and resistant to change (Provenza and Cincotta, 1993). Accordingly, food and habitat selection should be studied as dynamic behavioral processes rather than as static events that reside at some optimum.

Conservation and management programs should operate with this kind of dynamic in mind. The spotted owl is an excellent example. There is growing evidence that the spotted owl is not endangered. Instead, it occurs from British Columbia to Mexico in habitats as disparate as young- and old-growth forests and desert scrub (Easterbrook, 1994). Recent studies suggest that the DNA is no different in individuals in any of those populations. What differ are the experiences of individuals with the environment, but that does not make them different species. As Easterbrook points out: "If local variation in climate and diet convert creatures to different species, a black man who lives in Seattle, gets rained on and eats salmon would be a different species from a white man who lives in stifling humidity in Louisiana and dines on gumbo. By this theory the human race contains hundreds of species." The distinction between what has been shaped by the environment during an animal's lifetime and what has been shaped by evolution over millennia makes all the difference in the world concerning understanding of the status of spotted owls.

Acknowledgments—This paper is based on a talk given at the 11th Annual Meeting of the International Society of Chemical Ecology as part of a symposium titled "Plant-Herbivore Interactions: Quo Vadimus?" It is published with the approval of the Director, Utah Agricultural Experiment Station, Utah State University, Logan, as Journal Paper number 4628. The work was supported by grants from the Cooperative States Research Service and the Utah Agricultural Experiment Station.

REFERENCES

- ANDERSON, R. 1991. Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. *J. Appl. Ecol.* 28:102-108.
- BERMUDEZ-RATTONI, F., FORTHMAN QUICK, D.L., SANCHEZ, M.A., PEREZ, J.L., and GARCIA, J. 1988. Odor and taste aversions conditioned in anesthetized rats. *Behav. Neurosci.* 102:726-732.
- BIQUAND, S., and BIQUAND-GUYOT, V. 1992. The influence of peers, lineage and environment on food selection of the criollo goat (*Capra hircus*). *Appl. Anim. Behav. Sci.* 34:231-245.
- BRETT, L.P., HANKINS, W.G., and GARCIA, J. 1976. Prey-lithium aversions III: Buteo hawks. *Behav. Biol.* 17:87-98.

- BURESOVA, O., and BURES, J. 1973. Cortical and subcortical components of the conditioned saccharin aversion. *Physiol. Behav.* 11:435-439.
- BURRITT, E.A., and PROVENZA, F.D. 1989. Food aversion learning: ability of lambs to distinguish safe from harmful foods. *J. Anim. Sci.* 67:1732-1739.
- BURRITT, E.A., and PROVENZA, F.D. 1990. Food aversion learning in sheep: Persistence of conditioned taste aversions to palatable shrubs (*Cercocarpus montanus* and *Amelanchier alnifolia*). *J. Anim. Sci.* 68:1003-1007.
- BURRITT, E.A., and PROVENZA, F.D. 1991. Ability of lambs to learn with a delay between food ingestion and consequences given meals containing novel and familiar foods. *Appl. Anim. Behav. Sci.* 32:179-189.
- BURRITT, E.A. and F.D. PROVENZA. 1995. Effect of experience and prior illness on the acquisition and persistence of conditioned food aversions in lambs. *Appl. Anim. Behav. Sci.* in press.
- CEDERLUND, G., and OKAMA, H. 1988. Home range and habitat use of adult female moose. *J. Wildl. Manage.* 52:336-343.
- CEDERLUND, G., SANDEGREN, F., and LARSSON, K. 1987. Summer movements of female moose and dispersal of their offspring. *J. Wildl. Manage.* 51:342-352.
- CHAPPLE, R.S., and LYNCH, J.J. 1986. Behavioral factors modifying acceptance of supplementary foods by sheep. *Res. Dev. Agric.* 3:113-120.
- CHAPPLE, R.S., WODZICKA-TOMASZEWSKA, M., and LYNCH, J.J. 1987. The learning behavior of sheep when introduced to wheat. II. Social transmission of wheat feeding and the role of the senses. *Appl. Anim. Behav. Sci.* 18:163-172.
- COIL, J.D., HANKINS, W.G., JENDEN, D.J., and GARCIA, J. 1978. The attenuation of a specific cue-to-consequence association by antiemetic agents. *Psychopharmacology* 56:21-25.
- DAVIS, J.L., and BURES, J. 1972. Disruption of saccharin-aversion learning in rats by cortical spreading dispersion in the CS-US interval. *J. Comp. Physiol. Psychol.* 80:398-402.
- EASTERBROOK, G. 1994. The birds. *The New Republic*. March: 22-24.
- FESTA-BIANCHET, M. 1986a. Seasonal dispersion of overlapping mountain sheep ewe groups. *J. Wildl. Manage.* 50:325-330.
- FESTA-BIANCHET, M. 1986b. Site fidelity and seasonal range use by bighorn rams. *Can. J. Zool.* 64:2126-2132.
- FESTA-BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: Conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580-586.
- FORTHMAN QUICK, D. 1984. Reduction of crop damage by olive baboons (*Papio anubis*): The feasibility of conditioned taste aversion. PhD thesis. University of California, Los Angeles.
- GALEF, B.G., JR. 1988. Imitation in animals: History, definition, and interpretation of data from the psychological laboratory, pp. 3-28, in T.R. Zentall and B.G. Galef, Jr. (eds.). *Social Learning: Psychological and Biological Perspectives*. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- GARCIA, J. 1989. Food for Tolman: cognition and cathexis in concert, pp. 45-85, in T. Archer and L. Nilsson (Eds.). *Aversion, Avoidance and Anxiety*. Lawrence Erlbaum Associates, Hillsdale, New Jersey.
- GARCIA, J., and KOELLING, R.A. 1986. Relation of cue to consequence in avoidance learning. *Psychon. Sci.* 4:123-124.
- GARCIA, J., and GARCIA Y ROBERTSON, R. 1985. Evolution of learning mechanisms, pp. 191-242, in B.L. Hammonds (ed.). *The Master Lecture Series, Psychology and Learning*. American Psychological Association, Washington, D.C.
- GARCIA, J., LASITER, P.A., BERMUDEZ-RATTONI, F., and DEEMS, D.A. 1985. A general theory of aversion learning. pp. 8-21, in N.S. Braveman and P. Bronstein (eds.). *Experimental Assessments and Clinical Applications of Conditioned Food Aversions*. New York Academy of Science, New York.

- GEIST, V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. University of Chicago Press, Chicago.
- GREEN, G.C., ELWIN, R.L., MOTTERSHEAD, B.E., and LYNCH, J.J. 1984. Long-term effects of early experience to supplementary feeding in sheep. *Proc. Aust. Soc. Anim. Prod.* 15:373-375.
- GRIFFITH, B., SCOTT, J.M., CARPENTER, J.W., and REED, C. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477-480.
- GRUELL, G.E., and PAPEZ, N.J. 1963. Movements of mule deer in northeastern Nevada. *J. Wildl. Manage.* 27:414-422.
- HALL, S.J.G. 1988. Chillingham Park and its herd of white cattle: relationships between vegetation classes and patterns of range use. *J. Appl. Ecol.* 25:777-789.
- HISTOL, T., and HJELJORD, O. 1993. Winter feeding strategies of migrating and nonmigrating moose. *Can. J. Zool.* 71:1421-1428.
- HOWERY, L.D., PROVENZA, F.D., and BANNER, R.E. 1995a. Intraspecific differences in distribution patterns among individuals in a cattle herd. *Appl. Anim. Behav. Sci.* Submitted.
- HOWERY, L.D., PROVENZA, F.D., and BANNER, R.E. 1995b. The relative importance of mother and peers in perpetuating home range and habitat use patterns among individuals in a cattle herd. *Appl. Anim. Behav. Sci.* Submitted.
- HUNTER, R.F., and MILNER, C. 1963. The behavior of individual, related and groups of south country Cheviot hill sheep. *Anim. Behav.* 11:507-513.
- KALAT, J.W. 1974. Taste salience depends on novelty, not concentration, in taste-aversion learning in rats. *J. Comp. Physiol. Psych.* 86:47-50.
- KALAT, J.W., and ROZIN, P. 1970. "Salience": A factor which can override temporal contiguity in taste-aversion learning. *J. Comp. Physiol. Psychol.* 71:192-197.
- KALAT, J.W., and ROZIN, P. 1971. Role of interference in taste-aversion learning. *J. Comp. Physiol. Psychol.* 77:53-58.
- KEY, C., and MACIVER, R.M. 1980. The effects of maternal influences on sheep: Breed differences in grazing, resting and courtship behavior. *Appl. Anim. Ethol.* 6:33-48.
- LANE, M.A., RALPHS, M.A., OLSEN, J.D., PROVENZA, F.D., and PEISTER, J.A. 1990. Conditioned taste aversion: Potential for reducing cattle loss to larkspur. *J. Range Manage.* 43:127-131.
- LAWRENCE, A.B. 1990. Mother-daughter and peer relationships of Scottish hill sheep. *Anim. Behav.* 39:481-486.
- LAUNCHBAUGH, K.L., and PROVENZA, F.D. 1993. Can plants practice mimicry to avoid grazing by mammalian herbivores? *Oikos* 66:501-504.
- LAUNCHBAUGH, K.L., PROVENZA, F.D., and BURRITT, E.A. 1993. How herbivores track variable environments: Response to variability of phytotoxins. *J. Chem. Ecol.* 19:1047-1056.
- LEDoux, J.E. 1992. Brain mechanisms of emotion and emotional learning. *Curr. Opin. Neurobiol.* 2:191-197.
- LEDoux, J.E. 1994. Emotion, memory and the brain. *Sci. Am.* 270:50-57.
- LETT, B.T. 1985. The pain-like effect of gallamine and naloxone differs from sickness induced by lithium chloride. *Behav. Neurosci.* 99:145-150.
- LYNCH, J.J., KEOGH, R.G., ELWIN, R.L., GREEN, G.C., and MOTTERSHEAD, B.E. 1983. Effects of early experience on the post-weaning acceptance of whole grain wheat by fine-wool Merino lambs. *Anim. Prod.* 36:175-183.
- MARTIN, S.C., 1979. Evaluating the impacts of cattle grazing on riparian habitats in the national forests of Arizona and New Mexico, pp. 35-38, in *Forum—Grazing and Riparian/Stream Ecosystems*. Trout Unlimited, Denver.
- MIRZA, S.N., and PROVENZA, F.D. 1990. Preference of the mother affects selection and avoidance of foods by lambs differing in age. *Appl. Anim. Behav. Sci.* 28:255-263.

- MIRZA, S.N., and PROVENZA, F.D. 1992. Effects of age and conditions of exposure on maternally mediated food selection in lambs. *Appl. Anim. Behav. Sci.* 33:35-42.
- MIRZA, S.N., and PROVENZA, F.D. 1994. Socially induced food avoidance in lambs: Direct or indirect maternal influence? *J. Anim. Sci.* 72:899-902.
- NOLTE, D.L., PROVENZA, F.D., and BALPH, D.F. 1990. The establishment and persistence of food preferences in lambs exposed to selected foods. *J. Anim. Sci.* 68:998-1002.
- O'BRIEN, P.H. 1984. Feral goat home range: Influence of social class and environmental variables. *Appl. Anim. Behav. Sci.* 12:373-385.
- PHY, T.S. and F.D. PROVENZA. 1995. Sheep acquire preferences for substances that rectify lactic acidosis. *J. Anim. Sci.*, submitted.
- PORTER, W.F. 1992. High fidelity deer. *Nat. Hist.* May:48-49.
- PROVENZA, F.D. 1994. Ontogeny and social transmission of food selection in domesticated ruminants, pp. 147-164, in B.G. Galef, Jr., M. Mainardi, and P. Valsecchi (eds.). Behavioral Aspects of Feeding: Basic and Applied Research in Mammals. Harwood Academic Publishers, Singapore.
- PROVENZA, F.D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *J. Range Manage.* 48:2-17.
- PROVENZA, F.D., and BALPH, D.F. 1990. Applicability of five diet-selection models to various foraging challenges ruminants encounters, pp. 423-459, in R.N. Hughes (ed.). Behavioural Mechanisms of Food Selection. NATO ASI Series G: Ecological Sciences, Vol. 20. Springer-Verlag, Berlin.
- PROVENZA, F.D., and CINCOTTA, R.P. 1993. Foraging as a self-organizational learning process: Accepting adaptability at the expense of predictability, pp. 78-101, in R.N. Hughes (ed.). Diet Selection. Blackwell, London.
- PROVENZA, F.D., BURRITT, E.A., CLAUSEN, T.P., BRYANT, J.P., REICHARDT, P.B., and DISTEL, R.A. 1990. Conditioned flavor aversion: A mechanism for goats to avoid condensed tannins in blackbrush. *Am. Nat.* 136:810-828.
- PROVENZA, F.D., LYNCH, J.J., and NOLAN, J.V. 1993a. The relative importance of mother and toxicosis in the selection of foods by lambs. *J. Chem. Ecol.* 19:313-323.
- PROVENZA, F.D., LYNCH, J.J., and NOLAN, J.V. 1993b. Temporal contiguity between food ingestion and toxicosis affects the acquisition of food aversions in sheep. *Appl. Anim. Behav. Sci.* 38:269-281.
- PROVENZA, F.D., LYNCH, J.J., and NOLAN, J.V. 1994a. Food aversion conditioned in anesthetized sheep. *Physiol. Behav.* 55:429-432.
- PROVENZA, F.D., LYNCH, J.J., BURRITT, E.A., and SCOTT, C.B. 1994b. How goats learn to distinguish between novel foods that differ in postingestive consequences. *J. Chem. Ecol.* 20:609-624.
- PROVENZA, F.D., LYNCH, J.J., and CHENEY, C.D. 1995. An experimental analysis of the effects of a flavor and food restriction on the response of sheep to novel foods. *Appl. Anim. Behav. Sci.* In press.
- REINHARDT, V., and REINHARDT, A. 1981. Cohesive relationships in a cattle herd (*Bos indicus*). *Behaviour* 77:121-151.
- REVUSKY, S.H., and BEDARF, E.W. 1967. Association of illness with prior ingestion of novel foods. *Science* 155:219-220.
- ROATH, L.R., and KRUEGER, W.C. 1982. Cattle grazing and behavior on a forested range. *J. Range Manage.* 35:332-338.
- ROLL, D.L., and SMITH, J.C. 1972. Conditioned taste aversion in anesthetized rats, pp. 98-102, in M.E.P. Seligman and J.L. Hager (eds.). Biological Boundaries of Learning. Appleton-Century-Crofts, New York.
- SACKS, O. 1990. The Man Who Mistook His Wife for a Hat. Harper Collins, New York.

- SCOTT, C.B., PROVENZA, F.D., and BANNER, R.E. 1995. Dietary habits and social interactions affect choice of foraging location by sheep. *Appl. Anim. Behav. Sci.* In press.
- SQUIBB, R.C., PROVENZA, F.D., and BALPH, D.F. 1990. Effect of age of exposure on consumption of a shrub by sheep. *J. Anim. Sci.* 68:987-997.
- THORHALSDOTTIR, A.G., PROVENZA, F.D., and BALPH, D.F. 1987. Food aversion learning in lambs with or without a mother: Discrimination, novelty and persistence. *Appl. Anim. Behav. Sci.* 18:327-340.
- THORHALSDOTTIR, A.G., PROVENZA, F.D., and BALPH, D.F. 1990. Ability of lambs to learn about novel foods while observing or participating with social models. *Appl. Anim. Behav. Sci.* 25:25-33.
- WILSON, E.O. 1992. *The Diversity of Life*. Harvard Press, Cambridge, Massachusetts.
- YEATES, N.T.M., and SCHMIDT, P.J. 1974. *Beef Cattle Production*. Butterworth, Sidney, Australia.